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CENTRE FOR
ECOLOGICAL SCIENCES

METHODS IN BEHAVIOURAL ECOLOGY

A WORKSHOP SPONSORED BY
DEPARTMENT OF SCIENCE & TECHNOLOGY
GOVERNMENT OF INDIA
From 12th to 26th October 1992

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PROCEEDINGS

COMPILED AND EDITED BY

RAGHAVENDRA GADAGKAR

TECHNICAL REPORT NO. 24

CENTRE FOR ECOLOGICAL SCIENCES
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INTRODUCTION TO THE WORKSHOP

BY

RAGHAVENDRA GADAGKAR

PREFACE & INTRODUCTION TO THE WORKSHOP

This workshop on "Methods in Behavioural Ecology" was commissioned and funded by the Programme Advisory Committee in Animal Behaviour, Ecology and Evolution of the Department of Science and Technology, Government of India. The workshop was primarily meant for young research workers and university teachers who are engaged in or ready to embark on a career of research and/or teaching Animal Behaviour. The workshop had three components. Thirteen Introductory Lectures by myself, more specialized lectures by 28 invited speakers and laboratory sessions. Summaries of the introductory lectures and full texts of the specialized lectures are brought together in this Proceedings. The introductory lectures were based on J.R.Krebs & N.B.Davies - An Introduction to Behavioural Ecology, Blackwell Scientific Publications, Oxford. Second Edition, 1987.

It is with pleasure that I take this opportunity to thank all the invited speakers for delivering lectures of a uniformly high quality, all the participants for active interaction and all the volunteers without whose help this workshop would not have been possible. A special word of thanks to Mrs.Swarnalatha Chandran for assistance in compiling and producing this volume of the proceedings.

PROF.RAGHAVENDRA GADAGKAR

PROGRAMME

002

12TH OCTOBER 1992
MONDAY

0830 - 0930	REGISTRATION
0930 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to the Workshop.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 1 : The History of an un-named field. (Part 1)
1130 - 1230	SPEAKER : N.V.Joshi TITLE : Evolution of Polyembryony : When should a plant produce an extra asexual embryo ?
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 1: The History of an un-named field. (Part 2)

13TH OCTOBER 1992
TUESDAY

0900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 2 : The Theory of Natural Selection.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : A.V.Kharshikar TITLE : Modelling in Behavioural Ecology
1130 - 1230	SPEAKER : K.N.Ganeshaiah TITLE : Search paths and movement rules of foraging ants
1230 - 1400	LUNCH BREAK

003

1400 - 1700	SPEAKER : Talk by L.S.Rajpurohit Films by Rajpurohit, Balachander and Milind Watwe.
1700 - 1800	BREAK
1800 - 1900	SPEAKER : Raghavendra Gadagkar TITLE : Sampling Methods in Quantitative Ethology - Theory and an Illustration.

14TH OCTOBER 1992
WEDNESDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 3 : The Economics of Animal Behaviour.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : Anil P. Gore TITLE : Dynamic Modelling in Behavioural Ecology
1130 - 1230	SPEAKER : V.Nanjundaiah TITLE : The social behaviour of slime mold amoebae from the view point of Natural Selection.
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : R.Subbaraj TITLE : Behavioural Rhythms and their mechanisms.

15TH OCTOBER 1992
THURSDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 4 : Prey-predator Co-evolution.
1000 - 1030	COFFEE BREAK

1030 - 1130	SPEAKER : Ullas Karanth TITLE : Estimating Animal Abundance by line transects.
1130 - 1230	SPEAKER : R.Sukumar TITLE : Behavioural Ecology as a basis for management decisions
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK

16TH OCTOBER 1992
FRIDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 5 : Competition for resources.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : Milind Watwe TITLE : Host-parasite strategies.
1130 - 1230	SPEAKER : Meena Haribal TITLE : Chemically mediated animal behaviour.
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : Renee Borges TITLE : Foraging decision in arboreal herbivores - the dimensions of time and space.

17TH OCTOBER 1992
SATURDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 6 : When to live in Groups.

005

1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : Sahotra Sarkar TITLE : Voles and Cycles
1130 - 1230	SPEAKER : Uma Shaanker TITLE : Optimization of frequency distributions of seeds per fruit in plants.
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : Arun Venkataraman TITLE : Plausible ecological determinants of group size and mating systems in the Dhole *Cuon alpinus*

18TH OCTOBER 1992
SUNDAY

F R E E

19TH OCTOBER 1992
MONDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 7 : Selfishness and Altruism.
1000 - 1030	COFFEE BREAK
1030 - 1200	SPEAKER : G.Marimuthu TITLE : Biology and Behaviour of Bats.
1200 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : B.Mallik TITLE : Cost of increasing host diversity in polyphagous mites

20TH OCTOBER 1992
TUESDAY

0900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 8 : Social life in vertebrates.
1000 - 1030	COFFEE BREAK
1030 - 1300	SPEAKER : A.Raman TITLE : Insect - plant interactions : The Gall factor.
1300 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : K.Chandrashekara TITLE : Learning in Honey bees under different behavioural contexts - A case study.

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21ST OCTOBER 1992
WEDNESDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 9 : Social life in Insects. (Part 1).
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 9 : Social life in Insects. (part 2).
1130 - 1230	SPEAKER : Anindya Sinha TITLE : Molecular genetics of social wasps - A case study.
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : S.Subramanya TITLE : Foraging patterns of bird pests of crop plants.

22ND OCTOBER 1992
THURSDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 10 : Fighting and assessment.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : M.K.Chandrashekaran TITLE : Social synchronization of Biological clocks.
1130 - 1230	SPEAKER : Madhav Gadgil TITLE : Prudence and Profligancy : Behavioural Ecology of human resource use. I
1230 - 1400	LUNCH BREAK

1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1800 - 1900	SPEAKER : Presentation by participants Dr.Girish Maheshwari Mr.Rajendran

23RD OCTOBER 1992
FRIDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 11 : Battle of Sexes.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : M.D.Parthasarathy TITLE : From animals to human behaviour.
1130 - 1230	SPEAKER : Madhav Gadgil TITLE : Prudence and Profligancy : Behavioural Ecology of human resource use. II
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	SPEAKER : Presentation by participants Mr.John Peter Mr.Vedham
1800 - 1900	SPEAKER : Mr.R.Vasudev TITLE : Sibling competition and parent offspring interactions in plants.

24TH OCTOBER 1992
SATURDAY

900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 12 : Parental care and mating systems.
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : T.Veena TITLE : Interspecific associations and flocking in birds: Benefits and costs

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1130 - 1230	SPEAKER : Madhav Gadgil TITLE : Prudence and Profligancy : Behavioural Ecology of human resource use. III
1230 - 1400	LUNCH BREAK
1400 - 1700	PRACTICALS
1700 - 1800	BREAK
1700 - 1900	SPEAKER : Presentation by participants Dr.Rohini Balakrishnan Dr.Sudheendra Kumar Dr.Venkatesh Ms.Kaberi Kargupta

25TH OCTOBER 1992
SUNDAY

F I E L D T R I P

26TH OCTOBER 1992
MONDAY

0900 - 1000	SPEAKER : Raghavendra Gadagkar TITLE : Introduction to Behavioural Ecology 13: Multiple Strategies
1000 - 1030	COFFEE BREAK
1030 - 1130	SPEAKER : D.P.Abrol TITLE : Modern approaches in pollination biology.
1130 - 1230	SPEAKER : Raghavendra Gadagkar TITLE : Quantitative Ethology of Social Wasps - A case study.
1230 - 1400	LUNCH BREAK
1400 - 1700	SPEAKER : Report of Practicals by group representatives. Dr.L.S.Rajpurohit Dr.P.H.Pathak Dr.Sudheendra Kumar Dr.N.S.Kumaraswamy
1700 - 1800	BREAK
1800 - 1900	FREE

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INTRODUCTION TO BEHAVIOURAL ECOLOGY 1-13:

BY

RAGHAVENDRA GADAGKAR

INTRODUCTION TO BEHAVIOURAL ECOLOGY I
THE HISTORY OF AN UN-NAMED FIELD

SUMMARY

A definitive history of ethology has not been written although it eminently deserves to be. The following is then my own *ad hoc* history. I think it is reasonable to recognize five phases in the development of ethology. The first may be called *Pre-ethology* and happened prior to about the 1940s. During this phase animal behaviour was the passion and pastime of a few eccentric people and far from an organized academic activity. Notable players of the game during this period were Charles Darwin, who wrote the *Expression of emotion in man and animals*, the Russian physiologist Ivan Pavlov who discovered *classical conditioning*, the inimitable German Jakob von Uexkull who used the lowly tick to show that each animal lives in its own sensory world or *Umwelt* and Douglas Spalding, a family tutor to the Bertrand Russell household for whom it appears that the bright Russell children left enough time to do experiments on newly hatched chicks and prove that they are born with an innate ability to peck accurately at grain on the ground

The second phase may be called *Classical ethology* and lasted from about 1940 to about 1960. This period was characterized by two bitterly opposed schools of activity - the *Ethologists* in Europe and the *Behaviourists* in North America. Niko Tinbergen and Konrad Lorenz being prominent amongst the ethologists, formulated the systematic observational study of animal behaviour under natural conditions. The behaviourists such as J.B. Watson

and B.F. Skinner sought to treat virtually any available animal as a black box and use it in extremely well controlled artificial laboratory conditions with the hope of understanding human behaviour. Not much came out of this hope but the experimental and statistical techniques that they and their followers developed are coming in handy as the *Ethologists* are maturing into doing more and more experiments.

The third phase is that of *Modern ethology* which I will argue lasted for just about ten years in the 1960s but had a profound influence on the future of ethology. Two activities of great significance can be traced to this period. One is the integration of ethology and neurobiology to give rise to neuroethology in the hands of such people as Eckhard Hess, Jack Hailman, Donald Griffin and others. The second is the shedding of the naive interpretation of natural selection as acting for *the good of the group or species* and the realization that, except under very special circumstances, the good of the individual (selfishness) overrides the good of the group (altruism). This idea, championed by people like G.C. Williams and formalized by W.D. Hamilton was directly responsible for the subsequent growth, the present widespread practice and the glorious future expected of ethology.

The fourth and present phase is often labelled as *Behavioural Ecology and Sociobiology*. I reckon its beginning in about 1970 and predict that it will lose its identity in the process of giving rise to an extremely multidisciplinary, as yet, unnamed field of activity at about the turn of the century. The

central theme of the present phase of the ethology is to understand every aspect of animal behaviour as an efficient adaptation engineered by natural selection. One can get a glimpse of the nature of behavioural ecology and sociobiology by glancing at its favourite topics of research, The economics of animal behaviour, Prey-predator co-evolution, When to live in groups, The battle of the sexes, Selfishness and altruism and so on.

The fifth phase is that of the future which will hardly be recognizable as the progenitor of the previous phases. There is no doubt that it will draw together such apparently diverse fields as Population biology, Physiology, Ecology, Genetics, Evolution, Molecular biology, Ethology, Anthropology, Psychology, Sociology, Economics and Political science. One only has to look at the following titles of recent research to see that this is no exaggeration. Consider for example, Seed abortion in plants - parent offspring conflict or sibling rivalry, The wave of advance model for the spread of agriculture, Evolution times of languages, The dynamics of a heroin addiction epidemic, Co-operation amongst nations as a prisoner's dilemma game, B chromosome in a parasitic wasp - the most selfish DNA known!

INTRODUCTION TO BEHAVIOURAL ECOLOGY II
THE THEORY OF NATURAL SELECTION

SUMMARY

Evolution by natural selection is at the heart of most modern ethological studies. Industrial melanism, the phenomenon by which a rare melanic form of the peppered moth *Biston betularia* increased rapidly during the early stages of industrialisation in England is an excellent example illustrating the principle of natural selection. Prior to industrialisation, the peppered form was well camouflaged when it rested on lichen covered barks of trees but the melanic form was very conspicuous and discovered very easily by birds. Hence the melanic form was rare and the peppered form common. With industrialisation, barks of trees began to be covered with soot killing the lichens and making the melanic form camouflaged and the peppered form conspicuous. The dynamics of this and other systems under natural selection are conveniently studied using the principle of Hardy-Weinberg equilibrium. This principle shows that the relative frequencies of different alleles will remain constant generation after generation, if we are dealing with a large, random mating population with no mutation, migration or selection. This principle also allows us to calculate the changes in allele frequencies when any of the following conditions are violated. Although the genetic basis of most behavioural traits is not understood, it is important to bear in mind that the language of modern ethology assumes differential selection of alternate alleles coding for different behaviours. It is true however that the genetic basis of some complex

behaviour is beginning to be understood. Perhaps the best example of this is the recent discovery of a genetic basis for such complex behaviours in honey bees as cleaning the hive, feeding the larvae and foraging.

It is important to realise that ethologists sometime investigate the proximate physiological causes of behaviour and at other times they focus on the long term evolutionary consequences of the behaviour. Both of these are necessary and important but they should not be mixed up. It is also now being increasingly realised that natural selection can act many different levels including DNA, genes, chromosomes, organelles, cells, organs, individual organisms, populations and communities. The history of ethology is full of controversies created by the lack of such realisation.

INTRODUCTION TO BEHAVIOURAL ECOLOGY III
THE ECONOMICS OF ANIMAL BEHAVIOUR

SUMMARY

One of the most powerful ways of studying animal behaviour is to treat it as a problem in economics. In other words, natural selection is expected to have designed animal behaviour so that animals behave in an optimal fashion. The job of the ethologists then is to predict the behaviour of animals based on optimality models and see if observations match predictions. If they do not, then one considers additional factors which the animals probably take into consideration, but our models did not. The fact that, the currency that different animals may be optimizing in different situations, can vary makes this approach rich. Consider for example a bird that forages for insects some distance away from its nest. If the bird goes back to the nest to feed its chicks every time it finds an insect, this may be very uneconomical as it has to make one trip per insect. On the other hand, it may not be a very efficient strategy if the bird tries to gather as many as insects as would fit into its beak before going back to the nest. This may be because its efficiency of catching a new insect may decline as its beak gets full. If we knew the energy required for flying from the nest to the foraging site and back as well as the efficiency of catching insects as function of what is already in the beak, we could predict the optimum number of insects that should be delivered in each trip. Here we are considering the maximum number of insects that can be delivered per unit energy spent in foraging. Our

prediction may or may not fit the observed behaviour of the bird. One reason why it may not fit is that the bird may not be minimizing energy expenditure in foraging; instead it may be trying to maximizing the number of insects delivered per unit time. It is easy to see that such an approach can be useful in a wide variety of situations that animals or even plants for that matter, encounter in their daily lives.

INTRODUCTION TO BEHAVIOURAL ECOLOGY IV
PREY-PREDATOR COEVOLUTION

SUMMARY

The evolution of behavioural interactions between predators and their prey constitutes one of the most fascinating areas in Behavioural Ecology because natural selection is expected to maximise fitness of both the prey and the predators. This may seem a bit paradoxical until we begin to view prey-predator coevolution as an arms-race where predator species are continuously selected to become better at detecting their prey and prey species are being continuously selected at detecting their predators before they themselves are detected. Camouflage, Warning Colouration and Mimicry are some of the most important mechanisms that have played a role in prey-predator coevolution. At first sight many descriptions of Camouflage, Warning Colouration and Mimicry appear exaggerated and imaginary. However, carefully controlled experiments using modern behavioural ecological methods have clearly confirmed many of these "stories". The dynamics of prey-predator interaction is very complex and neither verbal "stories" nor experiments can fully unravel the subtilities of such dynamics. For this reason mathematical models have been extensively used in this branch of behavioural ecology. When combined with the experimental approach, mathematical models can indeed be very powerful. For example a simple mathematical model was developed to predict when a predator should prefer large cryptic prey and when they should prefer small conspicuous prey. A cleverly designed experiment presenting great tits in a cage with a "cafeteria" of prey moving

past a conveyer belt, confirmed the predictions of the model.

Prey-predator coevolution can sometimes take very unexpected turns. For example, many species of birds parasitise other species of birds by laying their eggs in the nests of the "host" species. For all practical purposes this is no different from traditional prey-predator coevolution. Such brood parasitism is very common in birds and has become a very rich arena for studies in behavioural ecology.

INTRODUCTION TO BEHAVIURAL ECOLOGY V
COMPETITION FOR RESOURCES

SUMMARY

All organisms depend on uptake of resources from the environment. Usually, organisms are in abundance and resources are limiting. Competition is therefore the essence of natural selection. The simplest form of competition is what has been called "ideal free distribution". If resources are unevenly distributed, exploiters of resources should be distributed in a matching fashion. This may sound like common sense but the simple experiment by Manfred Milinski showing that fish in a tank distribute themselves at opposite ends of the tank depending on the rate of food supply at each end of the tank and that the fish can, within minutes, re-adjust their distribution if the rate of food supply changes, demonstrates that animals are capable of using the very same "common sense" that is so obvious to us. This faith in animals' ability to utilise resources in the best possible manner has encouraged the development of an elaborate theoretical frame work known as "Optimal Foraging Theory". It is easy to see how, starting with the simple ideal free distribution, progressively complex kinds of interaction take place between competing individuals. For example, when animals can defend resources, by establishing territories, then we get a mixture of ideal free distribution and resource defense such that individuals occupying less crowded areas (with lower density) average about the same fitness as individuals occupying more crowded areas (with high density). One can then add to this, differential competitive abilities on the part of individuals and

get a pattern which is still a form of ideal free distribution but now the resources drawn by different individuals are not equal but are proportional to their respective competitive abilities. As one might imagine, a further extension of this idea should lead to the elements of a theory of optimal territory size. But here again, the situation is slightly complex and requires mathematical modelling. The basic principle in the development of models of optimal territory size is that maintaining a territory has both costs and benefits. There are enormous energetic costs of maintaining a territory and there is also a cost simply in terms of time spent in territory defense which could have otherwise been used in feeding, mating, parental care etc. On the other hand, there are substantial benefits of maintaining a territory. Indeed in may bird species, individuals who do not succeed in establishing a territory simply do not breed that year. Once we begin to understand optimal territory size as a balance between costs and benefits, we begin to see that territory size will not simply be proportional to the strength of their owners but will also depend on the quality and quantity of resources it supports.

INTRODUCTION TO BEHAVIOURAL ECOLOGY VI
WHEN TO LIVE IN GROUPS

SUMMARY

Some animals spend most of their lives moving about solitarily and rarely interact with other members of the species. Other animals may spend all or part of their time with other members of their species. Yet other animals are obligatorily social - they are incapable of surviving outside the group. But what decides whether and when animals should live in groups? In the framework of behavioural ecology, this is naturally explored on the costs and benefits of group living. The fact that not all animals live in groups suggest that sometimes the cost of living in groups must outweigh the benefits and sometimes the benefit must outweigh the cost. There is good empirical evidence that this is indeed the case. Our analysis of the behavioural ecology of group living becomes much richer if we focus on specific factors that contribute towards the costs and benefits of group living. Especially with reference to birds and mammals, foraging efficiency and predatory avoidance are among the most extensively studied factors. It is fascinating to see that both foraging efficiency and predator avoidance can sometimes promote group living and at other times, the same factors can discourage group living. Groups may be more efficient at foraging because of cooperative hunting, better detection of prey or simply because the walking of a large number of birds might flush insects out of the grass. However, the ability to catch prey may depend on attack by stealth and a group may simply be too noisy.

Similarly, predators may be better defended and repelled by groups and at other times the only hope of escaping from the predator my be crypsis and a group may simply not be upto this. But there are other costs and benefits of group living also. For example, it was suggested many years ago by Amotz Zahavi that communal roosts of birds my act as information centers where unsuccessful birds may learn about better foraging sites from the more successful ones. As with most of Zahavi's suggestions, this seemed far-fetched when first proposed, but a surprising amount of evidence is now turningup in its favour. Yet another complicating factor in the context of costs and benefits of group living is the quite common occurrence of dominance hierarchies within groups. This means that not all individuals in the group benefit equally. But then the subordinates may nevertheless be better off in the group than outside it. It is also possible however that under certain situations the balance will tilt in favour of solitary living for the lowest ranked member of a group. Quite logically this leads to the idea of optimal group size, analogous to our discussion on optimum territory size. There are several other complicating factors such as genetic relatedness among group members which we will consider in subsequent chapters.

INTRODUCTION TO BEHAVIOURAL ECOLOGY VII
SELFISHNESS AND ALTRUSIM

SUMMARY

On the face of it, Darwin's theory of natural selection expects animals to be selfish in competing for environmental resources. But animals often cooperate with each other. This is not very surprising because cooperation yields benefits to both parties. However, occasionally animals appear to behave in an altruistic manner i.e. they behave in a fashion that reduces their fitness and increases the fitness of the recipient of the altruism. Altruism was considered paradoxical until Hamilton proposed his theory of inclusive fitness. Hamilton pointed out that the fitness of an individual does not merely come from its offspring but also comes from genetic relatives for whose survival it may be responsible. Thus inclusive fitness is computed as the sum of the direct component (through offspring production) and the indirect component (through caring for relatives). In order to be able to numerically add the two components, each component is devalued by the coefficient of genetic relatedness between the actor and the recipient of the altruism. It can be shown that altruistic traits can evolve through this process sometimes called Kin Selection. But a more precise statement is the so called Hamilton's rule which states that an altruistic trait will evolve if

$$b/c > 1/r$$

where b is the benefit to the recipient, c is the cost to the altruist and r is the coefficient of genetic relatedness between

the altruist and the recipient. All other things being equal, Hamilton's theory predicts that altruism towards close genetic relatives should be more common than altruism towards non relatives. There is considerable evidence in support of this prediction.

However, an adequate theory will have to consider, not merely genetic relatedness but various other factors that may influence the fitness of an individual. For example, an individual may behave altruistically by continuing to stay in its parental nest and helping the parents to produce another brood of chicks instead of going off to raise its own offspring. On the face of it this is altruistic behaviour and is more likely to be selected if such help is given to one's own parent rather than to some unrelated individual. However, in order to reasonably predict which individuals will make the decision to stay and help and which individuals will decide to leave, will depend on many factors. For instance, an individual that decides to leave may have a very small chance of finding a territory and successfully raising her own chicks, may be too inexperienced to find a mate and raise chicks or may simply be unable to ward off predators and supply enough food to the chicks without additional help. Similarly a helper may not only get inclusive fitness for helping relatives but may also be gaining valuable experience and may inherit the territories of its parent. All of these factors can be taken into consideration in developing an inclusive fitness model for selfishness and altruism.

There is a second kind of explanation for altruism which is often treated separately from inclusive fitness theory. This is the idea of Reciprocal Altruism according to which, aid may be given today if there is a good chance that it will be returned tomorrow. The prisoners dilemma frame work is a more precise way of analysing such reciprocal altruism. If altruism is given with the hope of return, clearly it need not be restricted to genetic relatedness. This is one of the reasons why reciprocal altruism or mutualism are sometimes treated as alternative models to kin selection. However, it is easy to see that genetic relatedness and other factors mentioned above can all interact and influence the evolution of reciprocal altrusim. Thus a major accomplishment of behavioural ecology has been to provide a sound theoretical framework for the apparently paradoxical coexistence of selfishness and altruism in the living world.

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INTRODUCTION TO BEHAVIOURAL ECOLOGY VIII
SOCIAL LIFE IN VERTEBRATES

SUMMARY

There are many examples of advanced social life among vertebrates. But the most spectacular examples come from cooperatively breeding birds and mammals where some individuals routinely give up reproduction in order to make it possible for other members of the group to reproduce successfully. Many excellent studies have been made of such phenomena using the framework of inclusive fitness theory. Since vertebrates are diploid, genetic relatives (example siblings) are as closely related as one own's offspring or are less closely related (example nephews, nieces, cousins etc.) than offspring but almost never more closely related than offspring. It is obvious therefore that genetic relatedness alone cannot tilt the balance in favour of altruism. For this reason most studies of vertebrate sociality have attached sufficient importance to ecological, demographic and other factors in addition to genetic relatedness. Thus in different bird species with helpers, explanations for the prevelence of helping behaviour are associated with increased productivity due to helpers, inexperience of first year breeders, shortage of territories and breeding site etc. This does not mean that genetic relatedness is unimportant; it simply means that genetic relatedness is only one of the several factors which play a role in the evolution of sociality. An extreme example of highly developed sociality in vertebrates is the case of the naked mole rat whose parallels with social insects is often highlighted. The naked mole rat

appears to have permanently sterile worker castes much like in the case of bees and wasps. The naked mole rat is therefore the only universally accepted example of eusociality among vertebrates.

INTRODUCTION TO BEHAVIOURAL ECOLOGY IX
SOCIAL LIFE IN INSECTS

SUMMARY

The most highly developed examples of sociality are to be found in the insect orders Hymenoptera (ants, bees and wasps) and Isoptera (termites). The term eusociality is used to refer to the most highly developed level of sociality and is defined to include overlap of generations, cooperative brood care and reproductive caste differentiation. In addition to all termites and ants and many species of bees and wasps, a small number of species of aphids, beetles, thrips and the naked mole rat qualify for the term eusocial. Most discussion on the evolution of eusociality has been restricted to Hymenoptera because of their haplodiploid mode of sex determination. Hymenopteran full sisters are more closely related to each other (r=0.75) then parents are to their offspring (r=0.5). The repeated evolution of eusociality in the Hymenoptera has been considered as a striking evidence for the role of kin selection in the evolution of insect eusociality. However, there are quite severe conceptual problems. Hymenopteran females are related to their brothers by only 0.25 so that average genetic relatedness to siblings is not different from relatedness to offspring. This problem can be explained away if Hymenopteran workers can skew investment in favour of their sisters but their ability to do so is not well documented. Moreover, polyandry (multiple mating by queens) and polygyny (the presence of more than one queen either simultaneously or in succession) often breakdown the genetic

asymmetries created by haplodiploidy.

In the primitively eusocial wasp *Ropalidia marginata* for example, these phenomena bring down worker brood genetic relatedness to such an extent that even workers who can skew investment in favour of female brood are not better off than those who attempt to raise their own offspring. For all these reasons, attention is slowly shifting to factors other than haplodiploidy in explaining the evolution of eusociality. Benefits of group living arising from higher or more predictable productivity, relatively better insurance against loss of nest foundresses, demographic differences between solitary nest founders and workers and the benefits of serial division of labour leading to more assured fitness returns for workers are some of the factors presently under focus. The highly eusocial Hymenoptera such as honey bees and ants have fascinatingly complex social organisation but do not appear to hold much promise in understanding the evolution of eusociality. Nevertheless, their study has also yielded rich dividends in terms of understanding social organisation and division of labour. Social insects are also being increasingly used for other kinds of studies because of their large number of individuals who can often be easily trained to perform specified behavioural tasks.

INTRODUCTION TO BEHAVIOURAL ECOLOGY X
FIGHTING AND ASSESSMENT

SUMMARY

As Darwin realised, natural selection has two components. One has to do with the actual struggle for survival, while the other has to do with acquiring mates. The second component, often called Sexual Selection will be treated in a more detailed and general way in a future lecture. Here we restrict ourselves to one component of sexual selection that is usually confined to the males namely, fighting and assessment. For reasons that we will see later, in most sexually reproducing organisms, females are the limiting sex so that males compete with each other for access to females and females choose the "best" males. Male male competition need not always involve overt aggression. One such subtle form of competition has been termed the "war of attrition". For example male dung flies wait near fresh pats of cowdung for female dung flies to arrive. Males then mate with the females before the latter lay eggs. Here the competition between different males is in the form of deciding how long to wait at one pat of cowdung before abandoning it in search of another. Maynard Smith has introduced a game theoretic approach for analysing many such problems. In this case, it turns out that the evolutionary stable strategy is for the males to wait for a random period of time rather than a fixed period of time. This will ensure that males with different waiting times will have the same fitness. Empirical studies on dung flies confirm this prediction. Even when male male competition involves overt aggression, males do not necessarily fight to death; in fact they

do not always injure each other either. Fighting can often be ritualised and settled by various conventions. Ownership of territories, body size, plumage colour, quality of voice, are examples of ways by which animals assess the chance of their winning against a particular opponent so that fighting does not have to proceed very far. A classic example is the Harris Sparrow where dominant males have high levels of testosterone as well as dark plumage. When birds were artificially injected with testosterone they behaved like dominants but did not rise in dominant status because other males did not recognise them as dominants. When painted black they looked dominant but did not behave as dominants and therefore did not rise in status. Only when birds were both painted black and injected with testosterone did they rise in dominant status as they looked as well as behaved dominant. As with other aspects of animal behaviour it is not surprising that there is such a thing as optimum amount of fighting because there are costs and benefits of fighting.

INTRODUCTION TO BEHAVIOURAL ECOLOGY XI
BATTLE OF SEXES

SUMMARY

Most species of living organisms reproduce sexually. There is a vast and rich literature on differences in behaviour of females and males. But it was not possible to understand all of this in a unified framework until the advent of behavioural ecology. Behavioural ecology attempts to provide a simple and unified theoretical framework to explain all kinds of sex differences, in plants as well as animals. The basic principle on which this framework is based is that females are the limiting resource and males the abundant resource. This fundamental difference began with the advent of anisogamy among single celled organisms. Whether it is the production of a few large, nutrition-filled, relatively immobile gametes and many small, "inexpensive", highly motile gametes by an algae or the production of millions of inexpensive sperm and very few expensive eggs by humans, the same principle holds. Because female gametes are the limiting resource and females have invested heavily in them, they are expected to be much more choosy in mate choice. Because male gametes are the abundant resource and males have invested little in them, they are expected to be less choosy. Thus there will usually be female choice and male competition rather than male choice and female competition. As a direct consequence of this, the variance in reproductive success of females will be low. Since male gametes are not limiting, almost no females will go without males and since female investment is very high no individual female can

produce too many offspring. On the other hand variance in reproductive success of males will be very high because of intense male male competition. Many males will get no mates at all and the relatively low investment on the part of males will make it possible for some of them to have an extremely large number of offspring. Perhaps there is no better way of illustrating this than to point out that the record for the largest number of children fathered by any human male in the Guiness Book of world records is 888 whereas the record for the largest number of children by any woman is only 69.

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INTRODUCTION TO BEHAVIOURAL ECOLOGY X11
PARENTAL CARE AND MATING SYSTEMS

SUMMARY

Mating systems and parental care are very variable in the living world. Mating systems can be monogamous, polygynous, polyandrous or promiscuous. Parental care may be provided by the male parent, female parent, both or none. Once again, there is a very extensive literature on these aspects and the attempt of behavioural ecology is to provide a unified theory that accounts for this variability. Following from the principles outlined in the previous lecture on the battle of sexes, one can see that polygyny should be very common and indeed it is. One might expect that monogamy will be favoured by natural selection if the duties of parental care are too much for one parent so that a male who fertilises many females and makes no further investment in the offspring may end up with fewer surviving offspring than another male who mates with only one female but continues to invest in the care of her offspring. This is perhaps one reason why monogamy is so much more common in birds than it is in mammals. When the constraint of requiring care from both parents is removed, the theory developed in the last lecture predicts that it is the male who must desert because he has invested less and has the capability of fertilising many more females. In many species, males establish territories and garner large amount of valuable resources. Given that there may be a lot of variability in the ability of different males to do so, a female might be better off choosing a male with a very good territory even though he is already paired rather than to choose an unpaired male with

a territory of very poor quality. Using the ideas developed earlier in the context of competition for resources, we can thus begin to understand variability in mating systems. There are a few examples of male parental care which are not as easy to explain. However, notice that when compared to the case of internal fertilisation where the male has relatively little assurance of paternity, in the case of external fertilisation, the male is often much more certain that the offspring he may care for are his own. Indeed, now it is the female who is less certain of the parentage of the offspring compared to the case with internal fertilisation. All other things being equal, theory would predict that female parental care should be more common when there is internal fertilisation and male parental care should be more common when there is external fertilisation. This is precisely what appears to be the case in many fish species.

INTRODUCTION TO BEHAVIOURAL ECOLOGY X111 044
MULTIPLE STRATEGIES

SUMMARY

It is a fundamental principle of natural selection that while the majority of the individuals are following one strategy, there is always scope for a small number of individuals to follow an alternate strategy. It is perhaps this fundamental principle that allows for the coexistence of the enormous diversity of life on earth. Behavioural ecology focuses on alternate strategies and attempts to explain them as an inevitable consequence of the theory which is meant to explain the more common behavioural strategies. In other words, the idea is not to develop a separate theory for alternative behavioural strategies. Take for example the case of large male bull frogs who attracts females through his deep croaks. The large males are capable of establishing good territories, are capable or producing calls that convey information about his quality to the females. Small males who are incapable of defending a territory and of giving matching calls sometimes sit silently outside the large male's territory and intercept the female during her approach to the large male. Usually the small male is relatively unsuccessful compared to the large one, but, given his small size and poor resource defending abilities, he may be doing the best of a bad job. Sometimes however he has an unexpected advantage. In some species the large calling males are relatively easily detected by predator bats where as the small non calling males are not. This gives an additional advantage to the small males thus bringing

about coexistence of large and small males.

A rather spectacular form of such multiple or alternate strategies that also fits in well with the theory is the case of sex change in fishes. In some species male male competition is very intense where as females have about the same fitness irrespective of their size. In such a situation it would pay for a young and small fish to be a female (and thus get more fitness than a male of corresponding size) and to change over to a male when it becomes older and larger (and now get more fitness than a female of corresponding size). Thus such protogyny is more advantageous when there is intense male male competition than in species where there is not much male male competition. When male male competition is less intense, female fecundity may be more dependent on body size than male fecundity so that it now pays for the fish to practice protandry i.e. be a male when small and young (and get more fitness than a female of corresponding size) and change into a female when old and large (and get more fitness than a male of corresponding size). There are examples among fish which match both these predictions. Such alternate strategies may be entirely behavioural or they may have a genetic basis. As an example of the latter, there are crickets in which the calling and the non calling phenotype is genetically determined. Callars have more reproductive success because they are better in attracting females but compared to non callars, they also suffer more parasitism because there is a fly that tracks them by their calls.

EVOLUTION OF POLYEMBRYONY : WHEN SHOULD A PLANT PRODUCE AN EXTRA ASEXUAL EMBRYO?

BY

N. V. JOSHI

MATHEMATICAL MODELS OF THE EVOLUTION OF POLYEMBRYONY

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1. POLYEMBRYONY AND ITS PREVALENCE IN PLANTS

The emergence of multiple seedlings from a single seed was first observed by Leeuwenhoek as early as 1719. This condition where seeds contain more than one embryo, referred to as Polyembryony (PE), is widely prevalent among angiosperms. About 244 species from 140 genera belonging to 59 angiosperm families are reported to exhibit PE. The bulk of these reports however constitute incidental observations and hence PE might be more prevalent than is believed, should an exhaustive and systematic survey be attempted Surprisingly, despite the wide occurrence, the evolution of PE is poorly understood.

Except for a few instances, PE generally refers to situations where both sexual and asexual embryos develop in the same seed. Thus PE generally results in the production of both sexual and asexual offspring. The asexual embryos in PE apparently cannot develop independently of the process of sexual reproduction and in most cases require the development of the sexual embryo. Thus to the extent that this process involves the cost associated with the features of sexual reproduction such as the production of floral sex organs, pollination, fertilization and development of the zygotic embryo, PE is not equivalent to asexual propagation. In other words, PE is not associated with the same advantages as that of asexual reproduction. Hence the arguments developed for the evolution of asexual reproduction are inadequate to explain the evolution of PE.

Though we are not aware of the adaptive significance of producing both asexual and sexual embryos in the same seed, we assume that such a strategy harvests the advantages associated with both sexual and asexual reproduction. Our interest in this paper is not to offer arguments for the advantages of PE, rather to develop genetic and inclusive fitness models to arrive at the conditions that favour its evolution.

2. INCLUSIVE FITNESS AND GENETIC MODELS : ASSUMPTIONS

We wish to obtain the conditions under which the allele which leads to the production of additional nucellar embryos can invade a purely sexually reproducing population (i.e., one which does not produce nucellar embryos). It must be noted that the fixation of this allele is in fact subject to the condition that the sexual embryo survives and has some positive fitness value. Hence, we consider the formation of zygotic embryo as a prerequisite for PE.

The model assumes the following :

1. Offspring fitness increases non-linearly (Figure 1) with resources invested in seeds (R). This relation is given by

$$\text{fitness} = (R-c)^x \quad , \text{ where}$$

R= resource invested in seeds
c= minimum resource threshold for positive fitness to be attained
x= constant describing the shape of the curve , and $0 < x < 1$.

2. Before the invasion of PE, there exists an optimal allocation of resources (R^*) to seeds given by $c/(1-x)$, emerging out of the assumed fitness function.

3. The maternal parent does not alter this optimal resource (R^*) allocated to the seed in which additional embryo is formed; hence, the nucellar embryo obtains certain resources K, from R^*. K, however can range between the limits of c and (R^*-c). Since the minimum resource needed to obtain a positive fitness is c, we need $K > c$. The resource available for the zygotic embryo when the additional embryo is formed is R^*-K, and, by a similar argument, needs be a greater than c. Hence, $K < (R^*-c)$ and $c < K < (R^*-c)$. Since we have assumed that both the zygote and the nucellar embryo have non-zero fitness, each of them gets at least "c" units of resource. Therefore the total resources (R^*) should be greater than 2c. Thus we get, $c/(1-x) > 2c$ or $x > 0.5$. Thus from assumption 1 above, it follows that $0.5 < x < 1$.

4. The power (x) of the fitness function does not differ between the sexual and nucellar embryos. In other words, we assume that the fitness functions of the two genotypes, that of the sexual and asexual embryos, are identical. This may not always be true, since the sexual embryos generally enjoy heterozygous advantage (hybrid vigour). However, in a highly cross pollinated species, the nucellar embryos can be expected to be as heterozygous as the sexual embryo and hence would have the same hybrid vigour.

3 THE INCLUSIVE FITNESS MODEL

Let N be the number of offspring (seeds) produced by the mother in her clutch, each with a zygotic embryo. The inclusive fitness of the mother is given by

$$Mf = N.(R-c)^x.\ r_{zm}, \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

r_{zm} = genetic relatedness between the offspring and the mother.

Now, consider a mutant that produces an additional embryo from the maternal tissue in each seed, drawing K amount of resources from the zygotic embryo. Since the additional embryo is genetically identical to the mother ($r_{zm}=1$), the inclusive fitness of the mother is given by,

$$Mf' = N.(R-K-c)^x.r_{zm} + N(K-c)^x \qquad \ldots\ldots\ldots\ldots\ldots\ldots (2)$$

Maternal parent would favour PE if Mf'>Mf. From equations (2) and (1), after rearranging the terms, we get

$$\frac{(K-c)^x}{(R-c)^x - (R-K-c)^x} > r_{zm} \qquad \ldots\ldots\ldots\ldots\ldots(3)$$

Note that the numerator of the LHS represents the benefit (Bt) or fitness accrued through each nucellar embryo and the denominator the cost (Ct) in terms of the loss in fitness of the zygotic embryo due to the reallocation of resources to an additional nucellar embryo. Thus equation 3 shows that benefit to cost ratio (Bt/Ct) of producing a nucellar embryo should be greater than r_{zm} for maternal parent to favour polyembryony.

Without loss of generality, we can take c to be equal to unity. Consequently, the optimal investment, R^*, is seen to be equal to 1/(1-x) (see assumption 2). The Bt/Ct expression can then be written as

$$\frac{(K-1)^x}{(x/(1-x))^x - ((x/(1-x))-K)^x} \qquad \ldots\ldots\ldots\ldots(4)$$

Further, expressing K as a fraction 'f' of the total resource, 1/(1-x), we get

$$Bt/Ct = \frac{((f-(1-x))^x}{x^x-(x-f)^x} \qquad \ldots\ldots\ldots\ldots(5)$$

Since $1 < K < (1/(1-x)-1)$ (from assumption 3), we get, $(1-x) < f < x$; Further it can be seen that as f increases from 1-x to x, Bt/Ct first increases, and then decreases to $(2x-1)^x/x^x$.

By differentiating the expression for Bt/Ct (equation 5) with respect to f, we get f, the value of f at which Bt/Ct is maximized as :

$$f = x - \frac{(2x-1)}{x^x}^{(1/(1-x))} \qquad \ldots\ldots\ldots\ldots(6)$$

As x increases from 0.5 to 1, f increases from 0.5 to $1- \exp(-1)$ (≈ 0.63) and the Bt/Ct increases non-linearly from 0 to 1 .

For polyembryony to be favoured, Bt/Ct has to be greater than r_{zm} (eqn. 3). Obviously there are some values of r_{zm} for which the maternal parent does not favour nucellar embryony. Since in a randomly mating outbreeding population, $r_{zm} = 0.5$, the maternal parent favours polyembryony only for Bt/Ct > 0.5.

Substituting values of f in equation 6, it is seen that Bt/Ct is greater than 0.5 only for values of $x > 0.5758$. This further limits the condition under which the maternal parent can favour PE. Substituting this value of x in $R^* = 1/(1-x)$, we find that PE can evolve only if $R^* > 2.358$ times c. That is, in situations where the optimum seed size (R^*) is very small relative to c, PE cannot evolve because at this low R^* levels, re-allocation of resources would result in resource levels of nucellar (K) and zygotic (R-K) embryos less than required for their survival (i.e., c).

4. THE GENETIC MODEL

Our interest is to obtain the conditions under which the allele causing the formation of the additional (nucellar) embryo can successfully invade a population which is otherwise purely sexually reproducing. We construct simple, one locus two-allele models.

Let the purely sexually reproducing genotypes be denoted by NN. Let the fitness of these individuals be A. The allele for polyembryony, P, leads to a reallocation of K amount of resources from the sexual zygote to the differentiation and development of the nucellar embryo. Let the fitness values of the nucellar and the sexual embryos be C and B respectively.

The allele P induces the nucellar tissue to differentiate into embryos if it is present in the maternal tissue, irrespective of the genetic constitution of the zygote and the endosperm. This is akin to the maternal parent regulating the formation of nucellar embryo and hence the scenario is similar to that of the Inclusive fitness model where the maternal parent favours the formation of additional embryos. Under this model, the condition under which the allele P, as dominant or recessive, is able to successfully invade a population of N is given by (see appendix),

$$C > (A - B)/2 \qquad \ldots\ldots\ldots\ldots (7)$$

On the other hand, the condition under which the allele N, as dominant or recessive, invades a purely polyembryonic population is given by

$$C < (A - B)/2 \qquad \ldots\ldots\ldots\ldots (8)$$

Thus, regardless of whether polyembryony is controlled by dominant or recessive allele, for $C > (A-B)/2$, polyembryony goes to fixation and for $C < (A-B)/2$, non-polyembryony goes to fixation.

Following the assumptions listed earlier and expressing the fitness of embryos as in the Inclusive fitness model, we write,

$$A = (x/(1-x))^x \qquad \ldots\ldots\ldots\ldots (9)$$

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$$B = ((x/(1-x))-K)^x \qquad \ldots\ldots\ldots\ldots\ldots\ldots (10)$$

and $$C = (K-1)^x \qquad \ldots\ldots\ldots\ldots\ldots\ldots (11)$$

Substituting these in equations 12 to 15 and rearranging, we get the conditions that permit the invasion and spread of P in a population of N.

It can be seen that the expression for Bt/Ct for the formation of the nucellar embryo is identical to that obtained under the Inclusive fitness model. Hence the region in the x-K space permitting the evolution of polyembryony under the genetic model is the same as that obtained under the inclusive fitness model. Further, the conditions permitting the spread of P through maternal regulation (Model a) is a special case of the inclusive fitness model (equation 5) where $r_{zm} = 0.5$. It is thus clear that nucellar embryony is favoured for Bt/Ct >0.5 when it is under maternal regulation.

5 Altered resource allocation to embryos under the Evolutionarily Stable Strategy

In section 3 we showed that Bt/Ct can be maximized by investing K=f.R amount of resources into the nucellar embryo (see eqn. 5). Such an allele would spread rapidly against a non-polyembryonic allele. This however may not be uninvadable by another allele that maximizes its fitness instead of Bt/Ct.

Under the condition where maternal parent favours polyembryony (i.e., where C > (A-B)/2), it can be shown that the allele with an investment of

$$K^* = \frac{((x/(1-x)) + 2^{(1/(x-1))})}{1 + 2^{(1/(x-1))}}$$

in the nucellar embryo is uninvadable by any other allele (i.e. an allele with any alternative amount of investment). In other words K^* represents an ESS.

Further, if f^* denotes the fraction of R^* invested in the nucellar embryo, (i.e. $K^*=f^*.R^*$), we get

$$f^* = \frac{x + 2^{(1/(x-1))}(1-x)}{1 + 2^{(1/(x-1))}}$$

The evolutionarily stable allele always invests more resources into the nucellar embryo than the Bt/Ct maximizer. However, in a dynamically competing population of three alleles, where a population of the non-polyembryonic allele is invaded by both Bt/Ct maximizer and fitness maximizer, it is always the frequency of Bt/Ct maximizer that increases rapidly. Nevertheless, once the the frequency of the non-polyembryonic allele reduces and when the Bt/Ct maximizer and the fitness

maximizer are the main competing alleles, the latter always wins.

In conclusion, we have demonstrated here the conditions (as characterized by the values of x) under which polyembryony is likely to evolve. We have also derived the Evolutionarily Stable Strategy, denoting an optimal resource allocation between the nucellar embryo and the zygotic embryo.

An examination of eqn. 1 suggests x to be a measure of the efficiency of the plant to convert resources into fitness; a high value of x implies a higher efficiency. The model demonstrates that polyembryony can evolve only for values of x higher than 0.5758. This suggests that polyembryony is likeky to be more prevalent for higher values of x, i.e. in more efficient plant species. This qualitative prediction may be used to test the model by examining the extent of polyembryony in plant species of varying degrees of efficiency. Such an exercise is in progress.

6. MATHEMATICAL APPENDIX

Population genetic models for the evolution of polyembryony

We consider an infinite, panmictic random mating population with nonoverlapping generations. Let P and N denote alleles which code for polyembryony and for nonpolyembryony respectively. Let n, y and z denote the frequencies of NN, NP and PP genotypes. Let A be the fitness of the zygotes produced by a nonpolyembryonic phenotype, B, by the polyembryonic phenotype and C, the fitness of the nucellar embryo.

We consider a pure population of one allele, subjected to invasion by the other. The success on otherwise of the invasion is investigated in most cases by linearized stability analysis.

(a) *Nonpolyembryonic population (N) invaded by a dominant polyembryonic allele (P).*

Let y, z ($\simeq$ 0) be the frequencies of NP and PP respectively.

The frequency of P is then $\frac{y}{2} + z$

The following illustrates the contribution to the next generation from the various matings, involving the P allele, whose frequencies are nonzero to first order.

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to NN	Contribution to NP	Contribution to PP
NN	P	$(1-y-z)\left(\frac{y}{2}+z\right)$	No	-	A	-
NP	N	y	Yes	$\frac{B}{2}$	$C+\frac{B}{2}$	-
PP	N	z	Yes	-	B	C

If y' and z' denote the frequencies of NP and PP alleles in the next generation, from table B1, it can be shown that

$$\begin{bmatrix} y' \\ z' \end{bmatrix} = \begin{bmatrix} \frac{A+B+2C}{2A} & \frac{A+B}{A} \\ 0 & \frac{C}{A} \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix}$$

The dominant eigenvalue of the matrix is $\frac{A+B+2C}{2A}$, and

The condition for the spread of P is $\frac{A+B+2C}{A} > 1$

or $C > (A-B)/2$

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(b) *Polyembryonic (P) population invaded by a dominant nonpolyembryonic allele (N).*

Let y ($\neq$ 0) be the frequency of the NP genotype. Since N is nonpolyembryonic, NN homozygotes would be generated only by NN.N and NP.N matings, and the frequencies of these are zero to first order, so N would exists only in NP heterozygotes.

The following indicates contributions to the next generation from matings involving N

Maternal genotype	Pollen	Mating frequency	Whether polyembryony	Contribution to NN	Contribution to NP	Contribution to PP
PP	N	$\frac{y}{2}$	Yes	-	B	C
NP	P	y	No	-	$\frac{A}{2}$	$\frac{A}{2}$

The frequency of NP in the next generation, y' is obtained to be

$$y' = \frac{1}{B+C}\left[\frac{B}{2} + \frac{A}{2}\right] y$$

$$\therefore\ y' > y \text{ if } \frac{A+B}{2(B+C)} > 1$$

$$\text{i.e. if } \frac{A-B}{2} > C$$

which is the condition for a successful invasion by N.

MODELLING IN BEHAVIOURAL ECOLOGY

BY

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MODELLING IN BEHAVIOURAL ECOLOGY

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1. Very often the behavioural pattern under study is governed by many factors. A number of factors interact and give rise to the behaviour under observation. The picture becomes even more complicated when one takes into account the chance effect which also gets added. To understand this complex mechanism it is very essential to weed out less significant factors and consider only the more significant ones. If while building the model we try to take into account all the complexities, the modes becomes intractable. On the other hand, too much simplification takes the model away from reality. One has to strike a balance between these so as to finally reach a useful model.

2. To build up a model which will prove helpful in understanding the phenomenon under study, it is necessary

(i) to spell out the underlying assumptions in a clear manner,

(ii) to see the rules which will naturally emerge as consequences of the assumptions made, and

(iii) to have a few unknown parameters which lend flexibility to the model. For any good model such parameters have some physical interpretations.

When we operate the model to get 'the expected', which is then compared with 'the observed' the parameter values plugged in the model are such that they take 'the expected' as near as possible to 'the observed. If these two entities are close enough then the model is considered to be giving a good fit, and when they are at a sizable distance from each other, it becomes

necessary to have a fresh look at the assumptions made.

3. A good model always gives a better insight into what one is studying. It also makes possible applications to various other situations. Through comparison between the two sets of parameters, it makes it possible to look at two different situations in comparison. In general a good model enhances our understanding of the underlying mechanism and when coupled with data it enlightens us regarding the present state of affairs.

4. To elaborate on the above points, the following example regarding vigilance in bird would prove useful. (For further details and full discussion of this example one may refer to Dennis Lendrem's book entitled 'Modelling in Behavioural Ecology (1986))

A feeding bird, interrupts its feeding to look around and see if there is any predator. If it scans in this manner too often, its feeding would suffer. On the other hand if it does not scan often enough, it faces the danger of being killed. What vigilance pattern then should it follow ?

In reality this is a complex phenomenon. Pulliam (1973) gave the following model by weeding out the less important factors. His model was as follows:

(i) The attack of the predator lasts for T seconds. If during this predator approach time the bird happens to scan, then it detects the attack and flies away. If it fails to scan during this time, then it fails to detect the attack and

therefore perishes.

(ii) The scans are instantaneous and independent of each other.

(iii) The scans follow a Poisson process with rate λ i.e. in an interval $(t, t+\Delta t)$ of infinitesimally small length t, a scan occurs with probability $\lambda\Delta t$ and it does not occur with probability $1 - \lambda\Delta t$; further scans in non-overlapping intervals are independent of each other.

As a consequence of above assumptions probability that the bird fails to detect the approaching predator during an attack (which is of duration T seconds) is $1 - e^{-\lambda T}$. Let us write this probability as p.

Suppose the bird scans on average 10 times per minute. Then, when we take second as time unit $\lambda = 10/60 = 1/6$. If attack time is 6 seconds then $T = 6$. In this case $p = 1 - e^{-1} = 0.6321$.

If scanning rate is doubled, i.e. if the bird scans on average 20 times per minute then $\lambda = 1/3$ and $p = 1 - e^{-2} = 0.8647$.

What happens if we have a flock of N birds ? It is assumed that these birds scan independently of each other and even if a single bird detects the approaching predator it gives alarm and the entire flock flies away. Thus in this case the flock fails to detect the attack only if each and every bird in the flock fails to detect the attack. If we denote by p_g the probability of detection for the group, it is equal to

$$p_g = 1 - e^{-\lambda NT}$$

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Thus is vigilance rate is λ for a solitary bird, in a flock with N birds, it becomes $N\lambda$

Now if we assume that there is an optimal value of probability of detection and birds, whether solitary or in a flock, would scan only as often as to have this detection probability, it follows that individual scanning rate of a bird in a flock with N birds, would be N times less than that at a solitary bird. If we denote the individual scanning rate of a bird in a flock of size by λ_N, we have

$$\lambda_N = 1/N \ \lambda_1$$

or in other words, $N\lambda_N$ is the same for all N. The following table gives some values of λ_N for $\lambda_1 = 10$, denoting 10 scans per minute, taking minute as time unit.

N	1	2	3	4	5	6	7	8	9	10
λ_N	10	5	3.73	2.50	2	1.67	1.43	1.25	1.11	1

In practice what does one see? Does one find the scanning rate going down in this way in reality? Mark Elger and Carla Catterall of Griffith University, Brisbane fitted this model to flock-feeding sparrows and found that the model gives larger scanning rates for smaller flocks than what they actually found and smaller scanning rates for larger flocks than what they found in reality.

This discrepancy in what is observed and the expected picture as depicted by the model makes one reconsider the

assumptions made and modify them so as to come closer to reality.

The assumptions of Poisson process for scans has many implications which in reality may not hold. For example in reality too small interscan intervals or too large interscan intervals do not occur as often as the model tends to give. One may give up this assumption and may start by looking at interscan intervals. When one does that then one has to also examine the attacking behaviour of the predator. If the predator watches its prey and start its attack at the beginning of a feeding interval then it is said to follow 'wait and see' policy. On the other hand if it starts its attack at a random movement then it follows 'random attack ' policy. Probability of detection would depend upon the policy adopted by the predator. An appropriate model would be that one which takes into account the kind of predator the bird is facing.

5. In practice one has to go on making the model more complex as the situation demands. One model may provide a satisfactory fit and may explain one situation, but may need some modifications when applied to certain other situation which is similar to the first one in most respects but differs in some other respects only to make certain assumption, crucial for the model, somewhat untenable.

SEARCH PATHS AND MOVEMENT RULES OF FORAGING ANTS

BY

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SEARCH STRATEGIES OF FORAGING ANIMALS: PATTERNS AND RULES OF MOVEMENT

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The Optimal Foraging Theory (OFT) is constructed on the premise that the fitness of the animal increases with the food harvested and that the time (energy) available to harvest the food is limited. As a result, the theory assumes that, selection favours the strategies that increase the efficiency (ratio of food harvested to the time and or energy spent) of harvesting the food. The two important components of foraging activity are 1. Searching and 2. Handling the food. Obviously the limited foraging time has to be shared among these two activities and the selection should favour efficient strategies at both these levels. However a majority ($\simeq$ 95%) of the papers published following the celebrated work by MacArthur and Pianka (1966) and Emlen (1966) have addressed the foraging strategies adopted at the stage of handling the food and rarely ($\simeq$10%) the strategies at the stage of searching the food. This might be partly attributed to the diversity of the types of forager- prey combinations for which any single scheme of strategy may not hold: The foragers could be crawlers or hoverers, individuals or groups, while the prey could be distributed in random, clustered or any regular design on two or three dimensions.

It is nevertheless possible to define the efficient path of

forager using two criteria: 1. It should be the shortest (economical) possible path and 2. Should avoid recrossing its own path to minimise the revisitations to the foraged areas.

Randomly distributed resource spots

Keeping the above criteria as the measures of efficiency of the search path, there are few attempts to define the optimum rules of movement of the foragers that search for the randomly distributed food spots (Cody,1971, Pyke 1978a and b). There are few common and relatively robust predictions from these studies:

1. The animals foraging on an infinite area should maintain a correlation between the angle of arrival to, and the angle of departure from, the resource spot.

2. The foragers should turn alternately to left and right directions.

These predictions are well supported from the field studies on bumble bees and birds (Levis *et. al.* 1971, Pyke, 1978a,b & c, Cody 1971,1974), though under certain conditions that violate the assumptions, these predictions also are found violated (Zimmerman 1979,1982).

There are other situations as well where the foragers are found to follow such non-random movement patterns with minimum path recrossing. One of the most interesting system is described by Franks and Fletcher (1983) in army ants. These ants have two phases of their life cycle: saltatary phase in which they forage in radially placed raids from a static centre for about 15- 20

days and a nomadic phase in which they emigrate carrying their larvae searching and harvesting the food before settling on a new location every day. Franks and Fletcher (1983) have found that the radial raids are placed at 123^{0} from each other so as to avoid the temporal and spatial overlap of the subsequent raids, while the nomadic raids are non-randomly oriented such that they avoid recrossing their path and also facilitate placing any two centres of the static phases far away from each other.

Majority of the mass raiding ants forage in branched trails. We (Ganeshaiah and Veena unpublished) studied the branching pattern of the raids of *Leptogenys processionalis* using Horton's (1945) technique originally developed to analyse the branching pattern of the rivers and streams. Our study indicated that the branching patterns of the foraging raids are non-random and are similar to that of bronchial arteries in the human lungs. Using the arguments of the architects about the economy of the designs (Stevens 1973,1974), we have shown that these branching patterns are indeed the most efficient strategies of searching the food by the mass foraging ants.

Clustered distribution of the food

The foragers searching for the clustered distribution of the food exhibit an extensive random search of the area till they encounter a resource spot. On encountering the food and harvesting it they indulge in an intensive search of the surrounding area with increased turning rate and reduced velocity

of movement (Banks,1957; Bond,1980; Evans,1976). This behaviour is viewed akin to the extensive and intensive labour investment in various Farm enterprises depending on the benefits obtained from them.

Resource spots in regularly arranged designs

The foragers searching for the resource spots arranged in regular designs, as for instance, the florets in circular arrangement of the compositae heads (Gilbert, 1983) exhibit distinct movement rules specific to the design; They also exhibit an element of learning in exploring these various designs (Ganeshaiah and Veena, 1989). However it might me difficult to draw any common predictions about the rules of movement under these situations as they might change with the design on which they are foraging. However it is interesting that the foragers show non- random exploratory movements that avoid revisits to the resource spots and follow the least expensive paths (Ganeshaiah and Veena 1989, Veena and Ganeshaiah 1989, Gilbert 1983).

Foragers are also known to adopt the foraging modes that increase their efficiency of searching and reduce the cost of travelling (Pyke, 1978b). One interesting example is reported in the spider monkeys (Chapman *et. al.*1989) where the foragers select several but repeatedly the same centres for sleeping such that they reduce the travel cost while searching the food.

The theoretical work in the area of search patterns is much lacking. The few empirical studies have only served as the

pointers but have not been productive in providing the generalizations and the testable predictions; this might be possible only if more theoretical exercises follow these empirical studies.

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TECHNICAL SECTION

HOW ANTS EXPLORE THE UNKNOWN ?

Romanes (1883) in his book 'Animal Intelligence', quotes the following anecdote : "In Herr Gredler's monastry, one of the monks had been accustomed to put food regularly on his window sill for ants coming up from the garden. In consequence of Herr Gredler's communications, he took it in to his head to put the bait for the ants, pounded sugar, in an old ink stand and hung this by a string to a cross piece of the window and left it hanging freely A few ants were in the bait. They soon found their way out over the string with the grains of sugar and so their way back to their friends. Before long a procession was arranged on the new road from the window sill along the string to the spot where the sugar was, and so things went on for two days nothing fresh occuring. But one day, the procession stopped at the old feeding place on the window sill and took the food thence without going up to the pendent sugar jar. Closer observation revealed that about a dozen of rogues in the jar above were busily and unwearingly carrying the grains of sugar to the edge of the pot and throwing them over to their comrades below."

Citing this anecdote in his book, Wheeler (1910) considers it as another "story of ants, bees and wasps" glorifying their ability to "reason" out — a word very much out of use in modern ethology. Wheeler did not believe that insects could learn and incorporate their experiences into the behaviour. For him, insects were like the preprogrammed robots incapable of doing anything that is not instructed by the programmer and the programme *per se* being incapable of self correcting (on experience).

Wheeler's was apparently an underestimation of the potentiality of insect neural system. It is now clear that at least in few instances insects have shown the ability to learn and associate. They even have the memory — the short and long term memory — that shapes their behavior. With these abilities they are capable of exploring the new food patches in most efficient ways.

Infact without such ability to learn, the world would be chaotic for them. Consider a simple scenerio of a nectarivorous ant on a host plant with no information regarding the arrangement of the nectaries on it; such a foraging patch would be a complicated maze with no specific search path to follow. Hence, ants would waste much of their foraging time and energy searching randomly for the nectaries in this unknown world; besides, such random movements also lead to revisits to the foraged spots thus decreasing the efficiency of foraging.

But ants do not generally follow such random paths. Rather, after repeated visits to the foraging patches, they exhibit signs of the 'knowledge' about the pattern of arrangement of resource spots and modify their search behaviour accordingly. Few such examples are provided here to indicate the strategies used by ants while exploring their resource patches.

Camponotus serecius (Fabricius) forages on the nectaries of a locally wide spread weed *Croton bonplandianum* Baill. Croton bears nectaries at the base of pedicels of female flowers arranged linearly along the inflorescence axis. These inflorescences are borne regularly in a circle at every node; each inflorescence further bears four more inflorescences in the same pattern and such modules are repeatedly produced. As a result, the whole plant is composed of repeated modules of similar design. We (Ganeshaiah and Veena, 1988) asked whether ants repeatedly foraging on these plants, are capable of incorporating their experience of the design of the plant in to their subsequent search patterns such that they avoid revisits. Interestingly, individually foraging *Camponotus* ants follow one simple rule- they explore the cluster or each module consistently in left or right oriented circles i.e., after foraging on any inflorescence, the ant moves on to the o towards the left (or right) of it; this process continues till it explores all the inflorescences of one module (Fig. 1) and then moves on to another Such non-random search paths avoid revisits and are possible only if ant's behaviour has been shaped in accordance with the design of the plant Note that there are several other ways of avoiding the revisits. For instance, ant can move from A→B→D→C or A→C→D→B etc. But in these movements, to execute the correct third move they need to remember two previous moves on the module. But in a consistently left (L) or right (R) oriented search path, it suffices to remember just one step ie., the direction it turned previously.

Circular search paths are adopted by the insects foraging on other designs also. Gilbert (1983) has shown that the syrphids foraging on heads of some composite flowers forage in a circle and leave the head exactly at the

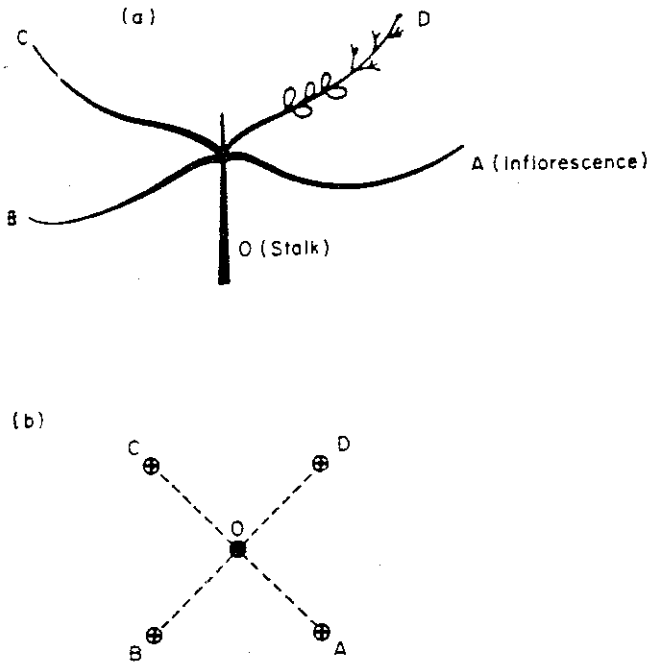

Figure 1. A cluster of four inflorescences of *Croton bonplandianum* (a) Actual, (b) diagrammatic top view.

same point where they landed and started to search. They mentally mark this finishing (starting) point using the solar cues. Indeed it is possible to fool them by rotating the head on its axis with respect to the sun's position - flies loose their angular bearing and exhibit errors while leaving in accordance with the direction and extent of rotation of head.

Aster heads and croton plants represent very simple patterns; ants could easily 'learn' these designs and accordingly modify their behaviours. But it is not clear if they are capable of assimilating the 'complex' patterns of the arrangement of the resource spots. Unfortunately, we know very little of the ways ants could circumvent such complex designs. Many more systems need to be studied before we can generalise the rules of their search patterns.

However the extent of repeatability of a complex pattern might influence the rate of feedback process of incorporating the design into the search strategy of ants. But how would ants behave when the design is not repeated? Consider predatory ants foraging on arthropods distributed randomly on the ground. The only repeatability of such patches is the randomness *per se* in the distribution of the food items. Franks and Fletcher (1983), studying army ants *Eciton burchelli* at Barro Colorado Island, have shown that ants have developed very ingeneous ways of foraging in such situations. These mass raiding ants leave their nest (a bivouac) every day in a column and forage through interconnected trails at the tip of the raid column. The raid columns of the subsequent days radiating from the nest are known to be seperated by around 123°. Franks and Fletcher have shown that this angle of seperation is indeed the optimum way in which ants avoid overlap of the raid columns of the subsequent days reducing the revisitation of the foraged patches before they are replinished by the fresh resources; this also helps in complete exploration of the area around the bivouac before the colony starts migrating. Thus ants seem to adopt search strategies specific to the design of the resource patch and the extent of the information they can gather about it.

It is interesting that in all the strategies cited above ants seem to adopt one common rule ie., they explore their patches moving in a circle around some reference point. Whether a three dimensional patch such as croton plants where the resource spots are regularly distributed or an undulating surface such as ground where food is randomly distributed, ants seem to translate them to a circular pattern and forage accordingly. It is not clear if such translation of all the complex arrangements of resource spots to circular patterns would minimise the complexity of the search strategies. Testing this needs more emperical stories from the field. Strangely enough, despite the long history of the foraging ecology, so little is known about the search strategies of animals in general.

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Topology of the foraging trails of *Leptogenys processionalis* – why are they branched?

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Summary. *Leptogenys processionalis* Jerdon forages on termites and other arthropods by raiding in branched trails. Growth and topology of these search trails were studied using Horton's (1945) technique orginally developed to analyze the branching pattern of river systems. Branching was always a bifurcating process and branches emerged symmetrically on either side of the main trail. Branching coefficients (R_b) were similar to those of a few biological branching systems, such as lungs, that are considered to be non-random in their branching pattern. The R_b values indicated that the rate of branching and growth of trails remained constant within each foraging bout. The length of trails became shorter as they grew out and branched. The branching process was a function of the spatial separation of food patches in the terminal search field. Ants in the terminal search field send signals on encountering prey. The recruits cannot discriminate between these signals if they arise from two food patches situated <40 cm from each other, and hence converge on them in a single trail. However, discrimination is possible when food patches are >40 cm apart and hence recruits congregate on them separately in two trails, resulting in branching. Thus, the branching process is a result of independent decision by the ants conforming to certain simple rules and not a collective decision of the whole colony. We argue that mass recruiting ants selected to forage by branching pattern of trails because of its efficiency over other topologies (Stevens 1973) in minimizing the cost of travel, both from the nest to the food patches and between food patches. Further, the branch angles appear to be a trade-off to minimize travel cost and the resistance to the flow of ants comprising the column.

Introduction

Foraging animals select for strategies that maximize the benefit-to-cost ratio of harvesting food (Cody 1971; Heinrich 1979; Levis et al. 1971; Pyke 1978a, b; Stephens and Krebs 1986; Zimmerman 1979, 1981, 1982). Systematic movement between the resource patches that minimizes the cost of travelling is one such strategy (Ganeshaiah and Veena 1988; Heinrich 1979; Pyke 1978a, b, c; Veena and Ganeshaiah 1991). Compared with flying insects, walking and crawling insects such as ants and caterpillars are highly constrained in their movement by the structural design of the substrate on which they move. These constraints could severely limit their foraging efficiency (Ganeshaiah and Veena 1988). Ants are adapted to overcome these constraints by utilizing information about the pattern of resource distribution and design features of the substrate on which they move (Ganeshaiah and Veena 1988; Cheverton 1982; Veena and Ganeshaiah 1991). However, they cannot always obtain such information about resource distribution. For example, predatory ants on the ground must find prey that is randomly distributed. Hence, despite the structural simplicity of the ground, developing an efficient search strategy is quite a demanding task (Franks 1989; Mirenda and Topoff 1980; Mirenda et al. 1980; Reyes 1986). Some ant species are known to have evolved peculiar strategies whilst searching for such unpredictably distributed food patches (Franks and Fletcher 1983).

In this paper, we report the foraging strategy of a predatory ant, *Leptogenys processionalis*, which searches for randomly distributed prey items and forms branched trails. More specifically, we studied these branched trails with regard to the following three questions.

1. Is the branching pattern of search trails random?
2. Is the observed branching pattern efficient in maximizing the ratio of area foraged (benefit) to the distance travelled (cost)
3. What are the extrinsic (environmental) and intrinsic (innate) factors regulating branching pattern?

To answer these questions, we analyzed the geometry of the branched trails using Horton's technique, originally developed to study the branching pattern of river systems (Horton 1945). We discuss the results in the context

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of fractal properties and the adaptive significance of the branching pattern of search trails. Search, in this context, is defined as movement pattern in space that increases the likelihood of finding the resource.

System

Leptogenys processionalis Jerdon (Formicidae: Ponerinae) is a group foraging ant which preys mostly on termites, but occasionally on other arthropods and annelids also (Musthak Ali 1981; Shivashankar 1985). These ants forage during the cool hours of the morning (between 0600 and 0900 hours) and evening (between 1600 and 1900 hours). Ants migrate once in about 35 days (range 15–60 days; Shivashanker 1985) and construct their own or occupy abandoned nests in the ground. Once established, the foragers generally leave the nest in a single trail. Ants mark their trails (paths) with pheromones (Shivashankar 1985), as is known for several mass-foraging ant species (Chadab and Rettenmeyer 1975; Topoff and Lawson 1979; Maschwitz and Schönegge 1983; Moffett 1988). At the leading front of the trail, ants fan out in several interconnected columns, resulting in a triangular field of ants actively searching for food (Fig. 1a). This actively moving search-field, hereafter called the "terminal search field (TSF)", has a moving front 60–80 cm in width (Fig. 1a, b).

After the trail has grown to a certain length (Fig. 1b) the TSF bifurcates, splitting the trail into two branches, each with a separate leading TSF. This process of bifurcation occurs repeatedly. However, not all TSFs move and bifurcate at the same rate; the result is a labyrinth of branched trails. Very rarely (<2%) do trails converge and form a loop. The terms "trail", "path" and "branch" are hereafter used interchangeably; "foraging bout" refers to the foraging activity from the time ants emerge from the nest until they all return.

As soon as prey is encountered, the TSF becomes a foraging front which harvests prey. The harvested food is transported back to the nest along the pheromone-marked trails. Thus, some of the trails nearest to the nest are repeatedly used for food transportation and for fresh recruitment to the foraging sites; hence, these paths become heavily trodden. On subsequent foraging trips ants move along these trodden paths, (hereafter called "permanent trails") without a TSF. However, as ants reach the end of the permanent trails, they again organize themselves into a TSF, set out in search of prey, and repeat the branching process. The new trails are transient (hereafter termed "temporary trails"), but may become permanent trails, depending upon whether they are frequently used or not.

Another mass-foraging ant, *Pheidolegeton diversus*, exhibits a similar pattern of foraging (Moffett 1988). The branching pattern of the foraging trails of this species was also studied to evaluate the generality of conclusions drawn for *Leptogenys processionalis*.

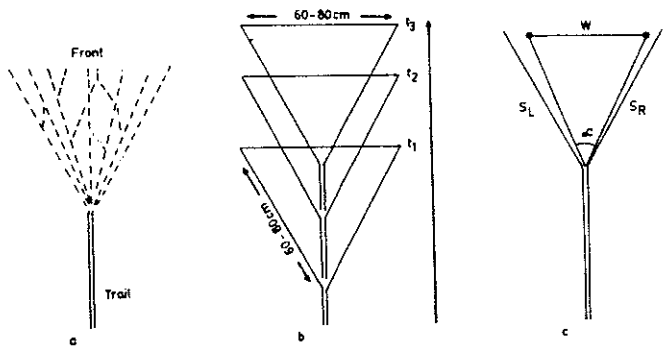

Fig. 1a–c. *Leptogenys processionalis*. **a** Terminal search field (TSF) with interconnected columns of ants, and **b** their movement in time (t_1–t_3). The TSF searches an area equivalent to width of its front as it moves along. **c** Food in TSF was placed along its front at various distances (W), and angle of the food was measured at the fork as $\alpha = 2*\sin^{-1}[W/2/(SL)]$. ($SL$: left side; SR: right side of TSF)

Methods

Data collection

Tracing the branching pattern. Four nests (N1 to N4) of *Leptogenys processionalis* were located in the open fields, free from vegetation (so that the physical obstructions did not affect the branching pattern) at Hebbal campus, University of Agricultural Sciences, Bangalore, India. Two nests (N5 and N6) of *L. processionalis* and one of *Pheidolegeton diversus* Jerdon (Formicidae: Myrmecinae) were studied in the Sukhalatti Forest near Shimoga, Karnataka. We carefully followed the ants emerging from a colony, and marked foraging trails by placing a thin strip of whitestone powder along their sides from the beginning until the end of each foraging bout. This powder did not deter the ants from foraging. The lengths of various branches were recorded, and the trails were later traced onto paper. Ants repeatedly used the permanent trails and a few of their branches for about 15–20 days; so, to avoid redundant data, we spaced any two tracings of a colony at least 20 days apart.

Branching angles. We define branch angle as the angle of deviation of branches to the left ($L\theta$) or to the right ($R\theta$) of the main trail at the fork. The obtuse external angles of left (Le) and right (Re) trails branching off a main trail were measured, and the branch angles were computed as $L\theta = (180\text{-}Le)$ for left and $R\theta = (180\text{-}Re)$ for right branches. The branch angles were thus computed separately for permanent and temporary search trails. These angles were also computed for the extreme left and right columns in the TSF.

Factors regulating branching. Winged termites (alates) attracted to artificial light were caught and preserved at 10° C and used as artificial food. Two termites were offered at various distances along the front (W) and sides (SL and SR) of the TSF (Fig. 1c). After 5 min, the fate of the foraging front was recorded as (a) branched (b) diffusely branched [where branching was seen but where daughter branches interconnected up to a distance of 20–30 cm by movements of ants (15–20 ants per 5 min) between them], and (c) not branched. The percentage of the TSFs showing branching was plotted against W, and α was computed as $\alpha = 2*\sin^{-1}(W/2/SL)$.

Horton's analysis of branching pattern

Horton (1945) developed a technique to analyze the topology of river paths in which rivulets, streams and rivers join before they

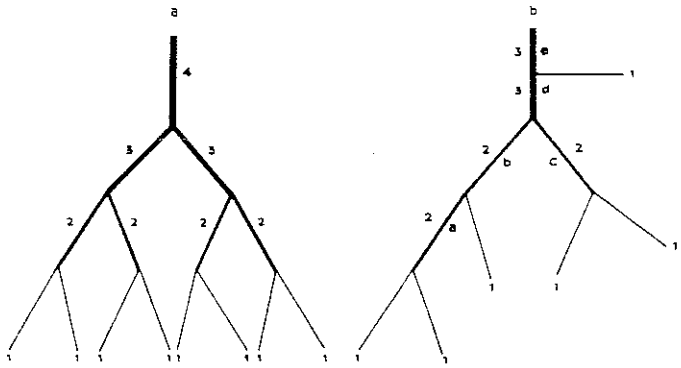

Fig. 2a, b. Strahler's (1952) method of ranking branches into hierarchial orders (1–4). Branches of same order are drawn in equal thickness. Note that symmetry of systematic branching in **a** breaks down as randomness enters **b**. In **b**, average length of order 2 branch $(L2)=[(a+b)+c]$ 2, while that of order 3 $(L3)=d+c$

end up in the ocean. His method, after slight modification (Strahler 1952) has been applied to the analysis of the branching patterns of various systems, such as bronchial trees, portal veins, pulmonary arteries, fungal colonies, geographical marked areas, trees, nerve cells and drainage systems (Leopold 1971; Barker et al. 1973; Stevens 1974; Horsefield 1980). The technique per se is very simple, and involves ranking the branches according to their hierarchical order. The terminal branches of any system are given order number 1 (Fig. 2a). If two branches of the same order join, the resulting trunk receives the next higher order while, if a leading branch of any order is joined by the low-order branch, the resulting trunk takes the order of the former (Fig. 2b). Horton showed that the log of the number of branches (log n) in an order plotted against the order numbers (0) decrease linearly, and the antilog of the slope of this line provides the branching coefficient (R_b), which indicates the average number of times any order branches; i.e., the number of branches of order i emerging from each branch of a higher order, $i+1$. It is obvious that the R_b value of a systematically bifurcating branching pattern is 2.0 (Fig. 2a); this increases as branching becomes random (Fig. 2b). The linear relation between log n and 0 holds for all the diverse branching systems analysed (e.g. human bronchial trees, Horsefield 1980; apple and birch tree, Barker et al. 1973), although these differ in their R_b values.

A second generalization by Horton about rivers was that the log of the average length of the branches, cumulated over subsequent orders (log CL; Fig. 2b), also follows a linear relation with the branch orders. Park (1985), however, recognized that this generalization is applicable only if the growth of the branches follows a specific pattern. Accordingly, he identified two kinds of growth patterns: (a) open unconstrained growth, where the average length of terminal branches is equal to or longer than that of the basal or higher order branches; (b) closed constrained growth, where the terminal branches are shorter than those at the base. By means of computer simulations, Park showed that while in the former pattern arithmetic cumulative length (CL) shows a positive linear relation with order number, in the latter pattern, log CL shows a positive linear relation with order number.

Statistical analysis

Branches in the tracings of the foraging bouts were ranked following Strahler's (1952) procedure, and the branching coefficients were computed for each tracing. The cumulative lengths and their log values were regressed over branch orders and analyzed for the significance of the fit of the linear regression coefficients. The mean branch angles and their vector lengths (r) were computed following Batschelet (1981).

Results

Branching pattern

Figure 3 shows a tracing of one of the foraging bouts and is representative of the topology of all other bouts traced. By Strahler's method of ranking, permanent trails emerging from the nest are given the highest order, and the terminal temporary trails the lowest. Conforming to Horton's first law, the log number of branches in an order (log n) decreased linearly with order number (0) in all the foraging bouts from all *Leptogenys processionalis* nests (Fig. 4) and also from *Pheidologeton diversus* nest.

The computed branching coefficients (R_b) ranged from 2.46 to 3.75 (Table 1). The R_b values of a few tracings were similar to those of other biological systems that are argued to be highly nonrandom (e.g., human lungs, 2.8), but compared with some other biological systems, such as trees ($R_b=4.83$; Leopold 1971; Barker et al. 1973), this is a very low range (Table 1).

When branching is a systematically bifurcating process, the R_b value will be 2.00. However, with deviations from systematic branching, this coefficient increases and, theoretically, has no upper limit. The R_b values of 5 out of 11 foraging bouts ranged between 2.46 (N4S1)

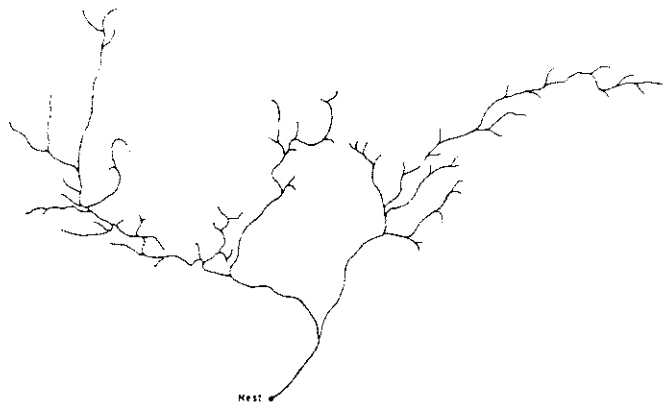

Fig. 3. Branching pattern of foraging bout of nest 4. After tracing the search trails, as detailed in text (Methods – Tracing the branching pattern "), grids of 20 × 20 cm were laid on the ground, and tracings were transferred to paper, using grid boundaries as reference points

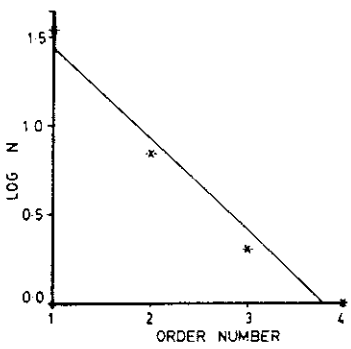

Fig. 4. Relation between log (n) and branch order (0) of N1S1

Table 1. *Leptogenys processionalis* branching coefficients (R_b) and regression coefficients of average length (L), cumulative length (CL) and of Log-cumulative length (log CL) with branch orders of search trails. N*i* refers to nests and *Si* to different times of tracings of the foraging bouts. Tracings marked with asterisks are how the trail appeared at the moment of observation; the other tracings indicate the trail patterns from the beginning to the end of the foraging bout; –: no data *P.d*: *Pheidolegeton diversus* data shown for comparison

Tracings	R_b	($P<$)	Regression coefficients					
			L	($P<$)	CL	($P<$)	Log CL	($P<$)
N1S1	3.28	(0.014)	98.79	(0.11)	184.95	(0.06)	0.335	(0.001)
N1S2	3.68	(0.001)	324.48	(0.10)	490.19	(0.09)	0.472	(0.0001)
N1S3	3.37	(0.013)	72.36	(0.26)	155.64	(0.06)	0.331	(0.035)
N1S4	2.91	(0.01)	55.92	(0.13)	140.59	(0.03)	0.312	(0.013)
N2S1	3.36	(0.0001)	557.01	(0.20)	674.40	(0.16)	0.468	(0.027)
N2S2	2.82	(0.006)	265.26	(0.02)	643.56	(0.03)	0.523	(0.021)
N2S3	3.75	(0.015)	–		–		–	
N3S1	3.17	(0.011)	225.04	(0.04)	406.48	(0.05)	0.546	(0.008)
N4S1	2.46	(0.001)	–		–		–	
N5S1*	3.46	(0.04)	–		–		–	
N6S1*	2.66	(0.043)	–		–		–	
P.d *	2.84	(0.0001)	–		–		–	

Table 2. Number [in brackets] and average length. L, cm (±SE) of branches of different orders of search trails

Order	N1S1	N1S2	N1S3	N1S4	N2S1	N2S2	N2S3	N3S1	N4S1
1	[35] 59.40 (±6.35)	[49] 60.72 (±10.49)	[32] 46.80 (±6.84)	[67] 52.5 (±8.25)	[37] 76.80 (±9.75)	[21] 60.30 (±7.46)	[14]	[31] 33.00 (±8.57)	[60]
2	[7] 77.10 (±51.06)	[12] 105.48 (±29.65)	[12] 133.80 (±22.20)	[10] 155.50 (±20.50)	[11] 115.50 (±31.11)	[7] 48.80 (±54.62)	[4]	[7] 77.10 (±40.85)	[17]
3	[2] 135.00 (±30.00)	[3] 351.00 (±186.42)	[2] 52.50 (±28.5)	[4] 93.75 (±52.40)	[3] 160.50 (±74.45)	[2] 1002.30 (±326.25)	[1]	[2] 469.00 (±330.0[illegible])	[5]
4	[1] 359.40	[1] 1060.50	[1] 315.00	[2] 241.65	[1] 1918.50	[1] 660.00		[1] 652.50	[2]
5				[1]					[1]

and 2.91 (N1S4; Table 1), indicating that the branching of trails is often systematic. However, six other foraging bouts showed R_b values ranging from 3.17 (N3S1) to 3.75 (N2S3). Branching patterns generated randomly under various sets of rules have been shown to have R_b values in the range 3.00–5.00 (Haggett and Chorley 1969; Stevens 1973). However, R_b values of 3–5, although a necessary condition, is not proof of random branching: branching patterns with R_b values in this range could still be systematic if their growth occurred by repeated addition of similar modules, with each trail giving rise to as many (3–5) branches as its predecessor (Stevens 1973). The foraging trails of *Leptogenys processionalis* seem to grow precisely in this manner. N1S1 to N1S4 refere to sequential tracings of the foraging bouts of colony N1 on different days from the establishment of the colony until it abandoned its nest after 3 months. Clearly, R_b values did not change with the age of the colony; nor did they change with the average length or cumulative length of the branches (Table 2; note that the foraging bouts differed considerably in their branch lengths).

Growth pattern of foraging trails

Cumulative length (CL) did not increase linearly with order number; the linear fit was not significant for 4 out of 7 foraging bouts analyzed (Table 1). On the other hand, log CL displayed a perfect linear relation with order number (null hypothesis, H_o: $b=0$ rejected for all traces; Table 1, indicating that the trails grew gradually shorter as they branched out. This is also evident from the average length (L) of branches of different orders (Table 2).

Branching angles

Left and right branches were highly symmetrically placed on either side of the parent trail (Table 3). The high vector lengths (r-values) indicate that the branches are significantly clustered around the mean angle, and hence are not randomly distributed. Similarly extreme left and right columns of the TSFs were significantly clustered and symmetrically placed. The resulting fork angles of the permanent (108.34°) and temporary (105.40°) branches and of the TSFs (110.10°) were also equal.

Factors affecting branching pattern. If the branching of a trail is a function of its growth, such that it occurs when the trail grows to a critical length, as in fungal colonies (Trinci 1973a, b), then the internode lengths (distance between any two successive branching points) can be expected to exhibit normal or unimodal distribution around this critical length. Our data did show such a pattern; the internode lengths were positively skewed

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Table 3. Branching angles of permanent and temporary trails and of terminal search fields (TSFs)

Branch level (n)	Branch angles								
	left branch ($L\alpha$)				right branch ($R\alpha$)				fork angle
	$x \pm SE$		r	P	$x \pm SE$		r	P	($L\alpha + R\alpha$)
Permanent (28)	55.28	2.13	0.91	0.01	53.06	2.79	0.93	0.01	108.34
Temporary (58)	54.10	2.10	0.96	0.01	51.40	2.42	0.95	0.01	105.40
TSF (30)	55.70	3.30	0.95	0.01	54.40	3.30	0.95	0.01	110.10

Table 4. Branching behavior of trails in response to food provided at varying distances (W) at front of terminal search field (TSF)

Distance (W) (cm)	Percent TSFs:			
	Branched	diffusely branched	not branched	(n)
3–10	0.00	7.14	92.86	(14)
11–20	0.00	50.00	50.00	(12)
21–40	46.67	53.33	0.00	(15)
41–60	88.89	11.11	0.00	(9)
61–80	100.00	0.00	0.00	(8)
>81	100.00	0.00	0.00	(11)

Table 5. Branching behavior of trails in response to food provided at varying angles from fork at front of terminal search field (TSF)

Angles	Percent TSFs			
	branched	diffusely branched	not branched	(n)
0–20	0.00	14.29	85.71	(7)
21–40	6.66	46.67	46.67	(15)
41–60	66.67	16.67	16.67	(12)
61–80	63.16	21.05	15.79	(19)
81–100	75.00	12.50	12.50	(8)
>100	87.50	12.50	0.00	(8)

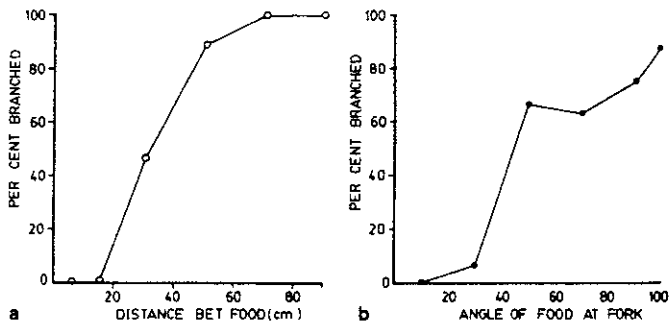

Fig. 5a, b. Percent terminal search fields showing branching, when food was provided **a** at various distances (W) along front, and **b** at various angles

with a long tail. However, such distribution might also arise if the branching is a function of encountering food at the TSF and if the inter-prey distance is also unimodally distributed.

Our preliminary observations indicated that if TSFs do not encounter food after moving for about 0.7 m (range 0.4 to 1.2 m), the ants retreat and join other trails. On the other hand, if food is encountered at the TSF, all the ants converge towards it. Accordingly, if food is encountered at two distinct places in the foraging front, the foragers congregate on these in diverging trails, resulting in branching. Hence, we hypothesized that the extent of the spatial separation of the food patches encountered regulates branching process. Our manipulation experiments supported this. Trails did not branch if prey (termites) were offered <40 cm apart at the front of the TSF (Table 4; Fig. 5a); branching invariably occurred if termites were offered >60 cm apart at the front. Similarly, branching was also found to be a function of the angle (α) that two food patches subtend at the fork of the TSF. The trails branched only if two termites were placed at $\alpha > 60°$ at the fork (Table 5; Fig. 5b). This relation, however, results partly from the association between W and α ($r = 0.63$, $n = 69$; $P < 0.001$). Since the width of the search front was limited to 60–80 cm (and sides ~80 cm), higher W values could be attained only if termites were placed at the extreme corners of the front of the TSF that is associated inevitably with higher α values. Thus, higher α values displayed a higher percentage of branching because they were associated with high W values. In fact, for W values <40 cm, only 20% of the TSFs showed branching, even when α was more than 60°.

Discussion

Our results indicate that all the foraging trails of *Leptogenys processionalis* and of *Pheidolegeton diversus* have similar topological features. We discuss below these features in the context of (a) their fractal properties, and (b) the rules regulating the branching process. Finally, we also suggest the possible adaptive significance of these features and of branched search trails in maximizing the benefit-to-cost ratios of harvesting.

Fractal properties

Foraging trails exhibited non-randomness in the following three topological features, leading to a self similarity in the branching pattern at different levels (orders):

Number of branches per node and branching coefficients A priori, there are no known factors preventing the formation of more than two branches at any node. However, the search trails always exhibited a bifurcated branching process; no trail split into more than two branches at a node. The illustrations of foraging trails provided by other workers (Mirenda et al. 1980; Reyes 1986; Moffett 1988) also suggest that the bifurcating branching system of *Leptogenys processionalis* is more a rule than an exception among mass-recruiting ants. However, trails did not grow and bifurcate at the same rate, and hence the trail of any order ends up in ≥ 2 branches of a lower order (as evidence by the R_b values). Nevertheless, such differential growth of branches persisted through all orders at the same rate within each foraging bout, as evident from the linear relation between log n and order number. This means that trails grow by the repeated addition of similar modules, resulting in a pattern that is self-similar at different levels.

Branch angles. The fork angles of permanent and temporary branches were similar, and the branches were symmetrically placed on either side of the parent trail, introducing additional self-similarity in the topology of search trails. This persistent similarity and symmetry of branch angles probably orginated from the fork angle of the TSF, where branching is actually initiated.

Branch lengths. The liniar relation between log *CL* and branch order indicates that the mean length of the branches of the higher order (near the nest) is higher than that of the lower order (away from the nest). Such constrained outward growth could be an inevitable consequence of the limitation of number of worker ants available for the transportation of food from distant spots.

Rules regulating branching process

In *Leptogenys processionalis*, the decision to branch occurs locally at the TSF, without any communication with the nest. Further, such peripheral decision making results in a self-structured branching pattern with certain nonrandom toplogical features. This can be achieved if all worker ants inherit a blueprint of the branching pattern of search trails that is insensitive to external influences, or if all the workers commonly exhibit simple movement-rules in response to the external stimuli (here, food). Our manipulation experiments indicated that the branching process is a function of the spatial distribution of the prey encountered by the TSF. Thus, it is not likely that ants follow an inherited guiding blueprint of branching pattern. Rather, they seem to adopt two simple response rules:

Rule 1. Ants in the TSF on encountering food, send signals to recruit other workers. We observed that, on encountering termites, individual workers of *Leptogenys processionalis* induce vigorous movements among ants up to 10 cm away. Workers thus activated become secondary sources of signals to recruit further foragers. Other mass-recruiting ants are also known to emanate signals on encountering food, thus inducing increased searching activity among the rest of the workers (Chadab and Rettenmeyer 1975).

Rule 2. Foragers converge towards the nearest food source, following signals from the neighboring workers. Foragers of *Leptogenys processionalis* cannot resolve the gradients of signals emanating from two resource spots if they are placed <40 cm apart at the raid front. Hence, they treat the two spots as a single patch and congregate on them by a single trail. However, they discriminate between the gradients of signals emerging from food patches that are more than 40–60 cm apart, and converge to the nearest of these. This results in the congregation of ants in the TSF at two locations, leading to the formation of two distinct trails or branches at the fork. Since the maximum width a search front can attain is 80–100 cm, ants seldom encounter more than two food patches at a time which are separated by more than 40–60 cm. This could constrain the formation of more than two branches at any node.

Why forage by branching?

All mass-recruiting ants have two tasks while foraging. (1) While exploring a given area they should minimize the total length of the foraging trail, such that the ratio of the area explored (benefit) to the length travelled (cost) is maximized. (2) Fresh recruitment to the newly discovered resource patches does not always occur from the nest; very frequently workers are recruited to the resource patches directly from other neighboring branches; hence, ants should minimize the average distance between any two TSFs (where trails encounter food), in such a way that the cost of travelling for the recruits on their reallocation to resource patches is reduced. Considering the potential foraging area around the nest to be an octagon, with the food patches evenly distributed, it is possible to show that the above two tasks can be most effectively solved if ants forage by branched trails. Comparing various architectural topologies such as spirals, meanderers, explosion and branching patterns that connect the points distributed in an octagon with its center, Stevens (1973, 1974) showed that while some of these minimize the total path length (that connects all the points with the center), others minimize the average path length between any two randomly chosen points (Table 6). However, among these, the branching pattern is a good trade-off in minimizing both the total path length (task 1) and the average path length (task 2).

Thus, the bifurcating branching system of the foraging trails of mass-recruiting ants appears to be an effi-

Table 6. Comparison of various topologies in regard to path length connecting all points of an octagon with center and average distance between any two randomly chosen points. Figure numbers in parentheses refer to those in Stevens (1974); tri and bi refer to trifurcating and bifurcating branching systems

Toplogy (Fig. no.)	Path length (cm)	Average distance between any two randomly chosen points (cm)
Spiral (23a)	90.00	45.00
Meanderer (23b)	90.00	45.00
Explosion (24)	331.00	3.37
Branching (tri, 25 d)	90.00	3.67
Branching (bi 120°) (26)	77.90	4.42

cient strategy that maximizes the ratio of benefit of harvesting food from a given area to the cost of travelling.

However, an additional condition for minimizing the length of the connecting links is that the angle of branching at the established nodes shall be 120° (Stevens 1973; Bern and Graham 1989). The pheromone-guided movement of ants, restricted to the width of the trail, is equated to the flow of fluids such as blood in vessels (Holt 1955; Taylor 1978). In such biological systems, the optimum branch-angle that minimizes resistance to flow when the main trunk divides into branches of equal width is predicted to be 70–80° (Murray 1926, 1927; D'Arcy Thompson 1942; Stevens 1974). Thus, while the branch angle of 120° minimizes length between the TSFs, that of 70–80° minimizes the resistance to the movement of ants. Interestingly, *Leptogenys processionalis* showed an average branch angle of 108° (Table 3); it is likely that this angle has evolved as a trade-off to minimize both the travel cost and the resistance to the flow of the ants in the columns.

Leptogenys processionalis thus seems to adopt the most efficient toplogy in laying foraging trails, which minimizes both the travel cost and resistance to the transportation of food. This pattern of branching seems to emerge more as a consequence of certain simple rules adopted by the individual foragers in TSFs than as an interactive decision of the whole colony. In this respect, the regulation of the foraging trails in mass-foraging ants is analogous to the functioning of the peripheral neural system as suggested by Franks (1989).

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Plant design and non-random foraging by ants on *Croton bonplandianum* Baill. (Euphorbiaceae)

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Abstract. *Croton bonplandianum* bears female flowers in inflorescences which are arranged in a regular pattern. Foraging individuals of the ant *Camponotus sericius* feed on the nectar in the nectary glands of female flowers. The pattern of movement of ants while foraging between these regularly placed inflorescences was highly systematic and distinctly exploratory. The ants tended to visit new inflorescences at each move and avoided revisiting inflorescences. They followed this foraging pattern by adopting circular movements either to the left or to the right and avoiding other complex but equally effective moves. This was probably due to memory constraints. The ants predicted the resource quality of the subset of a patch by sampling a part of it. The inflorescences within a cluster were similar in quality. Using this relation ants could make decisions about continuing to forage in a cluster after sampling any one inflorescence. If the first inflorescence visited was of good quality they continued to forage on the rest of the cluster, while if the first inflorescence was of poor quality they abandoned the cluster. This ensured efficient foraging with minimal expenditure of time and energy.

Insects foraging on nectar adopt certain strategies that maximize their net rate of energy intake (Levis et al. 1971; Pyke 1978a, b; Heinrich 1979; Zimmerman 1979; Morse 1986; Wetherwax 1986). The most prominent among these strategies are non-random movement between plants (Heinrich 1979) and prediction of patch quality based on the cues available before foraging in any patch (Zimmerman 1982; Morse 1986; Wetherwax 1986). There is also considerable evidence for the non-random movements of bird (Cody 1971, 1974; Gill & Wolf 1977) and fish (Kleerekoper et al. 1970) foragers. Non-random movement prevents the forager revisiting patches; it follows certain rules predicted by optimal foraging theory (Pyke 1978b). For instance, the insect leaves the patch (flower) in the same direction as its arrival to that spot and/or turns alternately to the left and right on departure (Pyke 1978b, c). However, these rules do not always seem to operate (Zimmerman 1979, 1982). When the probability of revisiting the same flower is low, insects need not follow a non-random foraging pattern (Zimmerman 1979, 1982); in such situations the mean angle of departure is uniformly distributed unlike the unimodal distribution predicted by optimal foraging theory (Pyke 1978b, c). Similarly, these rules might not operate in certain other situations. For instance, consider a plant as a patch and different inflorescences in it as subsets of this patch. Unlike the movement of a hovering forager between clusters of flowers, the movement of a crawling insect on a plant is constrained by the structural design of the plant. Hence, the rules governing the movement of a crawling insect between clusters could differ from that predicted for the hovering insect. If the structural arrangement of the inflorescences of plants is regular, the insects can increase their foraging efficiency, provided they can memorize and adopt such design into the rules governing their movements (Pyke 1978c). Such memory of the plant structure combined with sampling would also help them in accurately predicting the resource levels in other parts of the plants.

In this study, we used such a system where ants forage on the nectar of a plant whose inflorescences follow a regular design. We attempted to answer two specific questions: (1) Is the movement of ants between inflorescences in a cluster random or is it guided by certain rules formulated on the basis of the structural design of the plant? (2) Are ants capable of using the cues provided by the design and, thence, predict in advance the resource status of a cluster of inflorescences?

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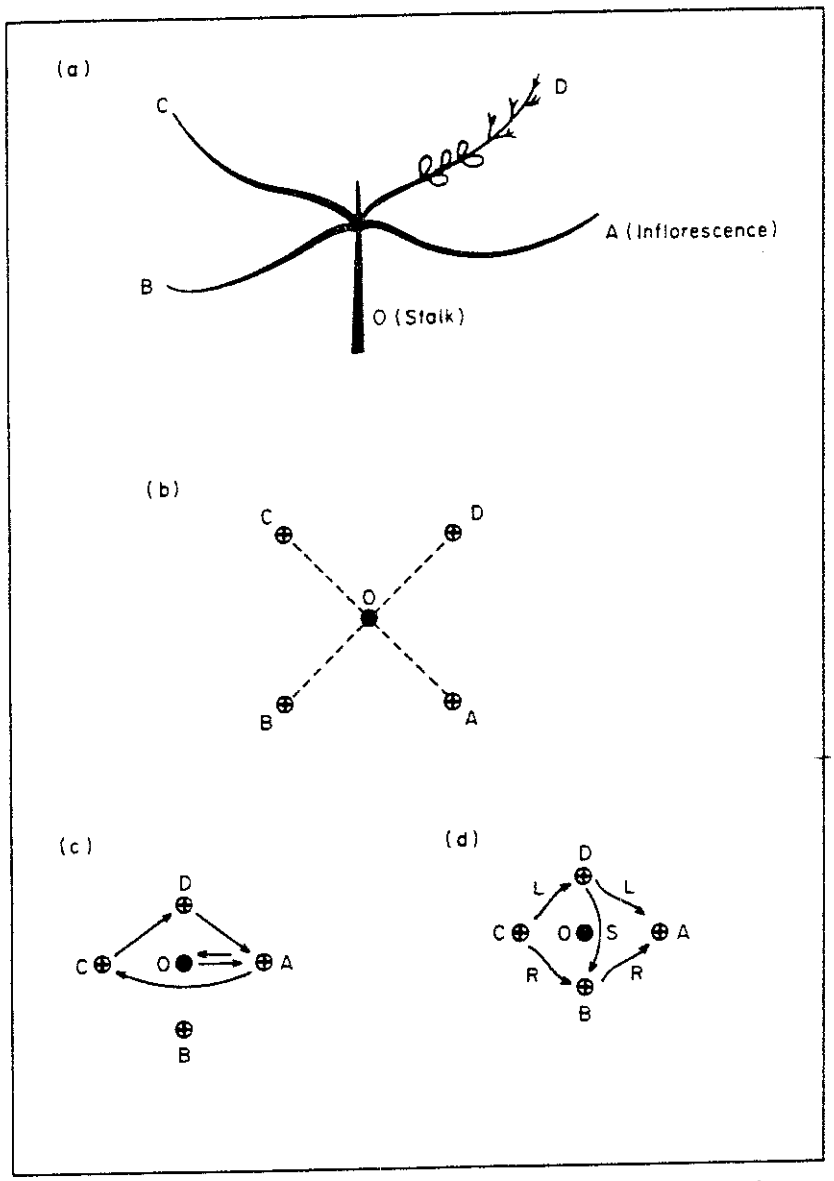

Figure 1. A cluster of four inflorescences. The actual (a) and diagrammatic top view (b). The first inflorescence is labelled A and the rest B, C, D in clockwise order. (c) The movement of an ant showing a sequence of O A C D A O. (d) The directions of moves: L: left; S: straight; R: right.

MATERIALS AND METHODS

The Study Species

Croton bonplandianum Baill. is a monoecious herb and bears inflorescences in clusters. Each cluster consists of generally four (80%), sometimes three (20%), inflorescences emerging from a single node around the stalk at equally separated angles (Fig. 1a). Thus, each cluster has a perfect and regular design so that a top view of the cluster exhibits four inflorescences at about 90° from the adjacent ones around the stalk (Fig. 1b). Each inflorescence bears male flowers at the top and females at the bottom; each female flower bears a nectary gland on the pedicel which starts to function after the ovules are fertilized. Inflores-

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cences are protogynous and female flowers open synchronously. As the flowers develop into fruits, the nectary gland starts to function and the amount of nectar produced increases gradually, attaining peak production when the fruits mature completely. Depending on the stage of the development of the majority of fruits, each inflorescence can be grouped into one of 12 classes of developmental stages (Fig. 4).

Croton harbours a set of ant species (Veena, Kumar & Ganeshaiah, unpublished data) of which *Camponotus sericeus* (Fabricius) was chosen for this study because of certain special features. This ant is an individual forager of nectar and is associated with the croton plant in almost all habitats. The foraging individuals are relatively big, forage faster than other species and are undisturbed even when closely observed so that it is easy to collect unbiased data.

Foraging Pattern

Individual ants were followed and their foraging sequences on each cluster were recorded. If an ant climbed onto an inflorescence in order to forage, that inflorescence was termed A, and the stalk O, and the other inflorescences were similarly labelled clockwise from A as B, C and D in that order (Fig. 1b). The foraging sequence of ants was therefore recorded as O (stalk) to A (first inflorescence); if the ant then moved to C, D and A and if it finally left the cluster via the stalk (O), the recorded sequence was OACDAO. In such a sequence A, C, D and A are considered to be 'visits' to the inflorescences. AC, CD and DA as 'moves' and ACD, CDA as 'runs' or sequences of three consecutive visits to inflorescences (Fig. 1c).

Test for Randomness in Foraging Pattern

When an ant has followed a sequence of OAC in a cluster of four inflorescences, after foraging on C, and given that it visits another inflorescence and not the stalk, it has three options: to move to B, or to D or to A. If the ant moves randomly the probability that it picks option A is 1/3, i.e. in a cluster of four inflorescences the probability that a randomly moving ant revisits an inflorescence after foraging on two inflorescences is 1/3. We tested whether the ant conforms to this prediction. For this, from the recorded data, only those sequences consisting of at least three or more visits to the inflorescences were selected. From these selected sequences all possible runs, i.e. sequences of three consecutive visits, were counted (N). From these runs, the number of runs in which the ant revisited an inflorescence in every third visit was counted (n), i.e. runs of the kind AXA, BXB, CXC and DXD were counted; using chi-squared tests these observed number of visits to the original inflorescence (n) were compared with that expected on the basis of random movement of the ant ($N/3$). Similar comparisons were also made for clusters of three inflorescences; the only difference is that, in these clusters, the probability of revisiting the original inflorescence is 1/2 as there are only two options for an ant after foraging on the second inflorescence.

The randomness was also tested by calculating the frequency of new inflorescences explored by the ant within a cluster, with an increasing number of visits in a sequence, and comparing it with that expected on the basis of random movement. On the first visit an ant forages on one inflorescence (A); on the second visit the ant goes to a second new inflorescence because the ants do not climb back to the inflorescence just visited. On the third and fourth visits, the ant might visit either an entirely new inflorescence or an already foraged inflorescence. The expected frequencies of sequences exploring new inflorescences with third and fourth visits were found by considering all possible paths based on random movements of the ant. These expected frequencies were compared with the observed frequencies of sequences leading to a different number of new inflorescences. The comparison was not made for the fifth visit onwards since by then the expected and observed frequencies were almost equal.

Rules of Movement

From the recorded sequence of data the directions of turns (left, right and straight ahead) in each step were decoded (Fig. 1d). For instance, a sequence of OABDAO shows that an ant has turned left (AB), gone straight (BD) and turned left (DA) in that order before leaving the cluster. A contingency table was set up indicating the frequency of these moves in the first and the second of any two subsequent moves. The independence of, and association (C) between, the first and second steps were then tested following Siegel (1956).

Table I. Frequency of expected and observed revisits to already visited inflorescences on every third visit in clusters of three and four inflorescences

Cluster type	No. of revisits to already visited inflorescences	No. of visits to other inflorescences	N	χ^2	P
Four inflorescences					
Observed (n)	(n) 30	($N-n$) 128	158	15 02	0 001
Expected ($N/3$)	($N/3$) 53	($2N/3$) 105			
Three inflorescences					
Observed (n)	(n) 13	($N-n$) 35	48	10 08	0 001
Expected ($N/2$)	($N/2$) 24	($N/2$) 24			

N: total number of sequences with three consecutive visits; n: total number of sequences with every third as a revisit

Prediction of Patch Quality

The index of stage of development of fruits (0–11) of two randomly chosen inflorescences from each of 64 clusters was recorded and Spearman's rank correlation coefficient was computed using these indices. Ten fruits corresponding to each index of development were protected from ant visits for about 1 h. The nectar accumulated was scooped on to a filter paper and its sucrose content was estimated (Nelson 1944). For a set of clusters ($N=78$), the number of inflorescences in a cluster visited by the ants and the developmental index of the first inflorescence visited in that cluster were recorded. From this, the percentage of ants that terminated foraging after one and after more than two visits in the cluster were calculated.

RESULTS

Foraging sequences in a cluster ranged from visiting just one inflorescence to as many as 13 visits with repeated foraging on some inflorescences. From these, only those sequences with three or more visits were considered for testing randomness in ant movement. Table I presents the observed number of three-visit sequences (runs) that showed revisits to the inflorescence on the third move, i.e. the observed number of runs of the kind AXA, BXB and DXD in clusters of three and four inflorescences. The observed number of revisits was significantly ($P<0.001$) smaller than that expected. This was true for clusters of both three and four inflorescences. Thus, the movement of ants between the inflorescences was clearly not random and they tended to avoid an inflorescence already visited. In other words, they appear systematically to explore the cluster before revisiting an inflorescence. This is also clear from Fig. 2. The observed frequency of sequences in which three different inflorescences in three visits were explored was more than expected. Similarly, the observed frequency in which four different inflorescences were foraged in four visits is also more than expected. This means that ants tend to visit new inflorescences more often than expected on the basis of random movement.

Figure 3a, b shows that the ants did not exhibit any bias in the direction in which they turned. The number of left, right and straight ahead moves were almost equal, though there were relatively few straight ahead moves ($\chi^2=2\ 12$, $P<0\cdot25$, for four-inflorescence clusters; $\chi^2=0\ 69$; $P<0\cdot25$, for three-inflorescence clusters). Chi-squared tests indicated that turns in the first and second moves were not independent and overall there was a positive association between the first and second moves (Table II). Of particular interest are turns to the left followed by left (LL) and right followed by right (RR). The LL and RR moves were more frequent than expected indicating that if an ant turns left it is more likely to turn left in the next move as well; similarly for RR. However, such association was not seen for SS. Indeed, SS moves were less frequent than expected. This can be reconciled if the contingency table is recast into two types: (1) the subsequent moves that lead to different inflorescences (LL, RR, RS, LS, SR and SL) and (2) the moves that lead to original inflorescences (SS, LR and RL). Type 1 moves were always more frequent than expected while type 2 moves were less frequent than expected. This was also true for ants foraging

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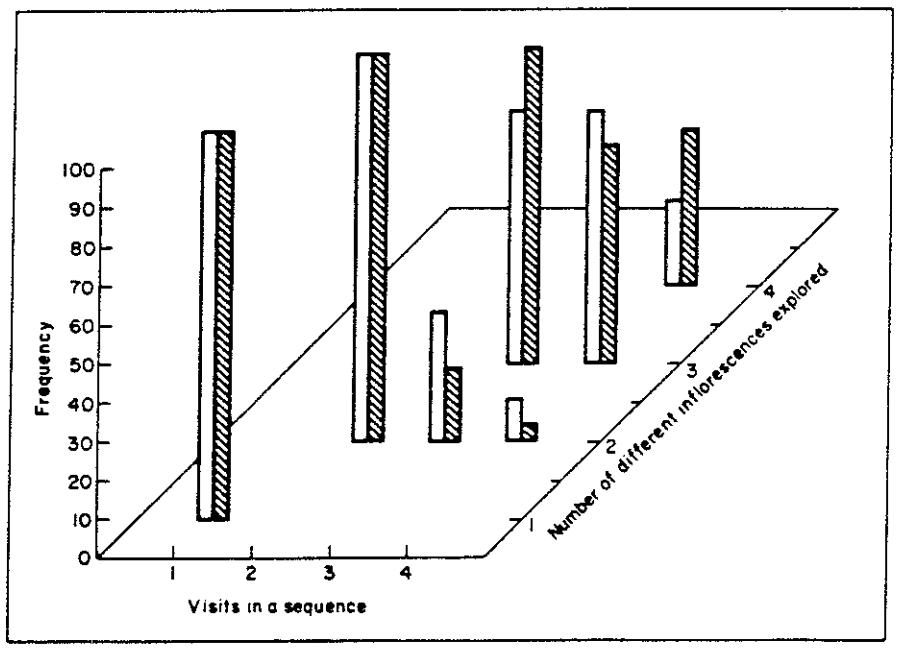

Figure 2. Expected (open bars) and observed (hatched bars) frequency of new inflorescences visited by an ant with an increase in the number of visits.

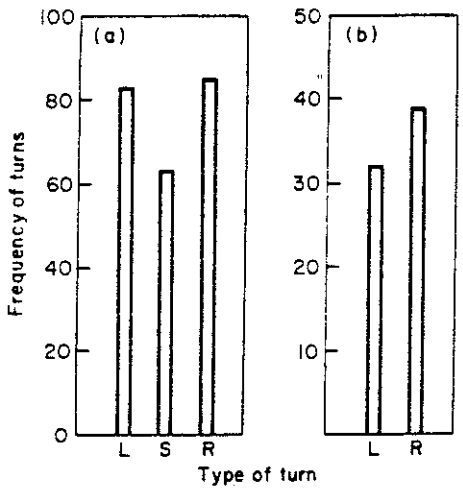

Figure 3. Frequency of left (L), straight (S) and right (R) turns taken by ants in clusters of four (a) and three (b) inflorescences.

Table II Frequency of left and right turns and straight ahead moves in the first and second of two subsequent moves in clusters of four and three inflorescences

	First move		
Second move	Left	Straight	Right
Four inflorescences*			
Left	31 (20 79)	17 (16 48)	14 (24 72)
Straight	14 (14 42)	7 (11 43)	22 (17 14)
Right	8 (17 74)	18 (14 08)	27 (21 13)
Three inflorescences†			
Left	16 (10 5)		8 (13 5)
Right	5 (10 5)		19 (13 5)

Values in parentheses indicate the expected frequencies
* $\chi^2 = 20\cdot85$, $P < 0\cdot0001$, $C = 0\cdot3414$ (C: association coefficient; see text for explanation).
† $\chi^2 = 10\cdot29$, $P < 0\cdot001$, $C = 0\cdot4193$

Table III Developmental stage and resource quality of the first inflorescence visited by the ant and the ant's subsequent behaviour

Stage of first inflorescence visited	Nectar status	Percentage of visits: No visits	Visits terminated after first inflorescence	Visits to more than two inflorescences	*N*
0 and 11	No nectar	36 84	50 00	13 15	38
1–4	Poor nectar	9 09	54 50	36 36	22
8–10	Moderate nectar	—	7 69	92 30	26
5–7	High nectar	—	10 84	89 19	37

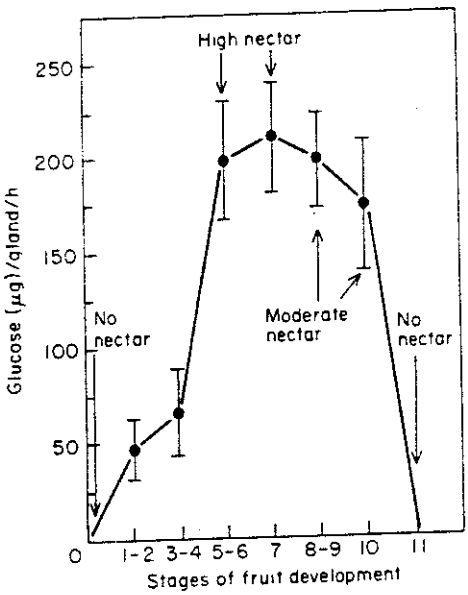

Figure 4 Amount of nectar produced in developing fruits of different stages. 1 and 2: just fertilized; 3 and 4: grown to 2–3 mm diameter; 5 and 6: fully grown (5 mm diameter), but seed not filled; 7, 8 and 9: seed-filling stage; 10: fruit dried and splitting; 11: all fruits split. Vertical bars indicate SEM

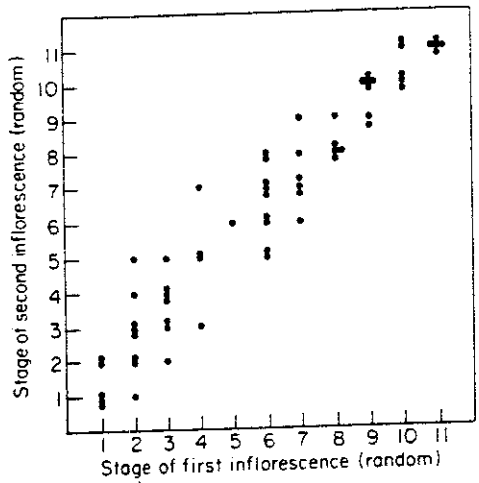

Figure 5 Correlation between stage of fruit development of any two randomly chosen inflorescences of a cluster. Stages as in Fig. 4. $N = 64$, $r = 0.96$, $P < 0.001$

on clusters of three inflorescences (Table II). Thus, the ant generally seems to follow at least one specific rule while foraging: to keep either left or right and to continue to forage in that direction.

Figure 4 shows the amount of nectar produced per h in nectary glands of fruits of different developmental stages. Stages 0 and 11 do not have any nectar while 5–7 produce 200 µg of sucrose per h. Accordingly, the stages were classified into four groups: no nectar, poor, moderate and high nectar (Table III). Any two inflorescences taken randomly from the same cluster belong to the same stage of development (Fig. 5). This means there is considerable synchrony in the development of inflorescences within a cluster. Since each developmental stage is also associated with a certain level of nectar production, we hypothesized that the ant would be able to predict the resource status of the whole cluster by sampling any one inflorescence. Table III presents the stage and resource quality of the first inflorescence visited by an ant and its behaviour following that visit. If the first inflorescence visited happened to be in the no-nectar group, the ants abandoned the first inflorescence itself; about 37% of the ants never went up to the top of the inflorescence and they terminated their visit halfway through; about 50% of the ants left the cluster after visiting the first inflorescence and only 13% of the ants continued to explore the cluster further. This is also true for the second group with poor

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nectar except that 36% of the ants foraged further after visiting the first inflorescence. In clusters of moderate and high nectar production, 90% of ants continued to forage after visiting the first inflorescence; only about 7% and 10% terminated foraging after the first inflorescence, respectively. Thus, ants make decisions about their commitment to forage in a cluster after predicting its quality using the information obtained by sampling one of the inflorescences. We did not test whether such sampling and decision-making processes continued further while the ants foraged through the cluster.

DISCUSSION

Ants foraged non-randomly on the plant and systematically explored the inflorescences in a cluster. By doing this, they avoided revisiting the inflorescences and thus increased the efficiency of foraging. However, in about 30% of visits, ants made more than four visits in a cluster, so that they inevitably revisited the inflorescence. These revisits may be explained as follows. Nectar is produced continuously in a gland. Hence, if the time elapsed after leaving a particular inflorescence and before completing foraging on other inflorescences in the same cluster is long enough, sufficient nectar may accumulate in the visited inflorescence. It then pays the ant to revisit this inflorescence rather than to go in search of another cluster because the inter-cluster distance in *Croton* is two to three times more than the inter-inflorescence distance within a cluster. Additionally, the ant also runs the risk of encountering the clusters with no or poor nectar when it is searching for new clusters. If the payoffs of leaving the cluster and searching for another cluster are low, then the ant should resort to revisiting the inflorescence (Krebs et al. 1974; Cowie 1977; Heinrich 1979; Real 1983). However, we have yet to work out whether the ant is optimizing its movements on the basis of these risks and costs of inter- and intra-cluster movements.

The systematic movement by the ant in a cluster may come about in any of the following ways. (1) The ant might mark the foraged inflorescence with a volatile chemical. This, however, is not likely because several ants were found foraging simultaneously on the same plant, although on different clusters. The volatile marker left by one ant is likely to interfere with the foraging by others. Thus, such marking would not be efficient unless it is highly volatile and short lived. But if it is highly volatile it might not help the marking ant because the duration of foraging time on an inflorescence in the same cluster before it can revisit is highly variable, ranging from 10 to 105 s per inflorescence. (2) The ant might learn the design or the pattern of arrangement of inflorescences in the cluster and move accordingly. (3) The ant might follow a set of movement patterns which are gradually selected through a continuous feedback system of rewards to the different moves that ants adopt in their repeated visits to the plant (Pyke 1978b, c). In the latter case, the ant need not learn the design of the plant, although the rules of movement are selected in direct relevance to the design. It is also true that if the ant is following both the second and third strategies it becomes difficult to delineate them. The data provided here support the third possibility; ants seem to adopt more often one specific rule. If they take a left turn in a cluster they continue to keep left; similarly for right turns. They do not, however, follow this principle if they take a straight ahead move at the first move because SS moves always lead to the original inflorescence. The data also indicated that all subsequent moves leading to the original inflorescence are less frequent than those leading to a different inflorescence. However, within these moves that lead to different inflorescences, SL, LS, SR and RS are less frequent than LL and RR. This can be explained by assuming that insects have memory constraints (Lewis 1986; Waser 1986). In a cluster of four inflorescences a continuous move of LLL leads to the new inflorescence in every move and the ant has to memorize just the previous move to execute the next move correctly; similarly for RRR moves the required sequence to be memorized is short and simple (R). But if the ant takes an RS move, then, in the third step, only one specific move i.e. L, leads the ant to a new inflorescence (RSL) while both RSR and RSS lead to one of the two visited inflorescences. This means that to execute the correct move at the third step the ant has to memorize the two previous moves of two different turns (R and S). This is true for any sequence involving S. If the insect exhibits memory constraints while foraging (Lewis 1986; Waser 1986) the best strategy for the ant would be to adopt LL or RR moves. Despite the fact that the moves involving S are complicated for the ant, S moves were not significantly less frequent than R and L turns. In other words, these LLL or RRR moves

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follow a circular exploration of the inflorescences It is interesting that in an analogous situation syrphid flies foraging on Compositae heads, where flowers are arranged in a circle, follow a similar strategy (Gilbert 1983) The flies explore the cluster by foraging 360° to the left or right before leaving the cluster It is not clear whether such circular exploration is specific to foragers on plants like *Croton* and Compositae heads or if it is a general strategy of all foragers foraging on a plant It would be interesting to enquire whether such circular moves lead to maximum exploration of resource spots in a bounded system, like a plant, irrespective of the pattern of arrangement of the flowers The tendency of the foragers to turn left or right is also established in bumblebees in in vitro conditions (Cheverton 1982); individual bumblebees consistently follow a particular direction as a sub-optimal strategy while foraging on resource patches arranged in a regular design

Ants make decisions regarding their commitment to forage in a cluster depending upon the resource quality of the cluster They assess this by the information obtained while foraging on the first inflorescence they visit and associating it with the resource quality of the rest of the inflorescences within the cluster In other words, they are capable of using the association existing between inflorescences within a cluster to predict the quality of the cluster by sampling a part of it Insects are known to be able to associate different patch characteristics with their resource qualities and to predict the quality of a patch by sampling a part of it (Heinrich 1979; Wetherwax 1986) Bumblebees, for instance, can quickly associate the colours of flowers with their resource qualities (Real 1983) Such sample-based prediction is also reported in birds (Gill & Wolf 1977)

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PRESENTATION BY PARTICIPANT

BY

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Sex Differences in Mortality among Langurs *(Presbytis entellus)* of Jodhpur, Rajasthan

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Key Words. Sex ratio · Mortality · Langur · *Presbytis* · Dispersal · Intrasexual competition · Infanticide

Abstract. In a population of about 1,300 Hanuman langurs *(Presbytis entellus)* living in one-male breeding structures at Jodhpur, Rajasthan, India, census data resulted in male:female sex ratios of 1.1 in infants, 1.5 in juveniles and 0.2 in adults. Long-term demographic monitoring of 144 known individuals up to the age of 30 months confirmed a higher juvenile female mortality. It is hypothesized that heavier maternal investment in males helps them to compete more successful. Once males emigrate from their natal troop, their mortality begins to exceed that of females. The strongly female-biased adult sex ratio seems to result from male-male competition: maturing males join male bands and are exposed to greater risks while traversing unfamiliar areas, occupying home ranges of harem troops and fighting with other males for possession of a female harem. A sample of 60 definitely known causes of deaths recorded over 21 years revealed that males died significantly more often than females in instantaneous 'spectacular' deaths from external causes, such as accidents, infanticide and predation, thus reflecting a high-risk, high-gain strategy. The sex difference in infanticide (18 males:9 females for 13 directly observed and 14 presumed cases) is not well understood because the commonly accepted hypothesis is that new harem residents try to shorten a mother's lactational amenorrhea by killing her unweaned infant regardless of its sex. However, it might be that harem residents select against future competitors of their sons and at the same time spare female infants with which they can reproduce if their tenure (mean: 26.4 months) is long enough.

Introduction

In many mammalian species, males suffer higher mortality rates than females (e.g. Belding's ground squirrel [1]; Soay sheep [2]; red deer [3]; humans [4–6]). It has been suggested that such differential mortality evolved in species characterized by pronounced male-male competition. The males of such species are selected to accept an aver-

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age reduction in the chances of survival as long as this is associated with a greater potential reproductive success in adulthood that can be achieved by the monopolization of females [7–9]. This hypothesis is tested here with data collected during a long-term field study on the Hanuman langur *(Presbytis entellus)*, a sexually dimorphic catarrhine primate with a harem breeding structure

Material and Methods

Jodhpur is located in the state of Rajasthan at the eastern edge of the Great Indian desert. The climate is dry, with a maximum temperature of up to 50 °C during May/June and a minimum temperature around 0 °C during December/January. Jodhpur receives 90% of its scanty rainfall (annual average 360 mm) during the monsoon period (July–September). The town stands on a hilly sandstone plateau covering approximately 85 km², surrounded by flat semi-desert. The natural vegetation is open scrub dominated by xerophytic plants such as *Prosopis juliflora, Acacia senegal* and *Euphorbia caducifolia*. Parks and fields are dependent on irrigation.

The Jodhpur plateau is inhabited by a geographically isolated population of about 1,200–1,300 Hanuman langurs *(P. entellus entellus)* that has been studied by various Indian and German research workers since 1967. There are no other langur groups within a radius of 100 km. According to censuses from 1983 to 1986, the population comprised between 1,130 to 1,298 animals. The reproductive units are bisexual one-male troops (harems) with a single adult breeding male. Each troop occupies its own home range of about 0.5–1.3 km². Troops containing several adult males are rarely found (< 10%). Long-term demographic monitoring of known individuals indicates that (with few exceptions) females remain in their natal troop throughout their lives. Males emigrate – usually as juveniles – and join all-male bands, whose home ranges can be up to 20 km². On average, adult males weigh 18.5 kg and adult females 11.7 kg [for details see ref. 10–12].

Due to fusions and fissions, the number of bisexual troops in the population has varied between 27 and 29, with an average troop size of 38.5 (range: 7–93). The number of all-male bands has remained about 13, with an average of 11.8 (range: 2–47). All-male bands invade home ranges of bisexual troops in an unpredictable pattern, sometimes resulting in either rapid or gradual replacement of the adult resident male. Residencies of single adult males in bisexual troops last from just a few days to at least 74.0 months, with an average of 26.5 months [13]. Jodhpur langurs breed throughout the year. Adult males defend their infants but never carry or feed them. A new resident male may kill the infants sired by his predecessor [e.g. ref. 14–16].

The habitat is greatly influenced by humans, particularly because the population of Jodhpur town increased markedly from about 350,000 in 1968 to about 750,000 in 1988. The whole plateau is subject to deforestation, except for a protected reserve of scrub forest with a total area of about 20 km². The langurs live in the open scrub forest, but several groups include human habitations (roofs, deserted buildings) and parks and field areas in their home ranges. All permanent water sources (tanks, artificial lakes, wells) are man-made. The diet consists of items from approximately 190 plant species. Most of the troops are fed by local people for religious reasons with wheat preparations, vegetables and fruits. Male bands are less frequently provisioned, because of their unpredictable patterns of movement. Some bands and troops raid crops. As they are considered sacred, however, the langurs are not hunted. Apart from feral dogs, natural predators are absent. The langurs are easy to observe, as they are not shy and spend most of the daytime on the ground.

Between July 1983 and October 1986, 7 censuses were carried out [17, p. 48; 18, p. 38; 19; V. Sommer, pers. observ.], from which sex ratios of different age classes were calculated. It should be emphasized that the counts covered the whole isolated population and had a high accuracy because all bisexual troops and male bands were included.

A detailed description of age-sex class classification is given in table 1. The categories for females are in accordance with a previous revision [11], especially concerning the fact that the category of 'subadult' females used by earlier workers on langurs was dropped. The average age of menarche (29.0 months) was calculated from individually known females [12, 20]. The categories for males were elaborated on the basis of a proposal made by Moore [21].

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Table 1 Age classification of *P. entellus*

Age class	Female	Male
Infant I	'black coat': from birth to the age of about 5 months, until completion of fur colour change	
Infant II	'white coat': after completion of fur colour change to completion of weaning, i.e. from about 5 to about 15 months of age	
Juvenile	15 months to the onset of menarche, i.e. about 2.5 years of age	15 months to about 4 years, testes internal in younger and descended in older juveniles, glans of penis generally not visible
Subadult	no subadult category in females	about 4–6 years of age; glans usually visible, ischial pads still undeveloped, canine teeth not yet fully erupted, capable of copulatory behaviour
Young adult	from regular cycling to birth of first infant; however, not older than 4 years	about 6–7/8 years of age; glans always visible, ischial pads small and usually pale, canine teeth fully erupted, teeth unworn; not yet full size
Adult	from birth of first infant, but latest from 4 years onwards	from 7/8 years onwards; full size; ischial pads pink often puffy

Results

The age and sex composition of the Jodhpur population is given in table 2. The sex ratio was apparently balanced at birth; the slight preponderance of male infants (1.1:1) is not statistically significant. There were 1.5 times more juvenile males than juvenile females. Further, with advancing age, male mortality increased dramatically, with 4.1 times more females than males among adults. Overall, there were 1.8 times more females than males in the study population.

At first glance, these results might be attributed to a methodological bias because the classification for juvenile males spanned a greater range (about 15–48 months of age) than that for juvenile females (about 15–30 months; table 1). However, long-term demographic monitoring of 144 known individuals born into 3 troops revealed the same tendency. The percentage of survival for males versus females was 69.2 versus 62.7% until 1 year of age, 55.7 versus 37.0% until 2 years, and 34.0 versus 27.3% until 3 years. A slight excess male mortality during the first 6 months of life (infant-I stage) was followed by a gradual increase of excess female mortality with a pronounced peak at 18 months of age (early juvenile stage). Thereafter, the percentage of excess female mortality dropped constantly up to 36 months of age (fig. 1) [see also survivorship curves presented in ref. 11, 12, which were based on smaller sample sizes]. No comparable data exist for the period beyond 36 months, because juvenile males emigrated from their natal troop with an average age of 2.7 years (n = 18, SD: 1.5 years) [unpublished data], and only some of them could be identified in male bands. Therefore, it is not known at which exact age the trend reverses towards excess male mor-

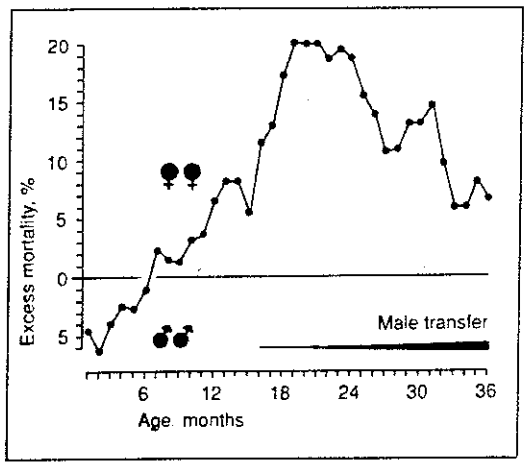

Fig. 1. Percentage excess mortality of females versus males during the first 3 years of life in Jodhpur langurs. Based on data of 144 individually known infants (86 males, 58 females) born into three troops (Kailana I, Kailana II, Bijolai, cf.) [11] between 1977 and 1988

Table 2. Sex ratios of different age classes in the langurs of Jodhpur (1983–1986)

Census date	Numbers of individuals and sex ratio (male:female)				Total individuals
	infants	juveniles	subadults + adults	overall	
Jul 83	195 unknown	135:123 (1.1:1)	141:536 (1:3.8)	unknown unknown	1.130
Apr 84	167:174 (1:1)	112:84 (1.3:1)	140:558 (1:4)	419:816 (1:1.9)	1.235
Nov. 84	146:149 (1:1)	152:91 (1.7:1)	136:575 (1:4.2)	434:815 (1:1.9)	1.249
Apr 85	169:150 (1.1:1)	168:108 (1.5:1)	124:560 (1:4.5)	461:818 (1:1.8)	1.279
Oct 85	154:143 (1.1:1)	171:115 (1.5:1)	141:574 (1:4.1)	466:832 (1:1.8)	1.298
Apr 86	163:149 (1.1:1)	186:96 (1.9:1)	126:571 (1:4.5)	475:816 (1:1.7)	1.291
Oct 86	154:127 (1.2:1)	187:102 (1.8:1)	148:564 (1:3.8)	489:793 (1:1.6)	1.282
Averages	158.8:148.7 (1.1:1)	158.7:102.7 (1.5:1)	136.6:562.6 (1:4.1)	457.3:815.0 (1:1.8)	1.252
Signi-ficance[1]	$\chi^2 = 0.33$ n.s	$\chi^2 = 12.00$ $p \leq 0.001$	$\chi^2 = 259.55$ $p \leq 0.001$	$\chi^2 = 100.55$ $p \leq 0.001$	

[1] Goodness-of-fit test, d.f. = 1, one-tailed

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tality However, it is likely that the mortality rate of males increased in connection with their emigration

Similarly, the age classification for subadult/adult males covered a range which is about 1.5 years *smaller* than that for young adult/adult females Nevertheless, this is a small fraction only of the postjuvenile life span, because female langurs can survive to at least 32 years of age and probably more than 35 years of age [23], whereas it is unlikely that males survive for more than 20 years. This assumption is supported by observations that many troops, for periods of several years, contained 1 or more old females whereas males of old physical appearance were seen very rarely and tended to disappear soon. Hence, there can be no doubt that the highly female-biased sex ratio obtained during censuses in fact reflects a higher mortality of postjuvenile males.

What caused the observed mortality? All cases of death reported by various observers between 1967 and 1988 were reviewed. During these 21 years, 151 langur corpses were found. For 19 corpses, the sex of the individuals was not recorded Four cases were abortions 44 corpses resulted from a case of mass dying in the course of which a troop of 82 animals reduced to 11 individuals [14]; these animals were poisoned by a local farmer because they had raided his crops [Mohnot, pers commun] In the remaining 84 cases, the age and sex of the dead individuals is known (table 3) In 60 cases (71 4%) the cause of death was observed directly However, only 3 cases (5.0%) of directly observed deaths could unambigously be attributed to 'internal' causes (starvation, disease), whereas 57 cases (95.0%) were due to 'external' sources (intraspecific killings, predation, accidents) resulting in sudden, 'spectacular' deaths

One sick juvenile died as a result of unilateral paralysis. Two infants died of starvation; in one case its mother had died; in the second case, an unweaned elder sibling suckled the milk that should have been taken by the neonate. 16 infants and juveniles were seen to be killed by individual adult males after the latter had occupied harem troops Likewise, 2 adult males and 1 adult female died because of wounds inflicted by males Five individuals were killed either by single or packs of dogs. The 33 cases of accidental deaths include: (a) 12 road accidents involving trucks and cars; (b) 15 electrocutions; the langurs were killed while climbing electric poles or touching wires installed on buildings; (c) 4 fatal falls; 1 adult male fell out of the canopy of a tall tree, probably after branches broke; 1 male juvenile fell into a well; 1 female infant and 1 male juvenile fell into a deep gorge; (d) 1 infant drowned; (e) 1 adult female was fatally injured by a stone thrown by a warden of a public garden.

The observed frequencies in individual death categories (table 3) were compared with those expected on the basis of the overall sex ratio for a given age class of the whole population (table 2). Significant sex differences existed within several age classes and categories. More male infants than expected became victims of infanticide (goodness-of-fit test, one-tailed, $df = 1$, $\chi^2 = 3.14$, $p \leq 0.04$). Apart from the directly observed cases included in table 3, another 18 infants were attacked and hurt by males and/or disappeared in connection with a change in the resident male: 2 cases [14]; 7 cases [25]; 5 cases [15]; 2 cases [16]; 1 case [Rajpurohit, pers observ.]; 1 case [Srivastava, pers. observ.] The sex of 14 of these presumed vic-

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Table 3. Eye-witnessed cases of death in the langurs of Jodhpur (1967–1988)

Sex ratio	Infant (23.3%)		Juvenile (20.8%)		Subadult/ adult (55.8%)		Overall population		Total	Source (cases)
	M	F	M	F	M	F	M	F		
	1.1	1	1.5	1	1	4.1	1	1.8		
External causes										
Intra-specific killings	10	3*	2	1	2	1	14	5***	19	[14] p. 188 (3); [10] pp. 67–69 (1); [25] p. 297 (1); [15] p. 168 (3); [18] pp. 51, 55–58, 64 (8); L.S. Rajpurohit, p.o. (2); [27] p. 313 (1)
Predation	–	–	3	1	0	1	3	2	5	[24] p. 297 (1); [17] p. 52, 64 (3); L.S. Rajpurohit, p.o. (1)
Accidents	4	5	8	1	7	8**	19	14**	33	[10] p. 67–69 (9); [24] p. 68 (1); [25] p. 297 (1); H. Loch, p.o. (2); [11] p. 4 (1); [15] p. 168 (1); V. Sommer p.o. (1); [17] p. 52 (4); L.S. Rajpurohit, p.o. (8); [27] p. 313 (2); A. Srivastava, p.o. (1)
Internal causes										
Starvation	2	0	–	–	–	–	2	0	2	H. Loch, p.o. (1); [15] p. 168 (1)
Disease	–	–	–	1	–	–	–	1	1	L.S. Rajpurohit, p.o. (1)
Unknown causes	3	0	0	3	12	6***	15	9**	24	[10] p. 67–69 (7); [26] p. 51 (1); P. Winkler, p.o. (1); [18] p. 52, 55–58, 64 (6); L.S. Rajpurohit p.o. (1); [27] p. 313 (1); C. Borries, p.o. (1); local people, photographic evidence (2)
Total	19	8*	13	7	21	16***	53	31***	84	
	27		20		37		84			

Goodness-of-fit test, d.f. = 1, one-tailed: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; all others n.s.
p.o. = Personal observation

tims of infanticide is known. If these cases (8 males, 6 females) are included in the sample (thus totaling 18 males:9 females) there is still a trend towards a male bias ($\chi^2 = 2.26$, $p \leq 0.06$, n.s.). Moreover, significantly more adult males than expected were killed in accidents ($\chi^2 = 6.97$, $p \leq 0.004$). When related to the total number of males and females, the preponderance of sudden 'spectacular' deaths in males was highly significant ($\chi^2 = 27.4$, $p \leq 0.001$).

Discussion

Age-specific differential rates of mortality in langurs are similar to those of other Old World monkeys [see review in ref. 28]. The overall death rate (table 2) of female infants and juveniles was higher than that of male infants and juveniles. Once the females approached reproductive age, their death rate was much lower than that of males, whose mortality rose sharply as they matured to subadult age. Among adults, the bias towards females observed here for langurs (0.2) is the most extreme so far reported for any catarrhine species [28].

At the proximate level, the overall sex differences in survivorship can be explained only partly by those causes of mortality for which we have direct evidence, because more male than female corpses were found at *all* ages (table 3). In this regard, it is important to note that, except for 3 cases of starvation and disease, all directly observed cases of mortality involved 'instantaneous' deaths. This might be due to the fact that observers can more easily identify 'external' sources of mortality [6], such as immediate deaths by accidents or intraspecific killings, than 'internal' sources, such as disease or senescence. Individuals that die slowly due to sickness, old age or other degenerative processes (e.g. starvation) do not attract attention so easily. Moreover, the individuals concerned are likely to hide until they die and are hence rarely discovered. Although some of the cases listed under 'unknown causes' might in fact refer to such individuals, accurate diagnosis would have required autopsies. Disappearances of individuals were not included in our sample. Indeed, females that disappear from their natal troops can be presumed dead, because female transfer is extremely rare. However, it is not possible to equate male disappearance with death, because males have very large total ranges of movement (> 50 km^2) over their lifetimes, and individually known males were repeatedly rediscovered at other places after more than a year.

The proximate explanations for the greater overall female mortality among infants and especially juveniles (table 2, fig. 1) remain particularly speculative. In this respect, langurs resemble other Old World monkeys, which generally show more surviving juvenile males than females [see review in ref. 28]. In several species of macaques, males weigh more than females at birth. In an elaboration of Trivers' [8] hypothesis, Dittus [29] assumed that such heavier maternal investment gives sons a 'head start' over daughters, permitting young males to compete more easily with female peers for food. Greater investment in sons also helps them to reach the larger size necessary for successful reproduction, which is linked with intense male-male competition. For langurs, the degree of food competition has yet to be quantified. However, because Maynard-Smith [30] argued that it is evolutionarily stable to invest in

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that sex for which the probability of survival is lower, it is interesting that interbirth intervals in Jodhpur langurs were significantly shorter after the birth of male infants (mean 15.4 months, n = 27) than after the birth of female infants (mean 17.1 months, n = 16) [22]. Therefore, an increased investment in females prior to weaning might be a reasonable option to reduce the higher risk of mortality experienced by female infants and juveniles [22].

Nevertheless, among infants and juveniles, there were more directly observed cases of death for males than for females. Especially, significantly more male than female infants became victims of infanticide. The functional explanation concerning infanticide favored by most primatologists (including the authors) is the reproductive-advantage hypothesis elaborated by Hrdy [31]: The death of an unweaned infant abbreviates its mother's lactational amenorrhea; accordingly, a new resident male in a harem reduces his waiting time to insemination of females by committing infanticide. However, the reproductive advantage which an infanticidal male would gain compared to a noninfanticidal counterpart should be independent of the infant's sex. Although a sample size of 27 cases from one site is a small one from which to argue for male-biased infanticide in this species, two factors might be crucial: (a) Possibly, harem residents select against future competitors of their own sons which will be sired with the troop females. Fatal attacks on older juveniles [as the 2 cases described in ref. 16] may reflect attempts by resident males to expel maturing males that would soon become direct competitors. (b) The residency of individual adult males varies between 3 days and at least 74.0 months (mean 26.5 months) [13], and the first conception might occur at an age as early as 31.0 months (mean 35.9 months) [15, 20]. Therefore, a selective force might exist to spare female infants from infanticide because they can potentially reproduce with the new male if his residency is long enough. Nevertheless, the rate of male infanticide is not high enough to bias the overall juvenile sex ratio in favour of females.

Increased mortality in subadult and adult males, on the contrary, is better understood at both proximate and ultimate levels of causation: maturing males leave their natal troop and join male bands, which move over large areas. The risk of accidental death therefore increases because males must pass through unfamiliar surroundings. Humans at least partially contribute to the increased risk of mortality by creating additional sources of accidents (electrocution, vehicles). However, this anthropogenic influence will not necessarily bias the sex ratio in favour of females, because it possibly offsets the reduced predator pressure typical of the Jodhpur habitat. Male migration has been identified as a main factor of higher male mortality in several other primate species such as toque macaques [29], rhesus macaques [32] or capuchin monkeys [33].

Moreover, there can be no doubt that the rates of intraspecific wounding are much higher among langur males than females [Sommer, pers. observ.; for supporting comparative evidence from Mount Abu, see ref. 34, table 4.3], because males are frequently involved in agonistic interactions during interband encounters and when they try to enter a harem troop [35]. However, outright killings by other males were rarely reported because, in contrast to infant-killing, instantaneous killing of an adult conspecific is far more difficult. On several occa-

Table 4. External causes of eye-witnessed cases of death in langurs outside Jodhpur[1]

Cause of death	Male	Female	Sex unknown	Site	Source
Natural					
Tiger predation	1 adult			Ranthambore/India	[36] p. 145f
	1 adult			Ranthambore/India	J. Moore, pers. commun.
Leopard predation	1 unknown age			Nepal	[37] p. 70
			1 unknown age	Abu/India	[34] p. 83
Dog predation	1 adult			Coromandel coast/India	[38] p. 101
	1 subadult			Gir/India	[39] p. 313
			infants	Sri Lanka	[40] p. 499
Python predation		1 adult		Gir/India	[39] p. 313
Lion predation			1 adult	Gir/India	[41] p. 564
Fall out of tree		1 adult		Nepal	[37] p. 70
Anthropogenic					
Car accident	1 adult	1 adult		Abu/India	J. Moore, S.B. Hrdy, pers. commun.
	1 inf. II			Jaipur/India	V. Sommer, pers. observ.
		1 adult		Abu/India	C. Vogel, pers. commun.
Electrocution	1 adult			Jaipur/India	M. Ratnani, pers. commun.
	1 inf. II			Pushkar/India	V. Sommer, pers. observ.
		1 juv		Abu/India	[34] p. 69
Sling shot	1 infant			Sri Lanka	[42] p. 44
Gun shot	1 adult	1 adult		India	[43] cited in [34] p. 81f.
Total number	11	6	> 3		

[1] Cases with unambiguously known causes only; infanticide omitted

sions, heavily wounded adults subsequently disappeared. Such individuals probably died in concealment.

The greater probability to die from external events in male langurs at Jodhpur may be common to the species generally. A review of unambiguously reported deaths at other sites (table 4) revealed that 11 males and only 6 females fell victim to (natural as well as anthropogenic) external causes.

An event observed by Moore [pers. commun.] at Abu graphically illustrates risk taking and costs in langurs: an adult male resident of a bisexual troop was killed by a truck during an encounter with a neighbouring troop while being chased by the other harem

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resident. Similarly, as a consequence of their dispersal, males of Belding's ground squirrels are run over by cars about twice as often as females and suffer frequent injuries in male-male clashes. Older age classes thus show an increasing proportion of females [1]. In langurs at Jodhpur, the all-male band structure and invasions into home ranges of bisexual troops are direct and indirect consequences, respectively, of male-male competition for access to females. Hence, the key factor in the predisposition to higher mortality seems to be the high potential reproductive success of a male [7, 9] leading to a high-risk, high-gain strategy in males.

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SAMPLING METHODS IN QUANTITATIVE ETHOLOGY – THEORY & AN ILLUSTRATION

BY

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Like all branches of Science, Ethology began with qualitative descriptions of the patterns of behaviour of different species of animals in different situations. With the accumulation of a large amount of excellent qualitative information, the transition from qualitative to quantitative ethology has begun to take place. While it is logical for any field of enquiry to begin in a qualitative way and mature into a quantitative science, I must emphasise that the qualitative phase is no way inferior and certainly cannot be dispensed with. Quantitative studies that are not based on adequate qualitative studies are likely to be flawed. It is therefore essential that careful qualitative descriptions should always precede quantitative studies. It is true however that quantitative ethology has its own unique methodological problems which are often ignored. Typically, quantitative ethology involves "measuring" animal behaviour. The first problem is that quantitative ethology, perhaps more than any other branch of biology, has the potential of generating completely useless information, if certain precautions are not taken. Animal behaviour is often transient and extremely context dependent. In addition it may also be very dependent on the internal state of the animal. Thus unless these variables are carefully controlled or adequately recorded, information gathered from measuring behaviour cannot be interpreted, or worse, can lead to misinterpretation.

An even more serious problem has to do with potential biases that often exist in measuring behaviour. To understand these biases let us first see what we mean by measuring behaviour. For example, different individuals show different levels of aggressive behaviour in a troop of monkeys. Quantitative ethology may attempt for example, to measure the rates of aggressive behaviour of different individuals and related these rates to the age of the animals, the presence or absence of females while the aggressive behaviour was shown and, whether or not the troop was in its home range when the aggressive behaviours were shown. In order to truly reflect the actual rates of aggressive behaviour shown by different animals, we should be either absolutely sure that we have recorded every instance of aggressive behaviour shown by every individual or be sure that we have recorded a truly random sample of the behaviours shown by each individual in each situation of interest. Many investigators do not appear to recognise that very often, we are only sampling the behaviour and not enumerating it. Because of the mistaken notion that we are enumerating rather than sampling, inadequate attention is usually paid to precautions that need to be taken to ensure a reasonably random sample. The possibility of obtaining a biased sample is especially high when we are observing not one but a whole group of animals and we are recording not one but a whole range of behaviours. There are rather simple ways of avoiding biased samples provided we accept that we are sampling and not

enumerating and we recognise the sources of bias. 097

COMMON SOURCES OF BIAS AND WAYS OF AVOIDING THEM

The following are four very common sources of bias and simple ways of avoiding them .

a) *Source of bias*
Some animals are more conspicuous than others.

Solution
Choose animals and behaviours randomly rather than because they are occurring at a particular time

b) *Source of bias*
Some behaviours are more conspicuous that others.

Solution
Use a predetermined duration of observation rather than decide it during the observation so that we dont (even sub-consciously) observe longer when something interesting and unusual is happening or stop sooner if it turns out to be a dull and boring session.

c) *Source of bias*
Behaviours are non-uniformely distributed over space and time.

Solution
Use time contingent rules of starting and stopping.

d) *Source of bias*
The human mind is more sensitive to habituation and fatigue than most of us suspect.

Solution
Odd as it may seen, observe less!

SAMPLING METHODS

Given these simple solutions, four methods of sampling suggest themselves.

1) *AD LIBITUM OBSERVATIONS:*

This means that one observes everything qualitatively without any specific rules such as those mentioned above. Data

from this method cannot be used to measure behaviour but such data are an essential prerequisite to plan appropriate sampling for any quantitative ethological study.

2)*FOCAL ANIMAL/GROUP SAMPLING:*

The idea here is simply to reduce the number of animals that need to be observed at a given time. Attention is entirely focussed on one or a small group of animals at any given time. If the decision as to when, which animal or which group is to be observed is made randomly, then both sources of bias listed above under a and d will be taken care of. Because the problem of habituation and fatigue are reduced, the source of bias arrising out of c (as listed above) will automatically be minimised. When the duration of observing each animal or group is predetermined and the observation sessions are governed by time-contingent rules of starting and stopping, almost all sources of bias are minimised.

3) *FOCAL BEHAVIOUR/GROUP OF BEHAVIOURS SAMPLING:*

As the name implies, here it is the number of behaviours recorded at any given time that is reduced. For exactly the same reasons as above, most sources of bias are minimised. Note that this method is not usually referred to in the literature as focal behaviour sampling and atleast a few behaviours are almost always observed simultaneously. We have used this method extensively by grouping together all relatively rare behaviours and following Jeanne Altmann, we call it " recording all occurrences of rare behaviours"

4) *INSTANTANEOUS SAMPLING:*

This method is often called Scan Sampling. Here the duration of observation is reduced rather than the number of animals or behaviours. Indeed, the duration of observation is reduced to an instant and therefore one usually is able to include the whole group of animals and all possible behaviours without introducing any significant bias. Observations made by this method can be thought of as obtaining a photograph of the whole group which shows the behaviour being performed by each animal at the instant the photograph was taken. By performing a number of such instantaneous scans, one can effectively compute the relative probabilities with which different behaviours are performed by different animals.

BEHAVIOURS AS EVENTS AND STATES

Every behaviour can be thought of as an event or as a state. For example, one can think of feeding as an event and compute the number of times that an animal feeds per day. Alternatively, one can think of feeding as a state of the animal and calculate how much time the animal spends in the state of feeding. Although any behaviour can be thought of either as a event or as a state, behaviours which are of long duration are more appropriately thought of as states rather than events (time spent in sleeping rather than number of times the animal sleeps) and short duration behaviours are more appropriately thought of as events (number of times an animal fights per day rather than proportion of time spent in the state of fighting). Similarly, information on

differences in the behaviours performed by different animals can be computed either as time spent in each behaviour or the rate at which each behaviour is performed. Scan sampling is a very convenient and widely used method for treating behaviours as states and computing time budgets and focal animal or focal behaviour sampling are convenient and widely used methods for treating behaviours as events and computing rates. During focal animals sampling it is relatively easy to keep a continuous record of all behaviours shown by the focal animal during the specified duration. This is not possible in scan sampling and is difficult in focal behaviour sampling. Focal animal sampling therefore is also a convenient method for understanding associations between different behaviours, by computing and analysing different sequences of behaviours. For example, one might want to know if wasps always groom themselves after feeding or if they rest after a foraging trip. Conversely, scan sampling is a convenient method for understanding associations between different animals. For example, one might want to know if the workers in a wasp colony work and rest in coordination with active and inactive states respectively of the queen.

A CASE STUDY

Using the principles involved in designing sampling methods in quantitative ethology as described above, I shall illustrate a case study taking the example of quantitative ethology of the primitively eusocial wasp *Ropalidia marginata*.

DYNAMIC MODELLING IN BEHAVIOURAL ECOLOGY

BY

ANIL P. GORE

Setting up good models of behaviour

Dynamic Programming in Behavioral Ecology M. Mangal and C Clark. Princeton University Press, Princeton, NJ, USA, 1988.

Dynamic programming is an optimization technique first developed in 1957 by Richard Bellman. It has been successfully applied to many problems in engineering and management. The present book is an exposition of how it may be used in modelling animal behaviour. Because animals encounter a random environment, the model has to be probabilistic. In particular, a decision to be taken at a given point of time is assumed to be Markovian, i.e. based on the state of affairs in the immediately preceding period. A discrete framework is used in the sense that time is counted in days, or hours, or other convenient unit. The variety of applications discussed in the book, both in terms of species and types of behaviour, is fascinating. Starting with group hunting by lions, we are carried, through parental care in birds, to diurnal migration of fish and zooplankton. In each illustration a particular behaviour of an organism is described and the current explanation of that behaviour available in the literature is presented. Finally the dynamic stochastic programming approach is worked out, which often yields a different/better explanation of the observed behaviour. It is of course assumed that behaviour has been so shaped by natural selection that it yields maximum benefit to the organism. While the standard definition of benefit is inclusive fitness, different surrogates have been used in different examples for operational convenience. The surrogate measure may be probability of survival, total energy reserve, or number of progeny at the end of a given period. In some examples the relevant period is 'natural' (e.g. in the case of nesting birds, from the time of egg-laying to the time when chicks become independent) but not in all. The optimization is dynamic in so far as there is feedback and updating of information at the end of each unit of time. In this the present approach differs from, say, optimal foraging theory (see Stephens, D. W. and Krebs, J. R., *Foraging Theory*, Princeton Univeristy Press, Princeton, 1986). Thus the marginal value theorem in the static formulation tells us that to get optimal result a forager should move from one patch to another as soon as the patch is depleted to a certain extent. But it does not take into account the state of hunger of the forager, which may have changed by virtue of its having spent some time in that patch. The dynamic-modelling approach gives the best decision as a function of the state of hunger as well as the remaining time on hand. Another distinguishing feature of the dynamic approach is that, given the values of all relevant parameters, the method yields precise numerical predictions and not just qualitative ones. This of course necessitates considerable computing, and for any significant application of the method, access to a PC is essential.

Do the answers arrived at using the dynamic-programming approach differ significantly from those based on a static approach? Indeed, and often enough to merit attention. One case that I found rather convincing is the following. An insect has to search for hosts of various types and to lay one or more eggs every time a host is encountered until the stock of eggs is exhausted or time runs out. As the number of eggs laid on a host increases, the probability that an emerging larva will reach maturity decreases, say due to competition. Then one can obtain the number of eggs to be laid on a host so as to maximize the expected number of mature offspring. This is the static optimum. Field observations show that actual number of eggs laid varies considerably from this optimum and is always on the lower side. The dynamic approach brings to our attention the fact that, early in the game, as the insect sets out in search of hosts, it is more profitable to lay one or a small number of eggs on a host since there exists a fair probability of finding many more hosts and providing a very favourable environment for each egg. As time runs out it is better to dump many eggs on each host. But it is never good to exceed the static optimum mentioned above, for the extra eggs laid cause excessive competition among the larvae, which may result in mortality among not only the larvae from the extra eggs but others that might have survived otherwise.

The two authors are excellent classroom communicators. They have adopted the same pedagogical style in writing this book, which is meant for biologists and not mathematical theoreticians. The result is a do-it-yourself book. If one has enough motivation and patience to follow the instructions given by the authors step by step, it should not be difficult to get the hang of their method. And this is where the rub is. Too many Indian biologists are divorced from mathematics (and some even from the hypothetico-deductive method). Some find it convenient to stick to descriptive natural history of behaviour rather than raise the question 'why'. There is the ever-present temptation to defend one's elementary work as 'benchmark' (first ever for that species/for that region/for that season). Would such a person want to work through this book? My own recommendation is that ecologists with any background should read this book, perhaps skipping all equations and such other details, to see if the findings are interesting enough to justify further investment of effort.

Statisticians will find this book interesting for another reason. It is well known that, whether it is the lifetime of a butterfly or an electric bulb, the same techniques of survival analysis are used. This book will show that it is also true of dynamic programming, hitherto taught only in courses of operations research and industrial statistics.

Ecologists inclined to modelling may feel deterred by the requirement of data (values of various parameters involved). My impression is that (a) formulation of the problem in the dynamic-programming framework can itself enhance understanding to some extent and (b) with only partial availability of data, the model can be used to indicate the field measurement more likely to be useful in prediction.

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Dynamic Modeling in Behavioral Ecology

by

M. Mangel and C. Clark

Princeton University Press (1988)

Lecture Notes by

A. P. Gore (April, 1990)

Axiom :

Organisms do have some way of getting near to optimal solutions of behavioral problems in situations that they normally encounter .

Corollary : Discrepancy between optima identified by a model and actual behaviour should suggest revision of the model.

Approach : At each stage the animal has to choose one action. Then comes next period and a new turn to choose. The optimization is over a well defined time horizon.

Patch Selection

$X(t)$ = forager's energy reserve at time t i.e. at the start of period t.

α_i = energy cost (per unit time) of choosing patch i

β_i = chance of being killed in 1 unit time at patch i.

λ_i = chance of finding food in 1 unit of time at patch i

Y_i = increment in energy reserve from 1 food particle in patch i.

$F(x,t,T)$ = maximum probability that forager survives from time t to T given energy reserve x at t.

$= \max P$ (survive from t to T / $X(t) = x$).

If $X(t)$ falls below a critical value x_c, forager dies. So that,

$$F(x,t,T) = 0 \text{ if } x \leq x_c.$$

The maximum of the survival probability is to be achieved through suitable patch selection decisions.

Boundary condition :

$$F(x,T,T) = 0 \quad \text{if} \quad x \leq x_c$$

$$= 1 \quad \text{if} \quad x > x_c \ .$$

If $X(t) = x$, patch choice is i, then

$X(t+1) = x - \alpha_i + Y_i$ if success (Prob λ_i)

$= x - \alpha_i$ if unable to get food (prob $1 - \lambda_i$)

chop (x, a, b) $= x \quad a < x < b$

$= a \quad x \leq a$

$= b \quad x \geq b$.

For reserve upper limit is C (capacity) and lower limit is x_c the critical level. Hence

$X(t+1) = \text{chop}\ (x - \alpha_i + Y_i,\ x_c,\ C)$ with prob λ_i

$= x'$ say

$= \text{chop}\ (x - \alpha_i,\ x_c,\ C)$ with prob $1 - \lambda_i$

$= x''$ say.

Strategy is to calculate backwards starting with t = T. Here there is no choice. No patch is chosen. F is also fixed. Go back 1 step in time.

$$F(x,\ T-1,T) = \max_i\ (1-\beta_i)\ [\lambda_i\ F(x',T,T) + (1-\lambda_i)\ F(x'',T,T)]$$

Thus the best result and associated choice of i can be found if β_i, λ_i, α_i, Y_i are all known. In general

$$F(x,t,T) = \max_i\ (1-\beta_i)\ [\lambda_i F(x',t+1,T) + (1-\lambda_i)\ F(x'',t+1,T)].$$

Thus you do the best at step t and the future steps get determined completely by the outcome during time period t. Recall again that choice of patch is at the beginning of the period. Consequences are accepted at the end of that period. Thus optimal decisions have to be computed.

A numerical example (p. 54, 55).

(A) 3 patches

	β	α	λ	Y
1	0	1	0	0
2	0.004	1	0.4	3
3	0.02	1	0.6	5

$x_c = 3$, C = 10

T = 20, X (19) ≤ 3 then death.

Let X(19) = 4. There is only 1 time period. Do what maximises chance of survival in one period.

Choose patch 1. X(20) = 3. No food gain. Death.
Choose patch 2. Survive → .996, fail to get food

→ .6 then X(20) = 3, death. Succeed in getting food → .4, then X(20) = 6. Survive. Chance .996 X .4 = .3984. Choose patch 3. Survive and succeed in getting food then X(20) = 8. OK. Chance .98 X .6 = .588. Hence F(4, 19, 20) = .588 . Optimal choice = 3.

(B) X(19) = 5 (or more)

choose patch 1 X(20) = 4 guarenteed. So why risk being killed in any other patch ?

F(5, 19, 20) = 1. Optimal choice = 1.

(C) X(18) = 4. We have to decide one step. Depending on X(19), next step is known from A and B above.

Choose patch 1. X(19) = 3. Sure death.

Choose patch 2. X(19) = 5. With prob. 0.3984 then survival guranteed
= 3 with Prob. (1-0.3984) then death.

Choose patch 3. X(19) = 8 with prob. 588 then survival guaranteed.

Hence F(4, 18, 20) = .588 and best decision is patch 3.

(D) X(18) = 5.

Choose patch 1 → X(19) = 4 Hence final survival prob. is 588.

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Choose patch 2 → X(19) = 4 with prob. .6 x .996, then onwards .588 .

So overall prob. of survival at T = 20 is .3514.

X(19) = 7 with prob. .4 x .996, then onwards survival guaranteed.

Hence survival to T =20 on choice 2 is .996

(.4 + .6 x .588) =.75.

Choose patch 3 → survive but fail to get food

Prob. = .98 x .4, X(19) = 4. Maximum Probability of onwards survival = .588. Overall → 98 x .4 x .588

survive and succeed → prob = .98 x .6, X(19) = 9

Probability of onwards survival 1. Overall → .98 X .6

sum total = .98 (.6 + .4 x .588) = 0.8185.

Hence F(5, 18, 20) = .8185. Optimal choice is patch 3. (The forth decimal place value not given in the book. I would round this as 0.819 which is different in the third place).

(E) Exercise : Show E (5, 17, 20) = .8185, best choice 3 and F(6, 17, 20) = .909, best choice 3.

Such detailed computations of course have to be programmed. Program listing for this example is given in the book on p. 90,99.

Quantitative features of the output (F values and best choices at various reserve levels and various time horizons) (Xerox copy of p.55 to be given to everyone). Fitness (F) is an increasing function of X the energy reserve, but inverse function of time horizon. Longer the time smaller the chance of survival. Best choice is a function of x, the energy reserve. If reserve is very high and time not too long, go far safe but unproductive patch. Thus we have feedback strategy here. Risky behaviour is optimal if reserve is close to critical level. If the time horizon is too long, choice is just a function of x and does not depend on the actual length of horizon. This is stationarity. We can choose alternative functions to be maximised.

Diet choice

Diet choice problem also can be posed in this framework . Instead of patch, we have to choose food type.

λ_i chance of encountering food of type i
λ_c no food is encountered in the period
α_i energy cost of handling prey type i
β_i chance that prey kills predator
Y_i energy content of prey type i.
τ_i handling time spent with food of type i.

$$F(x,t,T) = \lambda_c F(x - \alpha_c, t + 1, T) + \sum_{i=1}^{k} \lambda_i \max \{ F(x - \alpha_c, t+1, T), (1-\beta_i) F(x-\alpha_i + Y_i, t + \tau_i, T)\}.$$

Here we have a choice (accept or reject food item of type i) on encountering it. Also the chop function has to operate on reserve values as before. First term → no food encountered. First term in curly bracket - food type i ignored on encounter. Second term - prey type i chosen and prey does not kill predator.

Hunting behaviour of lion

Success in hunt (%)

lion group size	Thomson's gazelle	Wildebeast/ zebra	Other
1	15	15	19
2	31	35	9
3	33	13	20
4 - 5	31	37	25
6 +	33	43	0

If chance of success/no. of lions in group is a criterion, then groups of 3 or more seem quite unjustified no matter which is the prey. But abut 30 % of the hunts are in groups of 3 or more. Even the small gazelle is chased by large groups in 100 hunts while in 250 hunts 1 or 2 lions chase it (schaller). Why ?

One possibility is that a lion may get greater benefit by joining than going alone. Then the average feeding rate may not remain at the top. But the new lion joining the group does not care. It gains. Group size will thus go on increasing until the average feeding rate equals that of a single lion.

This and such other models give insights but cannot generate precise quantitative predictions.

Dynamic Model

Now we will not take the simple fitness function taking values one or zero depending on whether food reserve exceeds a critical value or not. Instead $F(x, T, T) = \phi(x)$, the terminal fitness; and

$F(x,t,T) = \max E \{ \phi(x(T)) / X(t) = x\}$

To maximise over n, the hunting group size.

$F(x,t,T) = \max_{n} \sum_{j} \lambda_{nj} F(x'_{nj}, t+1, T)$

where $x'_{nj} = x - \alpha_n + Z_{nj}$ where α_n is daily metabolic cost when hunting in a group of size n and Z_{nj} is food obtained,

$P(z = z_{n,j}) = \lambda_{nj} \quad j = 1,2,\ldots, J.$

If W is the weight of the prey, n lionesses hunt it, nq ($q > 1$) members of the pride share it, then food per lion is W/nq. If chance of success in hunt is p_n then

$P(Z = \frac{W}{nq}) = p_n$, $P(Z = 0) = 1 - p_n$.

If W is a random variable assuming values $W_1, W_2, \ldots, W_J$ with probabilities $\lambda_1, \lambda_2, \ldots, \lambda_J$ then

$P\left(Z = \frac{W_j}{nq}\right) = p_n \lambda_j$, $P(Z = 0) = 1 - p_n$.

Here state variable assumes nonintegravalues and some in terpolation is required to get F. See Sec. 8.3..

Prey : Thomson's Gazelle

α_n = 6 kg for all n. But capacity C = 30 kg.

$0 \leq X(t) \leq 30$. $E(W) = 11.25$ Kg. Lions chase upto 3 gazelles per day. So number of gazelles killed is binomially distributed with $(3, p_n)$ as the parameters.
$p_1 = .15$, $p_2 = .31$, $p_n = .33$, $n \geq 3$.
Under this set up, optimal group size (horizon 30 days) is 1 if $x = 5$ and 2 if $x = 10$ or more. The value $F(x, 1, 30)$ increases with x, from 0.06 to 0.35. Thus if gazelle is the only prey, survival is difficult even with the optimal strategy. So lions take other small prey also. There is some evidence that in stressful conditions lions hunt alone.

But even this model does not predict hunting groups larger than 2 (such groups are indeed observed). Perhaps the prey is mistaken for a large animal. Perhaps large groups sometimes get multiple kills. The latter could be incorporated in the dynamic model.

Zebra

Biomass 164 Kg. (enough for daily metabolic requirement of 27 lions). Now the optimum size is 6 in most cases, 4 or 5 in a few situations. But these groups are larger than average group sizes reported. This deficiency can be rectified by considering group sharing.

Suppose the group of females (pride) has N members and they have to divide into hunting groups of size n. For simplicity consider n which divides N. $m = N/n$ is the number of hunting groups. Suppose for each group the chance of success is p_n and all prey are shared equally by N lions. Then total daily kill Z has the distribution.

$$P(Z = j \mid W) = \binom{m}{j} p_n^j q_n^{m-j}$$

where W is the weight of an individual kill. What hunting group size will be optimal then ?

$$F(x,t,T) = \max_{n} \sum_{j=0}^{m} \binom{m}{j} p_n^j q_n^{m-j} F(x'_j,\ t+1,\ T)$$

Where $x'_j = \text{chop}\left(x - \alpha + \frac{jW}{qN},\ 0,\ C \right)$ where α is the net metabolic expenditure of a day, jW is the total kill, qN is the number of lions that share the kill and C is the gut capacity of a lion.

Using this formulation, optimal hunting group size is 2 and for a pride of N = 10, the survival is almost certain. Pride of size 6 or more seems viable.

Now the group size is small. Perhaps there are other benefits of larger hunting groups not noticed so far.

Reproduction in insects

Insect encounter a host, lay eggs and search the next host. No parental care. If c eggs are laid on a host, contribution to fitness in c $p_i(C)$, where $p_i(C)$ is the probability that an egg (in a group of c egges on host type i) reaches maturily. If we assume that $p_i(c)$ decreases linearily with c,

$$p_i(c) = 1 - \gamma_i c$$

then $c\ p_i(c) = c - \gamma_i c^2$ and its derivative is $1-2\nu_i c$. So the best clutch size is $\gamma_i/2$. This is called single host maximum (SHM). There is evidence to support the hypothesis of host recogition and for the existence of SHM. However obseved clutch sizes of certain wasps were always equal to or below SHM. There was enormous variation in clutch sizes (all below SHM). Small clutches were very common. Why ? See p 129-130

Apple maggots lay one egg per oviposition. They mark the fruit. A marked fruit is avoided normally. A fruit cannot support two larvae. As period of host deprivation increases, then marked

fruit is also accepted. After 5 minutes of host deprivation 10 % flies accept marked fruit. After 20 minutes, 65 %. After 80 minutes 90 % Why ?

X(t) = number of mature eggs remaining inside an insect from the stock it started with, X(0)=R. (No new ones to be produced). X (t) decreases as t increases.

$$X(t+1) = X(t) - c(t)$$

c(t) is the clutch laid in period t.

$\lambda_i(t)$ = P (host of type i is encountered in period t),

i = 1,2,..,h .

$\lambda_0(t) = 1 - \Sigma \lambda_i(t)$ = P (no host in encountered). Assume that at most one host is encountered in one period. $W_i(c,x,t)$ = increment in fitness by laying a clutch of size c in a host of type i at t given the reserve X(t) = x.

$\rho_i(c,x,t)$ = Pr(insect survives to period t+1 having laid a clutch of c eggs in a host of type i at t given X(t) = x)

$$\rho_0(t) = P \text{ (survival when no oviposition)}$$

T = lifespan, time after which laying eggs is useless as none will hatch, end of the day (so that leftover eggs will be resorbed) etc.

$$F(x,t,T) = \lambda_0(t)\ \rho_0(t)\ F(x,t+1,T) + \sum_{i=1}^{h} \lambda_i(t) \max_{0 \le c \le x} \{W_i(c,x,t) + \rho_i(c,x,t)\ F(x-c,t+1,T)\}.$$

Term 1 - no host encountered, insect survives, reserve x unchanged.

Term 2- i-th host encountered, W is additional fitness, if insect survives then reserve is x -c, to be used later.

F(x,T,T) = 0 because the reserve is now of no use.

Consider a particular case t = T -1.

$$F(x,T-1,T) = \sum \lambda_i(T-1) \max_{0 \le c \le x} \{W_i(c,x,T-1)\}.$$

since there is only 1 period, there is no future oviposition. Maximisation is after encountering the host.

Here the clutch laid is min (SHM,x). One should not go beyond SHM because that will reduce the total number of offspring. Obviously the clutch size cannot exceed the reserve size.

If t is far from T, the choice is between immediate and future oviposition. Hence a host that is not very useful may get no eggs. Hence :

1. For the same x, older insects shuld lay larger clutches than younger. Inferior hosts may not be acceptable to young insects but acceptable to older ones.

2. An insect cohort with the same initial egg number will, over time, experience differences in hosts encountered and hence number of remaining eggs will cover a wide range. Hence clutch sizes also will be widely different. If insects are subject to identical conditions, they should lay clutches of the same size.

This more or less answers the first question.

3. If you are more prone to predation, the future oviposition becomes less and less valuable. So larger clutches should be laid as survival probabilitee decreases.

For this the insect should be able to sense an impending disaster or increase in predation pressure.

Migration of Aquatic Organisms

Rise to surface at night, descend to deeper waters during the day (or vice versa). This is in response to changing light intensities (proximate cause). This is supposed to be due to trade off between potential feeding rates and risk of predation.

Who migrates ? Some Zooplankton, fish like Salmon. Reproduction is either continuous or a in single reproductive episode.

In one model we assume zero metabolic cost if no migration, energy cost of migration equals food eaten in time α, daily reproduction is proportional to net food intake and a fixed amount of (sexual) reproduction at the end of life T, if alive then. The option in a day is (1) feed at the surface the whole day and consume food = 24γ and risk predation with chance $\hat{m}$ or (2) feed for s_1 hours and get net every $(s_1 - \alpha)\gamma$ and experience a reduced chance of predation namely m_1. Given the length of time to be spent feeding, it has to be divided equally on either side of midnight to minimize exposure. So s_1 determines precisely the arrival and departure times (vis-a-vis the surface feeding zone). State variable is binary, alive or dead. The dynamic programming equation is

$$F(t,T) = \max_{s_1} [\ (1-\hat{m})\ (24\gamma + F(t+1,T)),\ (1-m_1)(\gamma(s_1-\alpha)+F(t+1,T))]$$

use $p_1 = 1-m_1$, $\hat{p} = 1-\hat{m}$, $f_1 = \gamma(s_1-\alpha)$, $\hat{f} = 24\gamma$.

$Fn = F(T-n,T)$, (lifetime fitness with n days to go). Then the above equation becomes,

$$F_n = \max [\ \hat{p}(\hat{f} + F_{n-1}),\ p_1(f_1 + F_{n-1})]$$

note $\hat{p}$ = prob. of survival without migration.

$\hat{p}_1$ = prob. of survival with migration.

Thus $\hat{p} < p_1$. Also $\hat{f} > f_1$. We can write $F_n = Q(F_{n-1})$.

$F_2 = Q(F_1)$, $F_3 = Q(F_2)$ etc. We can draw two straight lines $y = \hat{p}\ (\hat{f} + F)$ and $y = p_1(f_1 + F)$ and $Q(F)$ will be for every F, the larger of the two. Denote by $\hat{F}$ the intersection of these two lines. The third line is $y = F$ and at equilibrium, Q must lie on this line. $\hat{F}$ is the value at which optimum strategy switches from nonmigration to migration. Why ? Notice that slopes of the two lines are $\hat{p}$ and p_1. So the line representing migration has always a streeper slope. If $\hat{F}$ falls above the diagonal then equilibrium is on the line representing migration. Instead when $\hat{F}$ is below diagonal, it is best strategy at equilibrium not to migrate.

Copepods (Semelparous reproduction)

$X(t)$ weight of the reproductive tissue

S_1 – spend the whole day at surface

S_2 – spend the whole day at depth

S_3 – migrate back and forth .

risk of predation under these strategis : β_1 β_3 : $\beta_2 = 0$.

Food intake from strategy i is Z_i : random variable.

$Pr\ (Z_i = Y_{ij}) = \lambda_{ij}$, $j = 1,2,\ldots, J_i$

and

$E(Z_1) > E\ (Z_3) > E\ (Z_2) = 0$

α_i : metabolic cost under strategy i.

So,

$$X(t + 1) = X(t) + \gamma\ Z_i - \alpha_i$$

where γ is the coefficient of conversion of food to reproductive tissue. Also

$$0 \leq X(t) \leq C.$$

Mortality is only by predation and not by X(t) becoming zero. If $X(t) = 0$, metabolic cost is satisfied by some other tissue. Reproduction is only at the end and is proportional to $X(T)$. So $\phi(X(T)) = k\ X(T)$. The strategic aim is to maximise $E(X(T))$. The dynamic programming equation is

$$F(x,t,T) = \max_{i=1,2,3} (1 - \beta_i) \sum_{j=1}^{J_i} \lambda_{ij}\ F(x_{ij}, t + 1, T)$$

x_{ij} = chop $(x - \alpha_i + Y_{ij}\ ;\ 0,\ C)$. Here one must survive the period i and the state variable will be changed depending on the choice.

(1) If X(t) is large, i.e. near C, then it is better to choose S_2 because gain from feeding may not be worth the risk of predatin. Conversely for smaller values of X(t), feeding even at the risk of predation will be optimal.

(2) If forage is patchy and quantity of food consumed is highly variable, then a population should have a large variation in size. In that case, larger and smaller individuals should behave differently even if predation risk is independent of size.

(3) If predation is dependent on size, all we have to do is incorporate $\beta_i(X(t))$ instead of β_i.

Clutch size in birds

$X_p(t)$ = parent's reserve energy at t.

$X_n(t)$ = energy reserve for any one nestling (out of N identicalones in the group) at t.

Maturity /independence is at T. Options in any period, for the parent : Forage or not to forage.

β_p = chance of predation of parent while foraging.

β_n = chance of predation of chicks while parent is foraging.

λ_i = P(food item with energy Y_i is found) $i = 0,1,2,\ldots,I$, $Y_0 = 0$, $\sum_0^I \lambda_i = 1$.

Choice : Allocate fraction ϕ of food collected to chicks (divide equally), each getting $\phi Y_i/N$ and consume the fraction $(1-\phi)$. Choose ϕ .

Metabolic costs : α_p - for parent when not foraging, α_f - for parent when foraging, $\alpha_n(t)$ - for a nestling aged t_0

c_p - parental capacity.

$C_n(t)$ - nestling's capacity at time t (this increases with age).

($\alpha_n(1) = \alpha_p/20$, $C_n(1) = C_p/20$, both rising linearily to the parental value by time T/3) .

Critical (stravation) values for both parent and chicks are zero. (either every nestling survives or every one is dead)

The dynamic programming equation is :

$F(x_p, x_n, t, T, N)$ = max p (all nestling survive from t to T

given $X_p(t) = x_p$, $X_n(t) = x_n$, brood size N).

The maximisation is over the decision to forage or not to forage and choice of ϕ if food is gathered. This is for given N.

115 $$C(x_p, x_n, N) = N\,F(x_p, x_n, 1, T, N).$$

This is expected number of nestlings that reach maturity/independence, given x_p, x_n, N. N must maximise $C(x_p, x_n, N)$.

$$F(x_p, x_n, T, T, N) = 1 \text{ if } x_n > 0$$
$$= 0 \text{ otherwise.}$$

provided $x_p > 0$.

$F(0, x_n, t, T, N) = (1-\beta_n)^{T-t}$ if energy reserve of nestlings does not reduce to zero i.e. $x_n - \sum_{s=t}^{T-1} \alpha_n(s) > 0$. The value is the probability that no predator attacks.

$$= 0 \text{ otherwise.}$$

$$F(x_p, x_n, t, T, N)$$
$$= \max \{F(x_p - \alpha_p, x_n - \alpha_n(t), t+1, T, N);$$

$$\beta_p(1-\beta_n)\,F(0, x_n - \alpha_n(t), t+1, T, N)$$

$$+ (1-\beta_p)(1-\beta_n) \sum_{i=0}^{I} \lambda_i \max_{\phi} \{F(x_{p_i}(\phi), x'_{n_i}(\phi, t), t+1, T, N)\}.$$

First term applies if parent stays at the nest, second if it gets killed while foraging but nest is spared, third term applies if parent goes foraging and gets something and nest is not attacked.

$$x'_{pi}(\phi) = x_p - \alpha_f + Y_i(1-\phi) \text{ if it is between 0, } C_p$$
$$= 0 \text{ if the argument is positive}$$
$$= C_p \text{ if the argument exceeds } C_p$$
$$x'_{ni}(\phi) = x_n - \alpha_n(t) + Y_i\,\phi/N \text{ if it is between 0 and } C_n(t).$$
$$= 0 \text{ if the argument is positive}$$
$$= C_n(t) \text{ if the argument exceeds } C_n(t).$$

Other things remaining constant, survival chances increase with x_n and decrease with N. Parent should increase ϕ as T approaches.

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CHAPTER 7

Quantitative Models in Behavioral Ecology

In this last chapter we turn our attention from populations to individuals. We have done this earlier in Chapter 3 when modelling predation . In section 3.3.5 we invoked the concept of functional response, the relation between availability of food and rate of assimilation of a single predator . Now we will expand on variety of themes of this type .We will consider many types of behaviour , such as feeding , hunting , avoiding being hunted , fighting , parenting etc. We assume that in some sense the behaviour or any specific feature being considered is optimal . Why should we assume this ? A rather simplistic reasoning goes somewhat like this . Behaviour is (at least partly) inherited and is subject to natural selection . Hence in a population with behavioural variability caused by random mutations , suboptimal behaviour patterns decline progressively , leaving the optimal type or types to dominate the whole population . The object of the models considered here is to examine the nature of this optimality and to produce testable predictions . A logical follow up involves experiments and observations to test these predictions . But we shall not pursue this latter aspect . References to experimental work can be found in the literature cited . We will restrict ourselves to stating what are the decision variables , what is to be optimised and what is the nature of the optimal choice . There is a certain arbitrariness in this because we do not know that the objective function used is in fact sought to be optimised by forces of selection . However it is hoped that continuous interaction between this theory and observations will enhance our understanding of the nature of behaviour .

Two authoritative works on the material to be covered in this chapter are Stephens and Krebs (1986) and Maynard Smith (1982) . A delightfully written text is due to Lendrem (1986) . A specialised but very accessible work is due to Mangel and Clark (1988) .

7.1 Optimal Foraging:

Every animal must obtain nutrition for sustainence through foraging . Typically animals are selective in their choice of food . This may be for

various reasons . Some foods are more nutritious than others . Some are more time consuming to eat. Some are deficient in essential micronutrients. Others contain toxic substances that must be avoided . Some are easily confused with inedible or less desirable objects . The models to be discussed presently attempt to predict the response of an animal to this entire range of variation in a succinct manner .

Benefits of foraging have to be balanced with risks of predation . An interesting question to explore is how to combine vigilence with fod gathering for best overall results .

7.1.1.Diet choice :

Suppose a predator either sits and waits or searches for prey randomly . Various kinds of prey animals pass within its striking range . These encounters are assumed to be random . Every time the predator sees a prey , the decision open is either to attack the prey or to ignore it . What kind of decision rule will maximise the energy gain per unit time ? If prey types are all alike there is nothing to choose . But suppose some prey yield a higher energy reward than others . Further , once a decision to attack is made , it is assumed to be irreversible . During the time of attck , killing and ingestion (together called handling) predator cannot attack any other prey even if encountered . Hence it may be better to ignore a prey with poor energy reward so as not to miss any opportunity to attack a highly rewarding prey . Let us formalise this problem .

Suppose there are two prey types . An individual of prey type i , yields energy e_i and requires handling time h_i , i = 1 , 2 .The encounters with the two prey types are independent . X_i the time to the next encounter of prey type i has the probability density function

$$f_i(x) = \lambda_i \, e^{-\lambda_i x} \, .$$

Hence the expected waiting time is $1/\lambda_i$. Recall here the lack of memory property (see section 2.5) of the exponential distribution . As a result the origin from which we start measuring time is irrelevant . It could be the last encounter of the same prey type or either prey type or any other epoch . Further

$$P(X_1 < X_2) = \int_0^\infty \left(1 - e^{-\lambda_1 x_2} \right) \lambda_2 \, e^{\lambda_2 x_2} \, dx_2$$

which reduces to $\frac{\lambda_1}{\lambda_1+\lambda_2}$. Thus the probability that the next encounter is

with prey of type i is $\lambda_i/(\lambda_1+\lambda_2)$, i = 1 , 2 . Let p_i denote the probability that an individual of prey type i is attacked upon encounter . p_1 and p_2 are our decision variables . We wish to find values of p_1 and p_2 that maximise the rate of energy intake . For accounting purposes we divide total time T into search (or wait) time and handling time , so that we have in obvious notation , $T = T_s + T_h$. In a typical cycle , the predator searches or waits , then encounters a prey item , decides whether to attack it or not and implements that decision . Then the next cycle begins . The expected waiting time is E(min (X_1 , X_2)) which can be seen to equal $(\lambda_1 + \lambda_2)^{-1}$. The expected handling time is given by ,

$$E(T_h) = \frac{p_1 h_1 \lambda_1 + p_2 h_2 \lambda_2}{\lambda_1 + \lambda_2} .$$

This is because the encounter is with prey type i with probability $\lambda_i/(\lambda_1+\lambda_2)$ and the handling time is h_i if the decision made is to attack . The expected energy gain is

$$E(\text{energy gain}) = \frac{p_1 \lambda_1 e_1 + p_2 \lambda_2 e_2}{\lambda_1 + \lambda_2} .$$

This is because energy gain is e_i if prey type i is encountered and attacked. Hence the rate of energy gain , the objective function to be maximised is ,

$$R = \frac{p_1 \lambda_1 e_1 + p_2 \lambda_2 e_2}{1 + p_1 \lambda_1 h_1 + p_2 \lambda_2 h_2} .$$

To maximise R by suitably choosing p_i , we consider derivative of R ,

$$\frac{\partial R}{\partial p_i} = \frac{(1 + p_1 \lambda_1 h_1 + p_2 \lambda_2 h_2)\lambda_i e_i - (p_1 \lambda_1 e_1 + p_2 \lambda_2 e_2)\lambda_i h_i}{(1 + p_1 \lambda_1 h_1 + p_2 \lambda_2 h_2)^2} .$$

Curiously , the derivative has the same sign whatever the value of p_i . The derivative is positive if for i=1 ,

$$e_1 > \frac{p_2 \lambda_2 e_2 h_1}{1 + p_2 \lambda_2 h_2} .$$

In that case the best choice of p_1 is 1 . If the sign of the derivative is negative , the choice that maximises R is $p_1 = 0$. The fact that optimal choice of p_i is either zero or unity and never in between is sometimes calledthe zero-one rule . Thus the optimum strategy is nonrandomised . A prey type is either always ignored or always attacked on encounter .

Rearranging the above condition , we can write

$$e_1 > p_2\lambda_2 \ (\ e_2h_1 - e_1h_2) \ .$$

This is always satisfied if $e_1h_2 > e_2h_1$ because $e_1 > 0$. Hence $p_1 = 1$ if

$$\frac{e_1}{h_1} > \frac{e_2}{h_2} \ .$$

In other words the prey type which gives higher energy reward per unit handling time is always included in the diet . This is the second interesting feature of the diet choice .

Now suppose the above inequality is reversed , i.e. $\frac{e_1}{h_1} < \frac{e_2}{h_2}$. Thus

prey type 1 is not the better of the two . So p_2 will be 1 . What about p_1? It could still be 1 if λ_2 is sufficiently small . Thus inclusion or otherwise of the inferior prey type depends on the availability or abundance of the better prey type . If better type is plentiful it is optimal to ignore the inferior prey type . Otherwise not . In either case the decision is independent of the arrival rate or abundence of the inferior prey type . This is the third interesting feature of diet choice . A forager with the choice $p_i = 1$ for $i=1,2$ is often called a generalist while

the case with $p_1=1$ and $p_2=0$ is called a specialist.

These results can be extended to the case of several prey types . If we number prey types suitably so that

$$\frac{e_1}{h_1} > \frac{e_2}{h_2} > \ldots > \frac{e_k}{h_k} \ ,$$

then we can prove that (1) p_i is either 0 or 1 , i=1,2,....,k. (2) $p_1=1$ (3)if $p_i=1$ then $p_{i-1}=1$ (4) if $p_i= 0$ then $p_{i+1} = 0$ (5) whether p_i equals 0 or 1 is independent of λ_i .

7.1.2 Diet choice with constraints on intake of nutrients and toxins.

The above formulation has to be modified if the aim of maximising the

rate of intake has to be tempered by (a) the need to insure adequate intake of an essential micronutrient (b)the need to keep the intake of a toxin below acceptable limits .

Let us denote by v_1 and v_2 the quantities of a micronutrient of interest gained from a prey of type 1 or 2 respectively . Then given p_1, p_2, the expected intake of the micronutrient is ,

$$G = \left(p_1 \cdot \lambda_1 \cdot v_1 + p_2 \cdot \lambda_2 \cdot v_2 \right) / \left(\lambda_1 + \lambda_2 \right) .$$

The restriction on the diet choice is that G must be at least equal to G^* . How does this change the optimal choice of p_1 and p_2 ? (see fig 7.1.1) . If R the rate of energy intake is an increasing function of p_1 and also of p_2 , then the unrestricted optimal choice namely $p_1=p_2=1$ yields $G > G^*$ which satisfies the restriction and hence continues to be the optimal choice even under the restriction . On the other hand if R is an increasing function of p_1 but decreasing function of p_2 the unrestricted optimum is $p_1 = 1$ and $p_2 = 0$ is not admissible because G falls below G^* . Here the optimal choice is $p_1 = 1$ and $p_2 = p_2^*$. Thus an energetically less rewarding prey type may have to be ingested occasionally if it is rich in an essential micronutrient .

Let us denote by s_1 and s_2 quantities of a toxin gained from from a prey of type 1 and 2 respectively . Then given p_1 and p_2 , the expexted intake of the toxin is

$$H = \left(p_1 \cdot \lambda_1 \cdot s_1 + p_2 \cdot \lambda_2 \cdot s_2 \right) / \left(\lambda_1 + \lambda_2 \right) .$$

This intake must be held below H^* (see fig 7.1.2) . Suppose R is an inceasing function of p_1 but a decreasing function of p_2 . The unrestricted optimum is at $p_1 = 1$ and $p_2 = 0$. But the restricted optimum is $p_1 = p_1^*$ and $p_2 = 0$. What if R is an increasing function of both p_1 and p_2 ? The choice $p_1 = p_1^*$ and $p_2 = p_2^*$ is not admissible . The best choice choice has to be a combination of p_1 and p_2 that falls on the constraint line $H = H^*$ .To find it we rewrite the objective function R substituting for p_2 in terms of p_1 as

$$p_2 = \left(H^* \left(\lambda_1 + \lambda_2 \right) - p_1 \cdot \lambda_1 \cdot s_1 \right) / \left(\lambda_2 \cdot s_2 \right) .$$

Hence we get,

$$R = \left(p_1 \lambda_1 e_1 + e_2 \frac{(\lambda_1+\lambda_2)H^* - p_1\lambda_1 s_1}{s_2} \right) \Big/ \left(1 + p_1 \lambda_1 h_1 + \frac{h_2}{s_2} \{(\lambda_1+\lambda_2)H^* - p_1 \lambda_1 s_1 \right)$$

Here the sign of $\frac{\partial R}{\partial p_1}$ is determined by

$$\left\{ 1 + p_1 \lambda_1 \left(h_1 - h_2 \cdot \frac{s_1}{s_2} \right) + \frac{h_2}{s_2} (\lambda_1+\lambda_2)H^* \right\} \lambda_1 \left(e_1 - e_2 \frac{s_1}{s_2} \right) -$$

$$\left\{ p_1 \lambda_1 \left(e_1 - e_2 \frac{s_1}{s_2} \right) + \frac{e_2}{s_2} \left(\lambda_1 + \lambda_2 \right) H^* \right\} \lambda_1 \left(h_1 - h_2 \frac{s_1}{s_2} \right) .$$

Notice that the terms involving p_1 cancel out leaving ,

$$\frac{\lambda_1}{s_2} (e_1 s_2 - e_2 s_1) + (\lambda_1 + \lambda_2) \frac{H^* \lambda_1}{s_2^2} (h_2 e_1 - h_1 e_2) .$$

If this is posiive we choose the maximum permissible value of p_1 which is p_1^* and naturally p_2=0. If instead the above partial derivative is negative, our choice is p_1=0 and $p_2 = p_2^*$. We recall that $h_2 e_1 - h_1 e_2 > 0$. Hence a sufficient condition to ensure that the above derivative is positive is given by $e_1 s_2 > e_2 s_1$. Thus if energy gain per unit toxin absorbed is higher for the better prey type , then the optimal diet contains only the better prey type . If $e_1 s_2 - e_2 s_1$ is a sufficiently large negative number then the above partial derivative itself can become negative leading to the choice $p_1 = 0$ and $p_2 = p_2^*$.

7.1.3 Problem of recgnition:

So far we have assumed implicitly that each prey type can be recognised for what it is ,instantly , without error and without any cost . This assumption can be relaxed in various ways .

(a)Recognition with a cost: Suppose recognition of the prey involves a cost of r_t units of time and r_e units of energy .Suppose further that in the absence of these costs , the optimal solution of the diet choice problem as formulated in section 7.1.1 is $p_1 = 1$ and $p_2 = 0$. In other words the rate of energy gain is higher for the specialist that attacks only the better prey type, compared to a generalist that attacks either type of prey .Thus,

$$\frac{\lambda_1 e_1}{1+\lambda_1 h_1} > \frac{\lambda_1 e_1 + \lambda_2 e_2}{a+\lambda_1 h_1 + \lambda_2 h_2} \quad .$$

Now when recognition is not free , the expected energy gain for a specialist , in one cycle , is

$$\frac{\lambda_1}{\lambda_1+\lambda_2} e_1 - r_e \ ,$$

and the expected time spent is ,

$$\frac{1}{\lambda_1+\lambda_2} (1 + \lambda_1 h_1) + r_t \ .$$

Hence the rate of energy gain is

$$\frac{\lambda_1 e_1 - r_e(\lambda_1+\lambda_2)}{1+\lambda_1 h_1 + r_e(\lambda_1+\lambda_2)} \ .$$

It is better to be a specialist only if this rate exceeds the rate for a generalist . Notice that a generalist does not incur any cost of recognition since every prey encountered is attacked . Note also that when r_e or r_t increases sufficiently , it necomes inevitable to adopt a generalist strategy . When confronted with high cost of recognition , an optimal forager is expected to give up discrimination .

(b)Perfect mimicry: Suppose the better prey type perfectly mimics an inedible object in nature , say a twig . Encounter rate for twigs is λ_t and a handling time h_t is needed before the prey is recognised as a twig . If the choice is only to take the better prey the rate of energy gain declines to

$$\frac{\lambda_1 e_1}{1+\lambda_1 h_1 + \lambda_t h_t} \ .$$

Here , handling time is increased because of periodic encounter with twigs which does not add to the numerator at all . If the choice is to take either type of prey the rate of energy gain is,

$$\frac{\lambda_1 e_1 + \lambda_2 e_2}{1+\lambda_1 h_1 + \lambda_2 h_2 + \lambda_t h_t} \ .$$

Finally if only the inferior prey type is taken , the rate of energy gain is

$$\frac{\lambda_2 e_2}{a + \lambda_2 h_2} .$$

The largest of these three decides the best choice . As $\lambda_t h_t$ becomes very large , eventually the third option becomes attractive . Thus a prey item that mimics well , a commonly occurring inedible object is likely to be avoided by predators .

(c)Imperfect discrimintion: Suppose the two prey types are generally similar in appearence except for colour . The less desirable prey type is somewhat darker . However , discrimination between the two prey types based on darkness of colour is not error-free . There is some overlap .The predator has to decide upon the darkness threshold such that any prey darker than the threshold is ignored .

Whatever the threshold , two kinds of errors are likely to be made . Some good items may be ignored because they are too dark while some bad items may be selected because they are light . As the threshold is pushed towards darker shades , error of accepting a bad item becomes more probable. (see fig 7.1.3) . Let ϕ denote the probability that an undesirable prey type is attacked . Let ϕ^k denote the probability that a desirable item is attacked . If k=1 , the two prey types cannot be distinguished .A strategy based on darkness threshold is of some use only if $k < 1$. This parameter k is really an exogenous quantity and is treated as given . The problem is that of deciding the best level of the threshold .

Denoting by l and d the light and dark prey types , let λ_l and λ_d be the encounter rates , e_l and e_d energy yields and h_l and h_d the handling times respectively . Then expected energy gain as a function of the threshold chosen is ,

$$\bar{e} = \frac{\lambda_l}{\lambda_l + \lambda_d} \cdot \phi^k \cdot e_l + \frac{\lambda_d}{\lambda_l + \lambda_d} \cdot \phi \cdot e_d ,$$

and the expected handling time is

$$\bar{h} = \frac{\lambda_l}{\lambda_d + \lambda_l} \cdot \phi^k \cdot h_l + \frac{\lambda_d}{\lambda_l + \lambda_d} \cdot \phi \cdot h_d .$$

The expected waiting time $w = (\lambda_l + \lambda_d)^{-1}$ is independent of ϕ and the threshold chosen . We have to choose the threshold so as to maximise

$$R = \bar{e} \ (\bar{h} + w)^{-1} .$$

A direct method here would be to differentiate R with respect to ϕ and equate to zero . Instead consider a plot of $\bar{e}$ versus $\bar{h}$. Note that $\bar{e} / \bar{h}$ is the slope of the line joining origin and the point $(\bar{h} , \bar{e})$. R is the slope of the line joinning $(-w , 0)$ and $(\bar{h} , \bar{e})$.

First we note that $\bar{e}$ increases with $\bar{h}$ but at a decreasing rate . To see this consider

$$\frac{\partial \bar{e}}{\partial \bar{h}} = \frac{\partial \bar{e}}{\partial \phi} \cdot \frac{\partial \phi}{\partial \bar{h}}$$

$$= \frac{a_1 k \phi^{k-1} + a_2}{b_1 k \phi^{k-1} + b_2} \quad ,$$

where $a_1 = \frac{\lambda_l}{\lambda_l + \lambda_d} e_l$, $a_2 = \frac{\lambda_d}{\lambda_l + \lambda_d} e_d$, $b_1 = \frac{\lambda_l}{\lambda_l + \lambda_d} h_l$ and $b_2 = \frac{\lambda_d}{\lambda_l + \lambda_d} h_d$.

Clearly this derivative is positive since a_1 , a_2 , b_1 , b_2 , k and ϕ are all positive . Next , consider the second derivative .

$$\frac{\partial^2 \bar{e}}{\partial \bar{h}^2} = \left(\frac{\partial}{\partial \phi} \cdot \frac{\partial \bar{e}}{\partial \bar{h}} \right) \left(\frac{\partial \phi}{\partial \bar{h}} \right) .$$

On the right side $\partial\phi/\partial\bar{h}$ is positive . Hence the sign of the expression is determined by the first factor which is negative as will be shown .The sign of the first is determined by

$$\left\{ (b_1 . k + b_2 \ \phi^{1-k}) . a_2 . (1-k) . \phi^{-k} \right\} - \left\{ (a_1 . k + a_2 . \phi^{1-k}) b_2 (1-k) \phi^{-k} \right\} .$$

This simplifies to

$$k(1-k)\phi^{-k} \ (b_1 a_2 - b_2 a_1) .$$

So it suffices to show that $b_1 a_2 - b_2 a_1 < 0$. Substituting for a_1, a_2, b_1, b_2 we get,

$$b_1a_2 - b_2a_1 = \frac{\lambda_l\lambda_d}{\lambda_l + \lambda_d}\left\{ h_le_d - h_de_l \right\} .$$

But recall that the lighter prey type is more desirable by assumption . Hence ,

$$\frac{e_l}{h_l} > \frac{e_d}{h_d} .$$

Thus the above term is negative .To get the optimal value of the pair ($\bar{h}$, $\bar{e}$), we have to draw a tangent to the plot of $\bar{e}$ versus $\bar{h}$ (which passes through origin) from the point (- w,0)(see fig.7.1.4) .The interesting prediction here is that as w , the waiting time increases , the optimal pair ($\bar{h}$, $\bar{e}$) involves larger and larger values of $\bar{h}$ which means larger values of ϕ which implies a threshold increasingly to the darker side . Thus if the encounter rates are low it is better to include more items in the diet.

If encounter rates are high , it is better to be more choosy .

7.1.4 Marginal value theorem:

We now visualise a situation in which a foraging animal encounters , not individual prey but individual patches in which food is scattered . The forager's choice is the length of time to be spent foraging in a patch .As time progresses the patch gets depleted and eventually no food is left there .The forager can leave a depleted patch and go to another one which is richer . But this involves some cost in terms of search and travel time. A balance has to be struck .

Suppose there are p patch types . The encounter rate for patch type i is λ_i , i = 1,2 ... p. Suppose $g_i(t)$ is the total energy gain from spending time t in a patch of type i . We assume that $g_i(t)$ increases with t at a decreasing rate . In other words $g_i'(t) > 0$ and $g_i''(t) < 0$. Also $g_i(0) = 0$. We have to decide the value of t_i the length of time to be spent in a patch of type i so as to maximise the rate of energy gain R . Again if we consider a single cycle , the forager encounters a patch , spends time in it depending upon its type and then a new cycle begins . Hence the expected total energy gain is ,

$$\sum_{i=1}^{p} \lambda_i g_i(t_i) \Big/ \sum_{1}^{p} \lambda_i ,$$

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while the expected time spent is the sum of waiting time and foraging time i.e.

$$\left(1+\sum_{i=1}^{p}\lambda_i t_i\right) \Big/ \sum_{i=1}^{p}\lambda_i \ .$$

Hence

$$R = \frac{\sum_{i=1}^{i=p}\lambda_i g_i(t_i)}{1+\sum_{1}^{p}\lambda_i t_i} \ .$$

To maximise R , we equate its partial derivative to zero.

$$\frac{\partial R}{\partial t_i} = \frac{\left(1+\sum\lambda_j t_j\right)\lambda_i\, g_i'(t_i) - \lambda_i \sum \lambda_j\, g_j\,(t_j)}{(1+\sum\lambda_j t_j)^2} \ .$$

This equals zero when

$$g_i'(t_i) = \frac{\sum\lambda_j g_j(t_j)}{1+\sum\lambda_j t_j} = R \ ,$$

which is independent of i . Thus the time spent in any patch should be such that instantaneous rate of energy gain equals the average rate . This result is known as the marginal value theorem which is a terminology borrowed from economics . The particular case with only one patch type can be handled graphically too . Can you see how?

7.1.5: A linear programming formulation:

Here we consider the problem of choosing the right combination of two kinds of food so as to fulfill various requirements . The energy intake per day must be at least equal to m , the maintenance requirement . Total quantity to be digested must not exceed the daily digestive capacity c . The total intake of a micro-nutrient must not fall below v . Additional constraints of this type can be included without difficulty . We restrict to two kinds of food only to facilitate a graphical solution. Three or more food types can be handled algebraically . Rate of energy intake which was so far treated as the objective function to be maximised is included here as a constraint . Let q_1 and q_2 be the quantities of two kinds of foods to be ingested . Let e_i be the energy per unit , v_i the micro-nutrient content per unit and d_i the digestive capacity used up per unit of food type i ,

i = 1 , 2 . Then the constraints on q_1 and q_2 are :

$q_1 > 0$, $q_2 > 0$, $e_1q_1 + e_2q_2 \geq m$, $v_1q_1 + v_2q_2 \geq v$, $d_1q_1 + d_2q_2 \leq d$.

These can be conveniently expressed in a graphical for as shown in fig7.1.5. The hatched triangle is the feasible region consisting of all points that fulfill the restrictions . What is the optimal choice of q_1 and q_2 ?That depends on the objective function . In the linear programming formulation it is assumed that the objective function is linear just as the constraints are .The theory of linear programming tells us that the optimal choice of q_1 and q_2 is always one of the vertices of the feasible region . In the present case we have three vertices A,B,C. If we wish to maximise the energy intake $e_1q_1 + e_2q_2$, we can draw lines parallel to $e_1q_1 + e_2q_2 = m$, with increasing values of the total intake. The result is the point C . Similarly point A represents the choice that maximises the micro-nutrient intake while the point B minimises the demand on the digestive system .

What about search , handling and other considerations discussed earlier ? This approach has been developed with a herbivore animal in mind. It is assumed that the two kinds of foods are readily available and no search is involved .

7.1.6 Risk sensitive choice: Our discussion so far has focussed attention on maximising the expected gain . Now suppose we have to choose between decisions with the same expected gain but different variability . Which decision should an animal prefer ? Notice that we need a new criterion for making the choice since the expected gains are identical . We will now use the criterion of maximising the probability of getting adequate energy intake .

Let X denote the energy intake . We assume that X follows a normal distribution with mean μ and varience σ^2 . Suppose R is the energy requirement . Then we wish to maximise P (X > R) . In other words maximise $P(Z > (R-\mu)/\sigma)$ where Z is the standard normal variable . This probability is nothing but $1 - \Phi\left(\frac{R-\mu}{\sigma}\right)$ where Φ is the cumulative probability distribuion function of the standard normal variable .

Clearly P(X>R) is maximised when $\Phi\left(\frac{R-\mu}{\sigma}\right)$ is minimised . If $R < \mu$, as σ increases , the ratio $\frac{R-\mu}{\sigma}$ increases to zero . Hence Φ increases with σ . If $R > \mu$, Φ is a decreasing function of σ .

Thus , if if the expected energy gain is less than adequate , it is best to choose the option with greater variability . On the other hand if the expected gain is more than the requirements , the option with smaller varience should be selected . Intuitively speaking , an assured but inadequate intake is not attractive because it assures starvation . Here a highly variable option gives at least some hope of getting a bellyfull .

If on the other hand expected gain is adequate , a smaller varience is preferable . It reduces the chance of the disaster of a very low gain .

7.1.7 Vigilence : During feeding , animals periodically look up and scan the surroundings for signs of danger . We assume that acts of scanning are instantaneous and follow a Poisson process . The interscan intervals follow an exponential distribution with mean $1/\lambda$ and the number of scans follows a Poisson distribution with mean λ . Another simplifying assumption made is that there is a critical phase of time duration T in the attack of a predator . If the prey animal scans during this period , predator is detected and prey can get away .Therefore the probability of detection of an attacking predator is the probability of at least one scan during an interval of length T .The number of scans during time T has a Poisson distribution with mean λT .Hence probability of at least one scan is

$$P(\text{predator detection}) = 1 - e^{-\lambda T} .$$

If the prey animals forage in a flock of size n and scan independently of each other at the same rate λ , then the combined scanning rate is $n\lambda$ and the probability that at least one member of the flock detects the attacker (and runs away giving clear warning to the flock) is

$$P(\text{predator detection by a flock of size n}) = 1 - e^{-n\lambda T} .$$

This explains the benifit of group foraging in terms of increased vigilence.

Yet another formulation of the vigilence problem considers the best choice of the feeding rate $u(t)$. If the feeding rater is high , vigilence is poor and vice-versa . For best vigilence , feeding rate should be zero . But this is not practicable when the animal is hungry . Let $x(t)$ denote its food deficit . It seems reasonable to think of costs and benifits in terms of $x(t)$ and $u(t)$ together . Let us take the cost function

$$c(t) = k^2 . x^2(t) + u^2(t) ,$$

where k is a constant . Thus higher levels of food deficit and feeding rate

lead to more than proportionately higher cost . We wish to choose the function $u(t)$ under the forager's control so as to maximise

$$-\int_0^T c(t)dt \ .$$

Clearly the state of hunger $x(t)$ depends on the feeding rate $u(t)$. Let us assume that their relationship is defined by ,

$$\frac{dx(t)}{dt} = -ru(t) \ .$$

Thus higher the feeding rate , faster the reduction in food deficit .

We have now formulated the problem of choosing the best feeding rate as what engineers call an optimal control problem . We will solve it using the Pontryagin's maximisation principle discussed in the Appendix .

The optimal control function $u(t)$ maximises the Hamiltonian ,

$$H(x \ , \ u \ , \ t) = -\lambda ru - (k^2x^2 + u^2)$$

where λ is the so called costate or adjoint variable . Differentiating H with respect to u and equating to zero we get ,

$$\frac{dH}{du} = -\lambda r - 2u = 0 \quad \text{i.e.} \quad u = -\lambda r/2 \ .$$

But λ is unknown . It satisfies the following equations:

$$\frac{d\lambda}{dt} = -\frac{dH}{dx} = 2k^2x$$

and

$$\frac{dH}{d\lambda} = \frac{dx}{dt} = \frac{\lambda r^2}{2} \ .$$

Differentiating with respect to t again and eliminating λ we get

$$\frac{d^2x(t)}{dt^2} = \frac{r^2 d\lambda}{2dt} = k^2r^2x(t) \ .$$

By solving this second order differential equation we can get $x(t)$ and using it we will obtain $u(t)$.

Consider the following general second order differential equation

$$\frac{d^2x}{dt^2} + b\frac{dx}{dt} + cx = 0 \ ,$$

where b c are coonstants . To attack this equation we use the trial solution

$$x = e^{\delta t} .$$

Then we have

$$\frac{dx}{dt} = \delta e^{\delta t} \text{ and } \frac{d^2x}{dt^2} = \delta^2 e^{\delta t} ,$$

so that on substituting back we get ,

$$e^{\delta t}(\delta^2 + b\delta + c) = 0 .$$

Let δ_1 and δ_2 be the roots of the auxiliary equation

$$\delta^2 + b\delta + c = 0 .$$

Then the general solution of the differential equation is ,

$$x(t) = Ae^{\delta_1 t} + Be^{\delta_2 t} ,$$

where A and B are constants determined by boundary conditions .

In our particular case b=0 and c = $-k^2r^2$. Hence the auxiliary equation is

$$\delta^2 - k^2r^2 = 0 .$$

Cosequently the general solution is ,

$$x(t) = Ae^{-krt} + Be^{krt} .$$

Notice that as feeding progresses $x(t)$ must always decline since $u(t) \geq 0$. Therefore the first derivative of $x(t)$ must be negative .

$$\frac{dx}{dt} = A \cdot k \cdot r \cdot e^{krt}\left(\frac{B}{A} - e^{-2krt}\right) < 0 .$$

For this to be true for all positive values of k , r and t , we must have B = 0 . Otherwise for large values of k,r,t the term in the bracket and hence the entire expression may become positive. Further let the food deficit at t=0 be x_0 . Then A = x_0 and

$$x(t) = x_0 e^{-krt}$$

and

$$\frac{dx(t)}{dt} = - r\, u(t) = -krx_0 e^{-krt} .$$

Thus the optimal feeding rate is

$$u(t) = kx_0 e^{-krt} .$$

This means that the best strategy involves an exponentialy feeding rate as the food deficit declines . Consequently the cumulative intake over the

time interval (0 , t) is

$$x_0 - x(t) = x_0(1 - ke^{-krt}) ,$$

which can be compared with observations on feeding . Further , vigilence need not be against predators . It could be also against conspecifics i.e. other individuals of the same species . Many animals guard territories against attacks of such individuals. The above formulation could be used there too.

7.1.8 Egg laying: Consider a female insect that has a given number of eggs in her body . She searches for hosts and on finding one , lays a clutch of c eggs on it . Larvae emerge from these eggs and feed on the host. How many eggs should a female lay on a single host so that the number of viable offspring produced is maximised ? If c, the number of eggs laid is too large , then overcrowding , competition , starvation etc. reduce the probability of survival for a larva . Suppose this decline is linear and the probability of survival (to adulthood) for an individual larva in a group of size c is $1-\gamma c$, where γ is a constant related to the capacity of the host . Then the expected number of viable offspring resulting from c eggs laid on a host is $c - \gamma c^2$. This quadratic is maximum at $c^* = 1/2\gamma$. This is sometimes called the single host maximum (SHM) . Typically the female insect goes from host to host laying clutches on each till all eggs are exhausted or time is up (day ends or female dies etc.). So should the female lay the same number c^* on each host or is it possible that in some cases SHM is not the best decision ? This is indeed so . We shall show and why deviations from SHM may arise . This will be done using the technique of dynamic programming . We will treat time as discrete and explain how an equation can be written down to decide the optimal choice of c at each stage successively .

An entire book by Mangel and Clark (1988) is devoted to discussion of stochastic dynamic programming as applied to animal behaviour . Its 'do it yourself ' style makes the book very attractive . We shall use the notation of this book and describe the method through its application to the above problem of egg-laying discussed in the book.

In dynamic programming we have a state variable , a set of possible actions and associated pay-offs and costs . In a stochastic set up

considered here , consequences of decisions and actions are not fixed but random . The number of steps or decisions is fixed . The aim is to devise an optimal policy which gives the highest total expected pay-off over the period of interest . The following characterisation of an optimal policy , enunciated first by Bellman (1957) , is known as Bellman's principle of optimality :

An optimal policy has the property that , whatever the initial state and the initial decision are , the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision .

The set up is as follows . There are different types of hosts . In one unit of time the female insect can locate at most one host . $\lambda_i(t)$ is the probability of finding a host of type i , i = 1 , 2 , ... , k. The probability of not finding any host is given by ,

$$\lambda_0(t) = 1 - \sum_{1}^{k} \lambda_i(t) .$$

x(t) is the number of eggs in the female's body . It is our state variable. Note that no new eggs are produced after t=0 and x(t) is a decreasing sequence . c(t) is the number of eggs laid at time t . Clearly $0 \leq c(t) \leq x(t)$. This is the set of possible actions . $\rho_i(c,,x,t)$ is the probability of surviving to the next time period given the state x(t) and action c(t) on encountering a host of type i . The action c(t) changes the state variable to x(t+1) = x(t) - c(t) . It also adds a quantity $w_i(c,x,t)$ to the cumulative expected gain (in terms of viable offspring) . Time horizon of interest is from t to T . Let F(x,t,T) the total maximised expected gain upto time T starting with state x(t) at time t . We note that F(x,T,T) = 0 .When time is up , the remaining eggs contribute nothing to the total gain . What about F(x,T-1,T) ? There is one decision to be made . It depends on the host encountered if any . We can write ,

$$F(x,T-1,T) = \sum_{i=1}^{k} \lambda_i(T-1) \max_{0 \leq c \leq x} \left\{ w_i(c,x,T-1) \right\} .$$

Clearly the optimal policy is to lay eggs equal to SHM of the host type encountered , assuming availability of eggs . Note that the optimal policy itself is of greater interest to us than the value of the maximised gain .

The latter may depend upon many more parameters in addition to the optimal policy .

Let us go one step backwards and try to write an equation for F(x,T-2,T). A decision has to be made at stage T-2 only if a host is encountered . If a host of type i is met and c is the number of eggs laid , it has two cosequences . An expected gain of $w_i(c,x,T-2)$ is accumulated and secondly the state variable becomes x(T-1)=x(T-2)-c. If the insect survives to period T-1 , it is assured of maximised gain F(x-c,T-1,T) . Hence at stage T-2 we choose c so as to maximise the quantity,

$$w_i(c,x,T-2)+\rho_i(c,x,T-2).F(x-c,T-1,T)$$

The maximised gain equals this quantity with probability $\lambda_i(T-2)$, i=1,2,...,k. With probability $\lambda_0(T-2)$ no host is met and no gain accumulated in time T-2 .If the insect survives , it is assured a maximised expected gain F(x,T-1,T) . This is because the state variable is unchanged . Hence

$$F(x,T-2,T) = \lambda_0(T-2)\rho_0(x,T-2,T)F(x,T-1,T) + \sum_i^k \lambda_i(T-2) \max_{0 \le c \le x} \left\{ w_i(c,x,T-2)+\rho_i(c,x,T-2)F(x-c,T-1,T)\right\} .$$

In general at time t we have

$$F(x,t,T)=\lambda_0(t)\rho_0(x,t,T)F(x,t+1,T) + \sum_1^k \lambda_i(t) \max_{0 \le c \le x} \left\{w_i(c,x,T)+\rho_i(c,x,t)F(x-c,t+1,T)\right\} .$$

This is the dynamic programming equation satisfied by the gains resulting from an optimal policy . To repeat the reasoning , note that if no host is encountered and the insect dies , there is zero gain . If no host is encountered but the insect survives , then the state variable is unchanged but time progresses to t+1 yielding a gain of F(x,t+1,T) in the remaining time . This explains the first term on the right . If host of type i is encountered , the value of c is so chosen that expected gain at this step plus the future gain from the reduced egg-load is maximised . This equation

is deceptive and is not as easy to grasp as may seem . Numerical work of the type shown below , however helps clarify its nature .

Let us take a numerical example which is quite artificial and is designed to illustrate some points with minimum computation .

Let k=1 . That is , there is only one host type . Let $\lambda_0 = \lambda_1 = 0.5$. Let all survival probabilities ρ equal 1 .Let the gain function w depend only on

the choice of c . $w(0)=0$, $w(1)=1$, $w(2)=1.4$, $w(3)=1$, $w(c)=0$ if $c \geq 4$. Under this set up , we have ,

$$F(1,T-1,T) = \frac{1}{2} \max_{0 \leq c \leq 1} w(c) = \frac{1}{2} .$$

So if there is only one unit of time is available and only one egg is left, the best policy is to lay it if you find a host . Going one step further ,

$$F(1,T-2,T) = \frac{1}{2} F(1,T-1,T) + \frac{1}{2} \max_{0 \leq c \leq 1} \left\{ w(c) + F(1-c,T-1,T) \right\} = \frac{1}{4} + \frac{1}{2} .$$

Thus if there are two units of time and one egg , it should be laid at the first opportunity . Similarly ,

$$F(1,T-3,T) = \frac{1}{2} F(1,T-2,T) + \frac{1}{2} \max_{0 \leq c \leq 1} \left\{ w(c) + F(1-c,T-2,T) \right\} = \frac{3}{8} + \frac{1}{2} .$$

Now let us increase x(t) from 1 to 2 . Here ,

$$F(2,T-1,T) = 0.7 .$$

So , if there are two eggs available and one time unit , both should be laid if a host is met .

$$F(2,T-2,T) = \frac{1}{2} F(2,T-1,T) + \frac{1}{2} \max_{0 \leq c \leq 2} \left\{ w(c) + F(2-c,T-1,T) \right\}$$

The second term equals 0.35 if c=0 , 0.75 if c=1 and 0.7 if c=2 . Hence if there are 2 eggs and 2 time units , it is better to lay only one egg if a host is met . The second egg should be held back to take advantage of one more time unit available . Notice that the SHM here is c=2 . But the

incrementle gain from laying the second egg right away is 0.4 . Instead , if it is saved for the last time unit , a gain of 0.5 is expected . Such arguements do not contradict the conventional wisdom that a bird in hand is better than two in the bush . They only suggest that if there are ten or a hundred birds in the bush , the balance may tilt the other way . Indeed we have come across a similar situation in section 7.1.1 where an inferior prey in hand is found to be worth less than a better prey which 'may' arrive .

Let us go one step further and increase x(t) further to 3 .

$$F(3,T-1,T) = 0.7$$

Thus , if there are three eggs but only one time unit , it is best to lay 2 eggs if a host is found . In other words , one step away from T , if eggs are available plentifully , SHM is the optimal action given by dynamic programming . Now we go 2 steps away from T .

$$F(3,T-2,T)= \tfrac{1}{2}\ (0.7) + \tfrac{1}{2}\ \max_{0 \le c \le 3} \left\{ w(c) + F(3-c,T-1,T) \right\}$$

The expression in the curly brackets equals 0.7 if c=0 , 1.7 if c=1 , 1.9 if c=2 and 1.0 if c=3 . Hence it is best to lay 2 eggs if a host is met .

Some general comments are now in order . When eggs are abundant but time is limited , the best decision is to lay eggs equal to SHM .It is never benificial to lay more eggs than SHM . Hence any deviations from SHM will all be on the lower side .If eggs are few and time is more , it is better to lay fewer eggs than SHM to take advantage of the higher survival probability at lower density . Even if a group of females starts together, all with the same number of eggs , their encounter experiences will be far from identical . Some will meet more hosts than others .Some will meet better hosts than others . Hence assuming that they practise the same optimal policy , as time progresses , they will exhibit a considerable variation in their states (i.e. number of eggs remaining) . Hence clutch sizes chosen by them , all below SHM , will show commensurate variation . If the individuals do not start alike (some start earlier , some start with more eggs) the variation in observed clutch sizes is increased

further . Older insects will be pressed for time and hence will choose clutch sizes closer to SHM . A similar effect is expected if insect survival probabilities decline , thus in effect reducing the time available. Let us consider a simple numerical illustration of this .

In the example above , let the probability of survival in a time period be reduced to $\rho = 0.5$. Let $x = 2$. Then we have ,

$$F(2,T-1,T) = 0.7$$

$$F(2,T-2,T) = \tfrac{1}{4}\,(0.70) + \tfrac{1}{2} \max_{0 \le c \le 2} \left\{ w(c) + \tfrac{1}{2} F(2-c,T-1,T) \right\}$$

The term in the curly brackets equals 0.35 if c=0 , 1.25 if c=1 and 1.4 if c=2 . Hence the best decision is to lay both eggs if a host is encountered. Earlier when survival probability was assumed to be higher , we had found c=1 to be the best decision .

In problems with more realistic size , recursive calculations needed in dynamic programming have to be done on a computer .

7.2 Contests and game theory:

In this last section of the chapter and the book we shall consider contests between animals of the same species . We have already noted that such contests are the hallmark of the Darwinian theory of evolution . The contests may be for food , territory , mates , nesting sites , position in the social hierarchy etc.

The question of optimal strategy in a contest is somewhat different from optimisation problems discussed in 7.1 . This is because , while a contestant is free to choose his own strategy , the pay-off is determined by this strategy and the action chosen by the opponent . Such problems are the subject of the mathematical theory of games . For a very interesting introduction to the theory of games , see Williams (1954) . For a more recent and mathematical overview including the topic of interest here namely evolutionery games , see Thomas (1984) . We will first describe briefly the general appproach of game theory and then consider its application to animal contests.

7.2.1 Two person zero sum game:

This game consists of two players , say Blue and Red (to use terms in boxing). Each player makes just one move , without knowing what the other player is going to do . A move simply means choosing one out of a set of actions . Two moves chosen by the two players determine the outcome of the game which is a pay-off . A game is said to be zero-sum if pay-off to the Blue player necessarily comes from the Red palyer's pocket . In other words , gain of one player is loss of the other player . So a game is completely determined by lists of actions open to the two players and values of pay-offs associated with each pair of actions .

As an example consider a game in which Blue and Red have two options each , namely A and B . The resulting pay-offs are given in the following 2x2 matrix .

		Red	
		A	B
Blue	A	6	5
	B	5	4

Here if Blue and Red both choose option A , Red has to pay 6 units to Blue. Conventionally we write in the pay-off matrix quantities due to Blue . Anything payable to Red appears with a negative sign .

The theory of games assumes that a player seeks to maximise minimum possible gain (or minimise maximum posssible loss) that a choice of action entails. Under this assumption the target is choosing the right option . Let us see the game from the viewpoint of Blue . He wants to maximise his minimum gain . With option A the minimum gain is 5 while with option B it is 4 . Hence Blue should choose A . On the other hand Red wants to minimise maximum loss . His maximum loss with option A is 6 (which occurs when Blue also chooses A) and with opion B it is 5 . Hence Red should choose B .

We have found here the solution of the game . It has the remarkable property that knowledge of what the other player will do has no effect on the best option .

When , as in this case , maximum of row minima equals minimum of

column maxima , the game is said to have a saddle point (because seat of a saddle is at the minimum of the front-to-back curvature and maximum of side-to-side curvature) . A saddle point , when it exists , shows the the option for each player . However a saddle point may not always exist . The following pay-off matrix does not have a saddle point .

		Red	
		A	B
Blue	A	4	7
	B	6	5

Here the maximum of row minima is 5 and the minimum of column maxima is 6 . In this case knowledge of the other player's move does affect the best choice . If Red palys A , Blue should play B while if Red plays B , Blue should respond with A . Similarly , if Blue plays A , Red should play A while if Blue plays B red should respond with B . The situation seems not to have any resolution . A slight change in the formulation , fortunately , suffices to untie the knot . The change necessary is to allow mixed strategies and use expected gain as the criterion to judge a strategy .

A mixed strategy is a probability distribution over the set of available options , each of which is called a pure strategy . In the present problem it turns out that Blue can do better by using a mixed strategy instead of always playing B (which maximises his minimum gain) . Let us denote by the vector (0.25 , 0.75) , the probabilities with which to choose A or B . Then no matter what is the choice of Red , the expected pay-off of Blue is .25x4+.75x6=5.5 (which is also equal to .25x7+.75x5) . Similarly , Red can do better by adopting the mixed strategy (0.5 , 0.5) , instead of always playing A (which minimises his maximum loss) . The expected loss for Red is .5x4+.5x7=5.5 if Blue pays A . If Blue plays B , the expected loss is .5x6+.5x5=5.5 . Thus the expected loss is the same regardless of what Blue does .

Two questions come to mind . Do things always work out so nicely ? How does onr find out such a mixed strategy ? The answer to the first question is , yes . We shall state it formally as a theorem (without proof).

Minimax Theorem : Consider a two person zero sum game with pure

strategies A_1 , A_2 , ... , A_m for player 1 and B_1 , B_2 , ... , B_n for player 2 . Let $p' = (p_1 , p_2 , \ldots , p_m)$ denote a mixed strategy for player 1 , $q' = (q_1 , q_2 , \ldots , q_n)$ denote a mixed strategy for player 2 where $\sum_1^m p_i = 1 = \sum_1^n q_j$, and e_{ij} denote the pay-off received by player 1 when he plays A_i and player 2 plays B_j . Then

$$\max_p \min_q \sum_{i,j} p_i q_j e_{ij} = \min_q \max_p \sum_{i,j} p_i q_j e_{ij} .$$

The theorem asserts existence of a mixed strategy p that maximises minimum gain for player 1 and a mixed strategy q that minimises maximum loss for player 2 . Now let us see through an example how one may identify the best mixed strategy for each player .

In the problem discussed above , suppose Blue plays A with probability p_A and plays B with probability $p_B = 1-p_A$. Then his expected pay-off is $4p_A + 6p_B$ if Red plays A and $7p_A + 5p_B$ if Red plays B . For changing values of p_A these pay-offs change and can be depicted as straight lines in graph shown below . Notice that in the graph , if Red plays A and $p_A=0$, the pay-off to Blue is 6 . It reduces linearily to 4 as p_A increases to 1 .

The wavy line shows where the minimum expected gain is for a given value of p_A (whatever the strategy used by Red) . The minimum gain is maximised at the intersection where $4p_A+6(1-p_A) = 7p_A+5(1-p_A)$. Thus we get $p_A=0.25$.

A similar search for the best mixed strategy for Red is shown in fig.7.2.2.

Let q_A denote the probability that Red plays A . If Blue plays A , the expected loss for Red is $4q_A+7(1-q_A)$, while if Blue plays B , the expected loss for Red is $6q_A+5(1-q_A)$. Equating these we get $q_A=0.5$.

7.2.2 Evolutionarily stable strategy :

Maynard Smith (1982) showed that the framework of game theory can be used profitably to understand contests between animals . In the simplest formulation he assumed that each contesting animal can choose between two

pure strategies with colourful names hawk and dove . (A set up with more than two strategies will be considered later . In all these cases the strategy set for each contestant is the same .) A hawk strategist threatens the opponent and attacks if the opponent does not withdraw . A dove strategist withdraws when threatened . Hence when a hawk strategist (abbreviated as 'hawk') meets a dove , the latter gives up any claim on the contested resource of value V . When two hawks meet , a fight ensues , one player suffers a cost c of injury and the other player wins the value V. Either player is assumed to be as likely a winner as a loser . Hence the expected pay-off to a hawk meeting another hawk is (V-c)/2 . The complete pay-off matrix for the player 1 is as follows:

		Player 2	
		H	D
Player 1	H	$\frac{1}{2}$(V-c)	V
	D	0	V/2

Clearly , when two doves meet , there are no injuries and each player gets half of the value V .

So , as opposed to the games considered in 7.2.1 , the hawk-dove game is a non-zero sum game . This is not a radical departure . The mathematical theory of games does consider non-zero sum games . In such games , it can be shown that there exist mixed strategies p^* and q^* , for the two players, that together constitute what is called a Nash equilibrium . This equilibrium has the property that any player that shifts from his strategy unilaterally , while the other player sticks to his , the player that shifts is worse off . We shall not pursue this line of attack because Maynard Smith's approach departs from conventional game theory in terms of what constitutes an optimal strategy . In conventional game theory , optimal strategy is one that maximises the expected pay-off . Its counterpart in animal behaviour is the evolutionarily stable strategy or ESS . The whole idea of using game theory to study animal contests becomes clear once the concept of ESS is understood .

Assume that the choice of pure or mixed strategies is completely inherited and is passed on to the offspring produced asexually . This avoids the complication of two parents with different inherited strategies

contributing to the behavioural make up of the offspring .In our simplied set up , an offspring is an exact replica of the parent (except for rare mutations). Individuals exist in infinite populations and play the game against a randomly selected member of the population . The pay-off earned modifies the Darwinian fitness of the individual. Having played the game , a player contributes to the next generation , offsprings proportionate in number to the modified fitness . A population which is homogeneous i.e. consists of individuals that play the same strategy say dove , continues to be so in successive generations (is in equlibrium) . However , periodically , a small fraction of the individuals in the next generation turns out to be mutants that play a different strategy . Thus the equlibrium is disturbed . Will the original equilibrium be restored ? Not always . If the equlibrium is restored no matter what kind of mutation arises , then the original strategy played by all individuals in the population is said to be evolutionarily stable .To put it differently ,the original stratey is uninvadable by any other strategy .

Let us take some specific examples . Suppose a population consists of all doves (i.e. every individual plays the dove strategy) . Suppose in the next generation a small proportion p of individuals born is of hawks. To begin with , all individuals have the same base fitness w_0 . Now each individual plays the game with a randomly chosen adversary who is a hawk with probability p and a dove with probability 1-p . A hawk meets another hawk and hence gets the pay-off (V-c)/2 with probability p and pay-off V (when he meets a dove) with probability 1-p . Hence the expected pay-off is ,

$$p\left(\frac{V-c}{2}\right) + (1-p)V \ .$$

Thus the modified fitness of a hawk $w(H)$ is ,

$$w(H) = w_0 + p\,\frac{V-c}{2} + (1-p)V \ .$$

Similarly the modified fitness of a dove $w(D)$ is ,

$$w(D) = w_0 + p(0) + (1-p)\,\frac{V}{2} \ .$$

Now each hawk produces offsprings proportional to $w(H)$ and each dove proportional to $w(D)$. Hence the proportion of hawks in the next generation is,

$$p' = \frac{p.w(H)}{p.w(H)+(1-p)w(D)} .$$

If $w(D) = w(H)$ then p' = p . If $w(D) > w(H)$ then p' < p and if $w(D) < w(H)$ then p' > p . Now $w(H) > w(D)$ if

$$p \frac{V-c}{2} + (1-p) \frac{V}{2} > 0 .$$

In particular , if V > c , then for every p , p' > p . Thus the proportion of hawks goes on increasing . Clearly the dove strategy or D is not ESS . But the hawk strategy or H is .This seems intuitively reasonable . If the cost of injury is less than the value of the resource to be gained by attack , atackers should prosper .

Now suppose V < c . Even then $w(H) > w(D)$ as long as

$$\frac{V}{c-V} > \frac{p}{1-p}$$

or V/c > p . Thus when p the proportion of hawks is small it goes on increasing . When eventually V equals c.p the population reaches a stable equilibrium .The proportion of hawks will neither increase nor decrease .

This equilibrium is called dimorphic because the population consists of two kinds of individuals .There exists another interesting possibility . Suppose we allow for a mixed strategy . That is to say , the same individual plays hawk with probability p and dove with probability 1-p . Let us denote the mixed strategy by 'I' .In general if there are k pure strategies $A_1, A_2, \ldots, A_k$ possible , a mixed strategy I is a vector $(p_1, p_2, \ldots, p_k)'$ where p_i is the probability of playing A_i , $\sum_1^k p_i = 1$. When is a population of I-strategists uninvadable ? Let J be any other mixed strategy .(Pure strategies are automatically included as particular cases in which $p_i = 1$ for some i . Suppose a small proportion ε of mutants that play strategy J is introduced in the population of I players . Then ,

$$w(I) = w_0 + \varepsilon E(I, J) + (1 - \varepsilon) E(I, I),$$

and

$$w(J) = w_0 + \varepsilon E(J, J) + (1 - \varepsilon) E(J, I),$$

where $E(I,J)$ denotes the expected pay-off to an individual that plays I when faced with someone that plays J . For the population of I-strategists to be uninvadable we must have $w(I) > w(J)$ for each J distinct from I , and for very

small values of ε . A necessary condition for this is ,

$$\text{either } E(I, I) > E(J, I) \qquad (7.2.1a)$$

$$\text{or } E(I, I) = E(J, I) \text{ and } E(I, J) > E(J, J) . \qquad (7.2.1b)$$

These are referred to as ' standard conditions ' for a ESS .

Let us apply these considerations to the hawk- dove game . We see that D is not an ESS because

$$E(D, D) = V/2 < E(H, D) = V .$$

Suppose $V > c$. Then H is an ESS . Notice that if J is a mixed strategy $(q, 1-q)'$ then

$$E(H, H) = \frac{V-c}{2}$$

and

$$E(J, H) = q\,E(H, H) + (1-q)\,E(D, H) = q\,\frac{V-c}{2} .$$

Hence for every $q < 1$

$$E(H, H) > E(J, H) .$$

This proves that H is an ESS .

Suppose $V < c$. Then H is no longer an ESS . Since neither pure strategy is ESS , we may search among the class of mixed strategies . Is there any assurence that there exists an ESS ? The following simple result answers this question in the affirmative .

Theorem : For every two person game with two pure strategies , there exists an ESS (excluding the trivial case where pay-off is the same for either pure strategy) .

Proof: Let us continue to call the two pure strategies available D and H .Let the pay-off matrix for the player 1 be as follows:

Player 2

H D

	H	a	b
Player 1			
	D	c	d

Case 1. If a > c then H is an ESS , since E(H,H) = a > E(I,H)=p.a+(1-p).c , for every I such that p < 1 .

Case 2. If a=c and b > d then also H is an ESS . Here E(H,H)=E(I,H) . But E(H,I) =p.a+(1-p).b , whereas E(I,I) = $p^2.a + p(1-p).(b+c) + (1-p)^2.d$, which simplifies to $p.a +(1-p)(p.b+(1-p).d)$. Thus E(H,I) > E(I,I) for every I such that $p < 1$.

Case 3. If d > b then it is easily shown that D is an ESS .

Case 4. Let a < c and d < b . Suppose I = (p , 1-p) , p < 1 , is an ESS . Let J = (q , 1-q) , q ≠ p , be any other mixed strategy . Then

$$E(I,I) = p^2.a + p(1-p)(b+c) + (1-p)^2.d ,$$
$$E(J,I) = q.p.a + q(1-p).b + (1-q)p.c + (1-q)(1-p).d .$$

Hence

$$E(I.I)-E(J,I) = (p-q)\{p.a+(1-p).b-(p.c+(1-p).d)\} .$$

This difference must be nonnegative for every q if I is to be an ESS . This is possible only if the term in the curly brackets is zero . If not , the right hand side will have one sign when p > q and another when p < q . Hence ,

$$\frac{p}{1-p} = \frac{b-d}{c-a} \quad \text{or} \quad p = \frac{b-d}{c-a+b-d} .$$

At this value of p we get E(I,I)=E(J,I) . Therefore for I to be an ESS it must satisfy E(I,J) > E(J,J) . Verification of this is left as an exercise.

7.2.3 Games with more than two pure strategies :

While a game with only two pure strategies always has an ESS , this is not so in general . In this section we will present one example of a game with no ESS . Further , even when it exists , ESS need not be unique . We will consider an example of a game with more than one ESS . We will then consider two general results which help in the search for an ESS .

Example 1: Scissors-stone-paper game.

This game has no ESS . Intuitively speaking , this is so

because of the circularity among the three options available . Scissors can cut paper , paper can wrap up a stone and a stone can blunt scissors . The pay-off matrix for player 1 is given below.

		player 2		
		scissors	stone	paper
player 1	scissors	0	-1	1
	stone	1	0	-1
	paper	-1	1	0

Clearly no pure strategy can be an ESS because another pure strategy can invade it . If p = (p_1, p_2, p_3)' and q = (q_1, q_2, q_3)' are two mixed strategies then,

$$E(p, q) = q_1 - q_2 + p_2 - p_1 + 3p_1q_2 - 3p_2q_1 .$$

Hence

$$E(p, p) = 0 , \text{ for all } p .$$

So if q is an ESS it must satisfy

$$0 = E(q, q) \geq E(p, q) \text{ for every } p .$$

Consider the case $p_1 = 1$. It leads to the condition $q_2 \leq q_3$. The case $p_2 = 1$ leads to the restriction $q_3 \leq q_1$. Similarly two more cases namely $p = (0 , \frac{1}{3} , \frac{2}{3})$ and $p = (\frac{1}{3} , 0 , \frac{2}{3})$ together yield $q_1 \leq q_2$. Thus the only possible candidate for ESS is $q = (\frac{1}{3} , \frac{1}{3} , \frac{1}{3})$. But it cannot be an ESS because it fails to satify the standard conditions . (Hint: Check its performance against any pure strategy .)

Example 2: Hawk-dove-retaliator game.

This is an extension of the hawk-dove game cosidered earlier . Now we have a third pure strategy called Retaliator (R) which acts as an hawk against an hawk and as a dove against a dove . The pay-off matrix for player 1 is ,

		player 2		
		H	D	R
	H	-1	2	-1
player 1	D	0	1	1
	R	-1	1	1

In this game no pure strategy is ESS . A population of hawks can be invaded by mutant doves and vice versa . R is not ESS because any mutant doves do not get eliminated . A mixed strategy I = ($\frac{1}{2}$, $\frac{1}{2}$, 0) turns out to be ESS . To verify this first note that E (I , I) = 1/2 . Let J be any other mixed srategy given by J = (p_H , p_D , p_R) . Then ,

$$E (J , I) = \tfrac{1}{2} (p_H + p_D) < \tfrac{1}{2} \text{ if } p_R > 0 .$$

Hence if $p_R > 0$ then J cannot invade I . So consider strategies with $p_R = 0$. For such a strategy J we have E (J , I) = $\frac{1}{2}$. So the first standard condition is not satisfied . Consider the next comparison . We have,

$$E (J , J) = 1 - 2 (p_H)^2$$

and

$$E (I , J) = \tfrac{3}{2} - 2p_H ,$$

so that

$$E(I , J) - E (J , J) = \tfrac{1}{2} - 2p_H(1 - p_H)$$

which is positive unless $p_H = \frac{1}{2}$. Thus for every J $\neq$ I , E(I,J) > E(J,J) . But instead of demonstrating that there can be multiple ES strategies we have found a unique ESS . This lacuna is readily corrected if we change the pay-off matrix slightly so that R gets a slight advantage over D . The new pay-off matrix is ,

		player 2		
		H	D	R
	H	-1	2	-1
player 1	D	0	1	0.9
	R	-1	1.1	1

In this case pure strstegy R and the mixed strategy I = ($\frac{1}{2}$, $\frac{1}{2}$, 0) are

both ESS . The verification is left as an exercise .

Animals often seem to indulge in ritualised fights and to avoid full use of their fighting abilities . Serious injuries seem to occur much less frequently than what the highly developed weapons of war such as antlers , canine teeth , well built musculature etc. may lead one to expect . Perhaps the explaination lies in the fact that in the long run aggressiveness is not as good a strategy as retaliation .

We shall now state and prove two propertios of ES strategies in games with multiple pure strategies . The results hold even when the set of pure strategies is uncountably infinite . For proofs in the general case see Bishop and Canning (1978) .

The Bishop-Canning theorem : Consider a game with k pure strategies $A_1, A_2, \ldots, A_k$ for each of two players . Let $(p_1, p_2, \ldots, p_k)$ be a mixed strategy that is ESS . Then,

$$p_i > 0 \Rightarrow E (A_i , I) = E (I , I) .$$

Proof: Assume to the contrary . Let $p_1 > 0$ and $E (A_1 , I) < E(I,I)$, (why is the reverse inequality not considered?)i.e.

$$\sum_{j=1}^{k} p_j e_{1j} < \sum_j \sum_l p_j p_l e_{jl} .$$

The right hand side can be split into two terms and written as ,

$$\sum_{l=1}^{k} p_1 p_l e_{1l} + \sum_{j>1} \sum_l p_j p_l e_{jl}$$

which equals

$$p_1 E(A_1 , I) + (1 - p_1) E(X,I) ,$$

where X is a mixed strategy $\frac{1}{1-p_1} (0 , p_2 , \ldots , p_k)$, i.e. strategy I modified by excluding A_1 . Hence substituting back we get,

$$E (A_1 , I) < E (X , I) .$$

Notice that strategy I can be expressed as a mixture of 2 strategies , pure strategy A_1 and mixed strategy X in the prortion p_1 and $1-p_1$. Therefore , for any strategy J we can write ,

$$E (I , J) = p_1 E (A_1 , J) + (1 - p_1) E (X , J) < E(X,J).$$

Now putting J=I we get ,

$$E(I, I) < E(X, I),$$

which is impossible since I is ESS .

The theorem thus shows that every pure strategy included in an ESS I with positive probability performs equally well against I . This is a necessary condition only and a seperate check is necessary to confirm that a strategy that fulfills the condition is in fact an ESS .

Worthwhile pure strategies: If I is a mixed strategy $(p_1, p_2, \ldots)$ then a pure strategy A_j is said to be worthwhile in I if $p_i > 0$ .Pure strategies played with positive probabilities constitute the set of worthwhile strategies of I and the set is denoted by W(I) .

Lemma:If I_1 and I_2 are two ES strategies then $W(I_1)$ cannot be a subset of $W(I_2)$ (and vice versa) .

Proof:This proof is also by contradiction . Let if possible $W(I_1) \subset W(I_2)$. Now ,

$$E(I_1, I_2) = \Sigma p_i E(A_i, I_2) .$$

Further , $A_i \in W(I_1) \Rightarrow A_i \in W(I_2) \Rightarrow E(A_i, I_2)$ is constant say a. Hence

$$E(I_1, I_2) = E(I_2, I_2) .$$

Hence for I_2 to be ESS we must have ,

$$E(I_2, I_1) > E(I_1, I_1) .$$

But this cannot be because I_1 is itself ESS .

Corollary: If I is an ESS and W(I) contains every possible pure strategy , then I is the unique ESS .

7.2.4 A waiting game :

The framework of a finite number of pure strategies can be extended to a pure strategy set which is a continuum . In a waiting game each player chooses the length of time for which he waits . One that stays longer wins the resource .The cost incurred is proportional to the actual waiting period .

If player i chooses m_i as his waiting time , i = 1 , 2 , then player 1 gets the pay-off V-m_2 if $m_1 > m_2$ i.e. player 2 leaves earlier and gets $-m_2$ as pay-off . If $m_1 < m_2$ player 1 loses and gets $-m_1$ while player 2 gets V-m_1 . The strategy set is { m , m > 0 } . If $m_1 = m_2$, the resource is

shared equally .

In this game , no pure strategy can be evolutionarily stable .Any population consisting of pure m-strategists can be invaded by a mutant with pure stratyegy $m + \epsilon$; for

$$E (m + \epsilon , m) = V - m > \frac{V}{2} - m = E (m , m)$$

This does not mean that we should see an ever increasing value of m being adopted . That is is because for large m ,an effective counter-strategy is, not waiting at all . Specifically if there is a populaion with every individual adopting a pure strategy $m > \frac{V}{2}$ then a mutant strategy of zero waiting time can invade .

A mixed strategy here is a probability density function f(m) . We now state without proof an extension of the Bisop-Cannings theorem .

Result: If a mixed strategy given by the probability density function f(m) is ESS , then $\forall\ m \ni f(m) \neq 0$, E(m,f) is constant .

A generalisation of the associated lemma is as follows .

Lemma: If f and g are two ESS then W(f) cannot be a subset of W(g) and vice versa , where $W(f) = \{ m : f(m) \neq 0 \}$ and W(g) is defined analogously .

A rather surprising result here is that the waiting game has a unique ESS given by the exponential distribution . A detailed proof due to Bishop and Cannings(1978) is rather involved and is omitted . We will restrict ourselves to showing that exponential distribution is the only possible candidate for an ESS .

It is given that E(m,f) is constant . Suppose the mixed strategy chooses the waiting time to be x. Then the pay-off to the player using a pure strategy is V-x if m > x and - m if m < x . Hence the expected pay-off is ,

$$E(m,f) = \int_{x=0}^{m} (V - x)f(x)dx - \int_{m}^{\infty} mf(x)dx ,$$

which is independent of m . Let us verify that $f(x) = \frac{1}{V} e^{-x/V}$ satisfies this equation . Notice that ,

$$\int_0^m f(x)dx = 1-e^{m/V} , \int_0^m xf(x)dx = V\left\{ 1 - e^{-m/V} \left(1 + \frac{m}{V} \right) \right\}$$

which when substituted yields $E(m,f) = 0$.

Further in the class of probability density functions such that $f(x) > 0 \ \forall \ x > 0$ exponential distribution is the only ne with this property as shown below .

We know that $E(m,f)=E(m+h,f)$ for $h > 0$. i.e.

$$\int_0^m (V-x)f(x)dx - \int_m^\infty mf(x)dx = \int_0^{m+h} (V-x)f(x)dx - \int_{m+h}^\infty (m+h)f(x)dx ,$$

which simplifies to ,

$$\int_m^{m+h} (V-x+m)f(x)dx - h \int_{m+h}^\infty f(x)dx = 0$$

For small h this can be approximated by the equation,

$$h(V - \tfrac{h}{2})f(m + \tfrac{h}{2}) - h\,(1 - F(m+h)) = 0 ,$$

where $F(.)$ is the cumulative probability distribution corresponding to $f(x)$. It follows that

$$Vf(m) = 1- F(m)$$

or

$$\left(f(m)/(1-F(m))\right) = \tfrac{1}{V} \quad \text{for every } m > 0 .$$

This is in fact a characterisation of the exponential distribution

$$f(x) = \tfrac{1}{V}\, e^{-x/V}$$

as seen earlier in section 2.5 .

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THE SOCIAL BEHAVIOUR OF SLIME MOLD AMOEBAE FROM THE VIEW POINT OF NATURAL SELECTION

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The evolution of communication and social behaviour in *Dictyostelium discoideum*

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Abstract. Exceptionally for a developing system, the pathways of intercellular communication are fairly well characterised in the cellular slime molds. This paper attempts to provide adaptive explanations for the origin of the following features and consequences of communication between cellular slime mold cells: the tendency to congregate, chemotaxis to a released signal, signal relay from cell to cell, oscillatory signal release and an invariant ratio of the terminally differentiated cell types. For the sake of specificity attention is directed at the species *Dictyostelium discoideum*. Central to the entire analysis is the assumption that contiguous groups of feeding cells are, and in the past were, genetically identical. It is suggested that, in respect of most of the features listed above, the critical event which started things off must have been the acquisition by the cell membrane of permeability for a substance normally produced intracellularly as a response to the stress of starvation. An argument is presented for treating social behaviour in these organisms, and in particular the suicide by cells which differentiate into stalk, as an example of group selection

Keywords. *Dictyostelium*; slime mold; evolution; group selection.

1. Introduction

The aim of this paper is to advance adaptive explanations for some manifestations of organised behaviour in a primitive microorganism. A property will be said to be "adaptive" in the sense of being more useful for the survival and reproduction of the organism than the absence of the property and, sometimes, than other possible alternatives.

Almost by definition, communication or mutual signalling is a prerequisite for social behaviour (Wilson 1975). Excepting cases wherein sociality is only apparent and due to spatial proximity caused by other factors, the observation of social or cooperative behaviour indicates the existence of an underlying system of communication. Specifically, some form or forms of communication must be responsible for the integrated multicellular behaviour displayed by a developing organism. This leads one to the question of why any particular mode of communication, either identifiable directly or inferred from its effect on social behaviour, exists in development. In general there are two sorts of answer possible to such a question. One can think of a 'developmental' explanation, meaning basically an explanation in terms of whatever is known of the embryological process at a more basic level, ideally of its physics and chemistry. On the other hand one can aim for an 'evolutionary' explanation; that is, one can try to invoke natural selection. Seen in this light, the interesting questions which need to be answered are, in what manner is a particular form of communication adaptive? And how could it have evolved? Hardly anything is known about the details of

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intercellular communication in most developing systems for these questions to be considered seriously. The cellular slime molds, especially their best studied member, *Dictyostelium discoideum*, provide an exception to this general rule (Bonner 1967; Loomis 1975).

In *D discoideum* multicellularity arises on account of aggregation of single amoebae because of the emission of, and attraction to, a known chemical signal (Bonner 1967). During aggregation the signal is released periodically and also relayed from cell to cell (Gerisch and Wick 1975: Shaffer 1975; Roos *et al* 1975). Strong circumstantial evidence indicates that the cells continue to communicate—albeit by other, not yet understood means—in the multicellular aggregate (Raper 1940; Lokeshwar and Nanjundiah 1983). Eventually, after a series of morphogenetic movements, essentially all the cells in the aggregate differentiate into one of two types whose relative numbers are constant (Bonner 1967).

The present work is the result of an effort to look at the following 4 features of communication from an evolutionary point of view: aggregation by chemotaxis, periodicity of signal release and signal relay, patterning within the multicellular aggregate and cell number proportioning in the terminally differentiated structure. In order to fix our frame of reference we restrict our attention to *D discoideum*. A word about methodology: the approach—not necessarily in the same order—will be to (i) describe an existing property; (ii) suggest an adaptive value for it; (iii) conjecture an ancestral state (by which is meant, somewhat loosely, a state in which the property is missing); and (iv) point out that starting with the ancestral condition, the presently existing property could be acquired via plausible mutational steps.

In what follows I first sketch the development of *D discoideum* in just sufficient detail for our purpose and then go on to suggest specific evolutionary hypotheses for the 4 features mentioned above. General issues related to the hypotheses are discussed at the end. Comparative development in the cellular slime molds has been recently discussed in a paper by Bonner (1982) which has strongly influenced this one.

2. The life cycle of *Dictyostelium discoideum*

As this description is highly condensed, the literature (Bonner 1967; Loomis 1982 and references therein) should be consulted for a fuller picture. *D discoideum* is a free living soil amoeba. Controlled experiments performed in the laboratory enable one to build the following plausible account of its life in nature (figure 1). In their vegetative phase, individual cells feed on bacteria, grow and divide by mitosis. Under extreme environmental conditions cellular slime mold cells are capable of following one of two protective strategies, that of forming microcysts or macrocysts. Both are resistant structures. Microcysts are not known as yet in *D discoideum*, and macrocysts are the first step in the sexual pathway. Since they are not formed under standard experimental conditions, we will not refer to them any further (Bonner 1982 has considered their possible significance). In the laboratory, amoebae starved of food go through a seemingly quiescent phase for a few hours prior to aggregating. Aggregation is by means of chemotaxis, usually accompanied by relay of the chemoattractant. The attractant is a chemical, cyclic AMP (cAMP), which is produced and periodically released by the cells. A cell which senses external cAMP moves towards its source and in turn itself releases a burst of cAMP. Consequently local variations in cell density get amplified. Ultimately

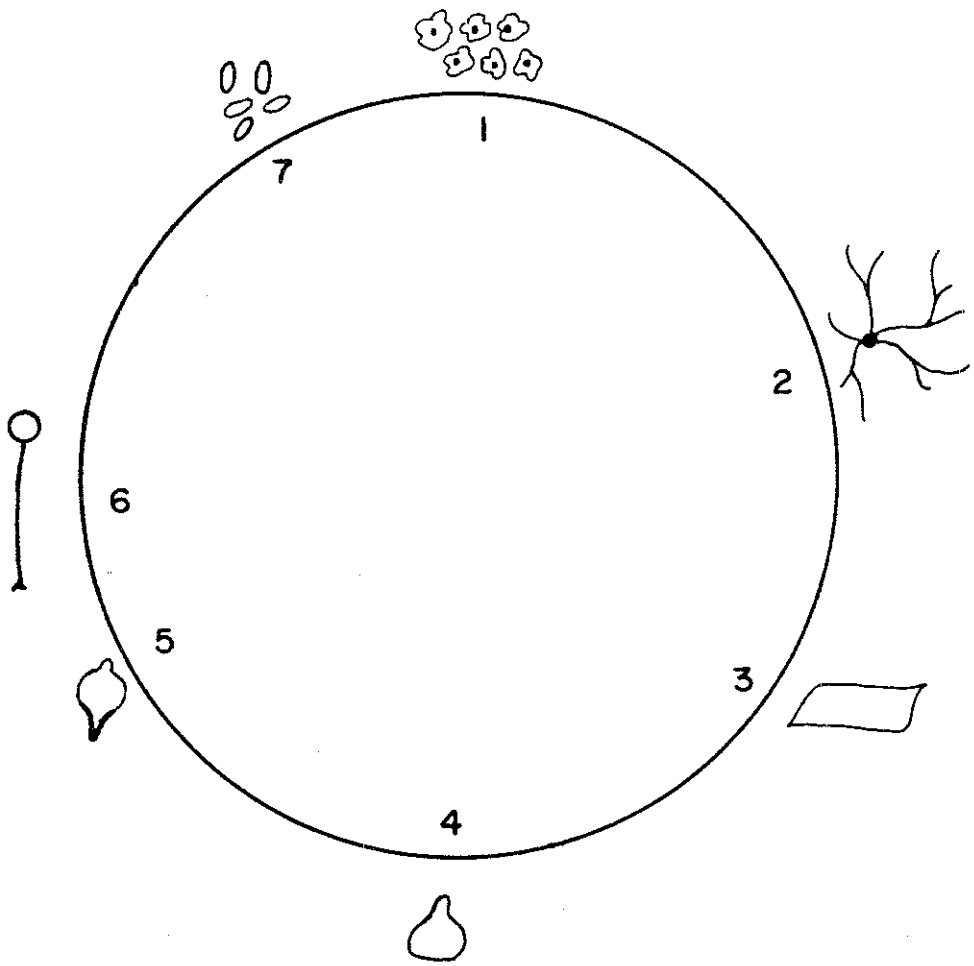

Figure 1. Schematic representation of the life cycle of *D. discoideum* (not to scale). (1). Free-living amoebae; (2). aggregation; (3). migrating slug, anterior to the right; (4). early culmination; (5). advanced culmination; (6). fruiting body with spore mass held aloft stalk; (7). spores

all the cells in a neighbourhood end up piled on top of each other in a mound which is held together by specific adhesion molecules. The aggregate—now called the slug—often falls down and adopts a cylindrical form with a nipple-like protrusion, the tip, at its anterior end. After moving for a length of time which depends strongly on external conditions as well as the genotype, the slug stops, reverts to a mound-like shape, and the cells in it move in the manner of water in a reverse fountain and the entire mass rises upwards (the words 'up' and 'down' mean away from the two-dimensional substratum on which aggregation has occurred, or towards it). Irreversible differentiation sets in concurrently, most of the cells either turning into spores or, alternatively, dying and turning into the units of a cellulose-sheathed stalk. The final structure, called the fruiting body, has a disc-shaped base (also made of dead cells), an erect stalk and, above the stalk,

a spheroidal mass of spores Under suitable conditions each spore can germinate and give rise to an amoeba, setting off the life cycle anew

3. Aggregation

If not the earliest, aggregation is certainly the most striking example of social behaviour in the cellular slime molds [mutual repulsion, observed in the vegetative phase of some slime molds, is conceivably a device for maximising the efficiency of feeding (Keating and Bonner 1977)] Since starvation is the primary trigger, it seems intuitively reasonable to suppose that aggregation, like the coming together of individuals in more evolved social groups, must be a behavioural trait which has evolved to improve the chances of survival of the individual itself or of its genetic relatives Therefore one must make it plausible that because of aggregation there is an increase, either in the probability that an amoeba turns into a viable spore or in the probability that a spore disperses to a favourable environment A large mass of spores probably stands a better chance of dispersal than many isolated spores (Bonner 1982) In a fruiting body, just the fact that the spores are on an elevation should also help in dispersal, and we will take this up later That apart, the assumption that aggregation might enhance sporulation seems justified, since cell-cell contact is normally a requirement for development, and so for sporulation (Gregg 1971; Newell *et al* 1971; Takeuchi and Sakai 1971) Precisely how contact aids development is not known; one possibility is that the binding or recognition of sets of cell-surface molecules is necessary Alternatively, from observations on mutants which can sporulate in the absence of contact if simulated by exogenous cAMP (Kay and Trevan 1981), we might conjecture that 'contact' really means a degree of proximity sufficient for some substance emanating from one cell to reach a level at the site of a second cell high enough to induce the latter to turn into a spore (extracellular cAMP by itself is a non-specific differentiation signal in present-day *D discoideum*; in conjunction with other substances it can influence either stalk or spore formation (Morrissey 1982)) The suggestion is, then, that in the ancestor of *D discoideum* a single cell could sporulate in isolation but that the process could be helped along by a stimulus emanating from another cell in the same condition What sort of substance would be appropriate to provide such a stimulus? A natural candidate would seem to be a chemical which was already being synthesised in the (ancestral) isolated cell during sporulation Such a substance would reinforce a cell's response to starvation if, in addition to being produced intracellularly, it moved from one cell to another through a 'leaky' membrane The leak itself would be selected for when it first arose by mutation This would be so since sufficiently small clusters of post-feeding amoebae very likely consist—and consisted—of clones; the mutation would be simultaneously expressed in an entire group of cells The possibility that the leak could be disadvantageous to a cell on account of its losing some of the signal substance must have been compensated by the benefit it conferred when it entered and stimulated other, genetically identical, cells To sum up, a group of amoebae which stayed together after feeding was over would hold a selective advantage over one whose members continued to move randomly and so drifted apart Thus the mechanism of 'aggregation', when it first arose, may have been nothing more than a decrease in cell motility once the density of food became too low to be reliably sensed; the effect may have been further strengthened by the acquisition of the ability by cells to adhere to one another

4. Chemotactic attraction

Continuing with the line of argument we have used so far, it is not difficult to see how mutual attraction, by decreasing the spatial spread of post-vegetative cells, would also have been selected for The agent of attraction could either be the same one that enhanced sporulation or, perhaps, a substance which worked inside the cell and guided cell movement by acting on contractile filaments, thereby causing local psuedopodial extrusion (the observed rapid accumulation of cytoskeletal actin in *D. discoideum* following an external cAMP stimulus (McRobbie and Newell 1984) could be a pointer to the original situation) The same substance entering from outside would have the same effect, but this time in a definite direction A mutation which made the cell membrane porous for this substance would polarise cell movement centripetally towards wherever the cell density was slightly higher than in the neighbourhood, or wherever—if development were not perfectly synchronised in all cells—the first cell to leak out the substance was situated

Until now I have tried to suggest how non-directed aggregation could be adaptive in itself, and how—by improving the efficiency of aggregation—a further beneficial adaptation could be conferred by either the simultaneous and mutual attraction of all cells in a neighbourhood or the attraction of most of the cells towards a center

5. Relay

Consider now the possibility that a primary chemotactic stimulus might excite a sensitive cell to act as a secondary source of the stimulus The advantage of having an attractant relayed outward from a centre, rather than having it released at about the same time by all cells, would seem to be the prospect of increasing the size of an aggregate Since the signal should have the same range whether it is released by a cell on its own or whether a cell releases it in response to an external stimulus, it appears that the ability to relay would not have been favoured if all cells had—in the course of their development—started to signal simultaneously In the absence of a means for synchronising development, simultaneous signalling does seem unlikely; the special care needed to achieve developmental synchrony in the laboratory suggests this Therefore, in order to associate a selective advantage with the ability to relay, it needs to be assumed that under natural conditions some cells in a group are developmentally more advanced than others and, specifically, are capable—purely on statistical grounds—of releasing the chemoattractant earlier than most others Given that relaying the chemotactic signal causes aggregates to increase in size, how might this be beneficial? It could be that large aggregates, with large volume-to-surface ratios, imply a reduction in the amount of the hypothetical substance which leaks to the outside world and is lost For the same energetic investment, the yield in terms of effective signal strength would be higher Another possibility, alluded to earlier (Bonner 1982), is that a large aggregate might improve the prospects for spore dispersal Significantly, large slugs of *D. discoideum* move faster than small ones (Bonner *et al* 1953) Consequently if the time available for dispersal (before sporulation begins) is limited, the distance of dispersal would be greater for cells contained in the larger of two slugs If this is to be used as a justification for increased aggregate size *via* relay, one will have to make the further supposition that

aggregate motility existed earlier, probably having being selected as an aid to dispersal by itself.

There is another way of looking at the phenomenon of relay (Nanjundiah 1978). So far we have assumed that chemotaxis-mediated aggregation came first and that relay was a later refinement. Suppose things had been the other way round: consider a stage in evolution at which a clone of cells, lying close to one another, were faced with starvation. Just as we made a case for the original aggregation signal being a pre-existing component of the cell's internal response, we can argue that the cell-to-cell transfer of a substance, until then produced inside the cell in response to starvation and remaining there, would have enabled an entire group of cells to cope with a deteriorating environment faster than they would have in the absence of relay. Both clustering and chemotactic attraction could have arisen, in this way of looking at things, as later adaptations. Note that the first hypothesis (relay as a device for increasing the range of the chemotactic signal) makes it essential that the relay substance and the chemoattractant be the same (as is indeed the case in *D. discoideum*); on the second hypothesis, though it would probably be of advantage to have them the same, they could well be different.

An interesting point regarding the origin of relay is that on the second hypothesis the relay substance must have been able to activate its own synthesis. In other words, the reaction pathway responsible for forming the substance must have had in it an autocatalytic (positive feedback) step. The critical mutational event would then have been, as already suggested, a specific membrane 'leak'. If, on the other hand, chemotactic aggregation had arisen as an earlier adaptation (the first hypothesis), the important mutation would have been the one which made chemoattractant synthesis autocatalytic: that is, an early step in the synthetic pathway would need to be activated by a later step.

6. Oscillations

Given relay, and therefore an autocatalytic step; given that the living cell is thermodynamically an open system; and given that most biochemical reactions *in vivo* operate far from equilibrium, oscillatory reaction fluxes are almost a "natural" consequence (Higgins 1967), meaning that no special adaptive explanations are called for. Goldbeter and Segel (1977) have in fact shown that the observed cAMP oscillations in *D. discoideum* can be successfully modelled by assuming that the condition for relay exists, that is that an extracellular cAMP stimulus activates the intracellular synthesis of cAMP. Oscillations are on the other hand ubiquitous in biological systems (Winfree 1980); in particular, morphogenetic oscillations are found in myxobacteria (Kaiser *et al* 1979) as well as in other cellular slime molds, possibly with the involvement of cAMP (Schaap and Wang 1984). Even temporal patterning in chemical communication, though rare, is not unknown (Conner *et al* 1980). So it is worth considering whether the relatively rapid (period ca. 8 min) oscillations of cAMP in *D. discoideum* might be adaptive after all.

Under certain conditions, the course of glycolysis in yeast is oscillatory, also with a periodicity of some minutes (Hess and Boiteaux 1971). Since these oscillations involve the adenine nucleotide pool and therefore the adenylate charge (Atkinson 1968) of the system, Goldbeter (1974) has conjectured that the cell benefits by partitioning each oscillatory cycle into distinct energy-utilising and energy-yielding phases, something which is supposed to make for an improved metabolic efficiency. How far this argument can be carried over to cAMP oscillations in *D. discoideum*, where ATP levels do not vary

significantly within a period (Gerisch *et al* 1977), is not certain. Richter and Ross (1981) have offered yet another adaptive explanation for the glycolytic oscillation. Using a quantitative model they have calculated that energy dissipation in the latter part of glycolysis (the pyruvate kinase step) is minimal precisely when an earlier step (the phosphofructokinase reaction) is periodic with a frequency within a defined range. Again, one does not know how good this explanation, depending as it does on the "tuning" of one reaction step by another, would be for the slime mold oscillations. The oscillations in this case occur—as far as is known, unlike glycolysis in yeast—both extracellularly and inside the cell, and it is easier to speculate on a possible adaptive role for extracellular oscillations. It has been shown (Nanjundiah 1973) that when the relevant parameters are assumed to have reasonable values, a pulsatile source of cAMP has a spatial range which is about an order of magnitude more than the range of an equivalent steady source which releases cAMP at the same average rate. The reasoning is based on the facts that (a) (in three dimensions) the concentration of a signal diffusing from a steady source falls off inversely with the distance, whereas the peak concentration due to an impulsive source decreases as the cube of the distance, and (b) the lower the frequency of successive pulses, the weaker the effect of the equivalent steady source. Then, given a plausible threshold for the sensitivity of a cell, either for the concentration of cAMP or for its spatial gradient, the threshold is reached at a farther distance from the source when the signal is released in a series of brief pulses than when it is released at a uniform rate. The conclusion remains valid even when the released signal profile is no longer a sharp pulse but is somewhat sinusoidal. However, in the latter case the range of the signal is enhanced by roughly a factor of two rather than by one order of magnitude. A periodic signal has two other advantages. One is that the receiver would not get adapted to it as readily as it might to a steady source. It is to be expected that a train of stimuli reiterated at an appropriately intermediate frequency would be much better at eliciting a response than the same train of stimuli applied either at a very low frequency (in which case each stimulus would—so to speak—be like the first stimulus, there being no reinforcement) or at a very high frequency (in which case there would effectively be one constant stimulus, to which the system could adapt). Just this has been observed in the case of *D. discoideum* cells with folic acid, a chemoattractant for feeding cells (Wurster and Schubiger 1977). Also, periodic pulses of cAMP are efficient at eliciting cell differentiation whereas steady levels are not (Gerisch *et al* 1975; Darmon *et al* 1975). Unfortunately, none of these experiments tested the effect of irregular pulses or different waveforms; one is still unsure as to precisely which stimuli constitute signals and which ones do not. The other advantage of a periodic signal is that at close distances there would be a lesser degree of ambiguity in locating a periodic source than a steady source (the amplitude of oscillations will, in any case, get damped with increasing distance from the source, the higher frequencies dropping out first).

7. Pattern formation and tissue proportioning

7.1 *Pattern in the slug*

The slug is a facultative migratory structure formed by an aggregate of *D. discoideum* before it differentiates into a fruiting body. It is in some ways a preparatory phase; the

future stalk and spore cells are identifiable in its front and rear portions (Raper 1940). Depending on the type of experiment carried out, this separation into pre-stalk and pre-spore can be seen either as an expression of autonomous cellular predispositions (Takeuchi *et al* 1977) or as a consequence of the relative positioning of cells along the long axis of the slug (Raper 1940). Probably both factors are important and reinforce each other. Whatever be the cause, a spatial separation of presumptive cell types occurs within a few hours after aggregation is completed. It is difficult to avoid the conclusion that this spatial segregation must have co-evolved either with, or following, the evolution of the process of fruiting body formation and the geometry of the fruiting body. The chain of events could have been first, the transition of an aggregate into a fruiting body of a certain structure (a spore mass held aloft on erect stalk) and later, the appearance of an intermediate migratory phase in which the form of the fruiting body was anticipated. Migration would most likely be on account of an extension in time of the mechanism of amoeboid movement. However, morphogenesis in two other cellular slime molds displays features which indicate that this cannot be the whole story. In *Dictyostelium mucoroides*, stalk cells are formed and continuously released from a common pool consisting of all the cells in the migrating slug; in *Acytostelium* the stalk, which is acellular, is made up of material extruded from cells. Bonner (1982) treats this in some detail and goes on to speculate that patterning might be related to some developmental constraint imposed by the use of cAMP in chemoattraction.

It must be mentioned that the reasons for believing that cells in the slug communicate with one another go beyond the facts of integration (in a general sense) and pre-stalk—pre-spore patterning (in particular). The oldest and most convincing reason is that slugs belong to the class of regulative embryos; a fragmented slug gives rise to a diminutive but normally proportioned fruiting body (Raper 1940). Regulation was probably an adaptation in response to the selective pressure provided by physical fragmentation (Bonner 1982). Quantitative studies (Lokeshwar and Nanjundiah 1983) directed at a very early event in regulation—the regeneration of a new tip at the anterior margin of tipless fragments—indicate the involvement of long-range communication within the slug. How communication actually occurs is not known; the evidence from experiments on the rate of tip regeneration in genetically mosaic slugs is in agreement with, but does not prove, cell-to-cell relay (Lokeshwar and Nanjundiah 1985). If this result is confirmed, and if the same signal is responsible for both the rate of tip regeneration and long-range communication in the slug, one might conjecture that cell-to-cell relay during aggregation was a preadaptation which facilitated patterning in the slug.

7.2 *Tissue proportioning*

Under constant environmental conditions the number of spore cells in a fruiting body is in a more or less constant ratio to the number of stalk cells. The data of Stenhouse and Williams (1977), as analysed by Lokeshwar (1983), shows that 87·6 % ± 4·5 % of the cells in small fruiting bodies (630–3901 cells) form spores; the corresponding figure for large fruiting bodies (8404–18301 cells) is 87·1 % ± 4·8 %. Lokeshwar also makes a case for neglecting, in comparison with stalk and spore, the number of cells which form the basal disc (less than 1·5 % of the total); his own studies reveal no undifferentiated amoebae in the fruiting body. Two questions follow: (i) Why is the ratio of spores to stalk constant? (ii) Why do a certain fraction of cells—those that form the stalk—die and so sacrifice

their genetic potential? Wilson (1975) and Bonner (1980) cite stalk formation in *Dictyostelium* as an example of altruistic behaviour and invoke kin selection in order to explain it. The following simple argument (V Nanjundiah, unpublished results) makes this explicit. However, I suggest (see later) that 'group selection' is a more appropriate term than 'kin selection' to describe the phenomenon.

The critical assumption will be that, at least under the conditions obtaining when the present form of the fruiting body first evolved, an aggregate consisted of genetically identical cells. The problem facing this aggregate would have been to transfer all or part of itself elsewhere because food was finished at the site of aggregation. Migration of the entire aggregate towards food (not known to occur in *D. discoideum* slugs), might have been a possibility. The alternative, given that some of the cells had committed themselves to form spores, would have been to ensure that as many spores as possible dispersed and helped to give rise to viable amoebae. With an erect stalk and a spore mass on top, the distance of dispersal would depend on the elevation of the fruiting body and so on the number of stalk cells, but too high a stalk would mean that there would not be many spores left to propagate. An optimal balance would be reached at some intermediate value for the proportion of cells turning into spores. The actual ratio of spore to stalk at this optimal balance will depend on the mode of spore propagation—which could be by means of water, insects or other small animals, or wind. Purely as an illustrative exercise let us imagine that the spore mass is detached by a gust of wind and free-falls on account of its own weight (turbulence being neglected). The distance of dispersal will be the horizontal distance covered by the mass in the time it takes to fall to the ground. For a fruiting body consisting of N cells of which N_1 are spores and $N_2 = N - N_1$ make up the stalk, the height of the structure will be proportional to N_2. Then the time of fall, and so the distance covered, will be proportional to $\sqrt{N_2}$ or $\sqrt{N - N_1}$. Now, suppose that the availability of food, and so the probability of a spore germinating, is proportional to the distance of dispersion. A single spore, N of whose clonal descendants formed a fruiting body, would give rise to $N_1\sqrt{N - N_1}$ (times some constant) spores. It is easily seen that the product $N_1\sqrt{N - N_1}$ is a maximum when $N_1 = \frac{2}{3}N$, that is, at a fixed ratio of N_1 to N. Therefore according to this highly simplified model, $\frac{2}{3}$ of the cells in an aggregate should differentiate into spores and the rest into stalk if reproductive fitness is to be maximised. This conclusion still leaves us with the difficult problem of speculating on the possible mutational steps leading to proportioning. An intriguing but attractive possibility would be for proportioning to have evolved in parallel with patterning and spatial segregation of presumptive cell types, either in the late aggregate or in the early fruiting body.

8. Discussion

I have tried to provide adaptive explanations for some observed and inferred examples of communication between cells of *D. discoideum*. The sequence of evolutionary stages is suggested to have been as follows (table 1): sporulation of single spores → non-specific aggregation and sporulation in a group → aggregation by chemotaxis → relay of chemoattractant and oscillations → formation of the fruiting body with division of labour into stalk and spore → motility and patterning in the aggregate. Relay could have preceded chemotaxis instead of following it. The types of mutational events which could

Table 1. A hypothetical sequence in which the later mutational events enhance, but do not otherwise interfere with, the effects of the earlier ones. The initial situation is supposed to be one in which cells sporulate individually when starved; 'X' is a substance synthesised intracellularly in the course of sporulation. For simplicity X is assumed to be the same in each step; this would correspond to the roles played by cAMP in *D. discoideum*

Effect of mutation	Consequence	Possible reason(s) for increase in fitness
Starvation-induced leak of substance ('X') through cell membrane	X can enter a cell from outside	(a) Improved ability to sporulate; (b) Cell responds to deteriorating environment more rapidly than it would have
Tendency of cells to stick to each other	Cells form clumps	Improved prospects for (post-feeding) dispersal, but probably also a decrease in feeding efficiency
Stickiness inducible by X	Cells clump only after feeding is over	As above, but no decrease in feeding efficiency
Chemotaxis to X	Cells actively congregate	Eventually, better dispersal
X relayed from cell to cell	Aggregate size increases	As above

have led to each new stage have been conjectured. In this discussion I confine myself to making a few general points regarding these explanations.

Two questions which occur at the outset are, how reasonable are adaptive explanations in this context? And how reasonable are the arguments that have been advanced suggesting a specific form of selective force for the appearance of a particular phenotypic trait? The answers to both of these questions will necessarily be indirect and partial, and so not conclusive.

Cellular slime molds differ quite a bit in their life cycles, but aggregation and the formation of fruiting bodies consisting of spore masses held aloft stalks are common to all species. The reason why the details of development differ from one species to another could have to do either with differing adaptations to different selection pressures or to the same selective pressures leading to more than one adaptive peak. The possibility that the more "primitive" species are in the process of evolving towards the *D. discoideum* state cannot be ruled out, but appears to be unlikely. More relevant, the adaptive explanation itself might be incorrect or, at any rate, no less likely than a non-adaptive one (Gould and Lewontin 1979). It has already been mentioned that the phenomenon of oscillations is a possible candidate for a selectively neutral trait, even though a plausible adaptive explanation exists. The extracellular release of a cyclic AMP phosphodiesterase might be a second such candidate; arguments for and against the viewpoint that this is a nonadaptive (or maladaptive) trait will be found in the literature (Nanjundiah and Malchow 1976; Gerisch 1976; Darmon *et al* 1978). So also the widespread occurrence of regulation—the constancy in relative proportions of adult cell types—

might well have a purely developmental, as opposed to evolutionary, explanation.

All the same, in the absence of a specific rival hypothesis—based on selective neutrality, developmental correlations, even maladaptation—presenting itself, experience indicates that it is a useful exercise to see whether an adaptive explanation can be constructed at all and if it can, whether the construction is natural or forced.

A necessary (though not sufficient) condition for a trait to have evolved by selection amongst differentially adapted phenotypes is that it be subject to genetic control; and a "natural" construction of an adaptive explanation is one that makes use of plausible mutational steps. In the case of intercellular communication in *D. discoideum* both these requirements are satisfied. Consider the following properties of known mutations in *D. discoideum*: (i) an ability to differentiate without cell-to-cell contact (Kay and Trevan 1981) or normal aggregation (Ishida 1980); (ii) a failure to produce cAMP (Bonner *et al* 1969); (iii) a failure to respond to cAMP by chemotaxis (Bonner *et al* 1969); (iv) an inability to amplify and so relay an external cAMP signal, with the consequent absence of oscillations (Wurster and Bumann 1981); (v) a failure of normal stalk-to-spore proportioning (Morrissey *et al* 1981); and (vi) the absence of a correlation between the spatial patterning of the presumptive cell types in the slug, which can be normal, and proportioning in the fruiting body, which can be highly aberrant (Morrissey *et al* 1981; Amagai *et al* 1983). The intention is not to suggest that these mutations must represent a reversion to an evolutionarily primitive situation, but rather to indicate the plausibility of the origin and evolution of (present-day) wild-type genes with the properties demanded. It must be admitted that in one respect this could be a misleading argument: because selection acts on the genotype and not on single genes, or in other words because the relation between genes and phenotypic traits is normally not one-to-one, the life cycle must have evolved as a whole—and not, as in a sense we have imagined, in bits and pieces. It might appear that caution is all the more warranted when discussing *D. discoideum*, given the manifold effects that extracellular cAMP has on its development (Loomis 1982). Nevertheless, if the effect of a mutation is such as to influence one aspect of the phenotype more than any other, and if the mutation arises early enough in evolution for phenotypic effects to be significant, one can assume, as a good first approximation, that the components of (in this case) the communication pathway have been independently selected (table 1).

Even if we accept that adaptive explanations for the various features of intercellular communication we have considered might be valid, could the same end result have been achieved by other selective forces? The forces we have taken into account have been (a) selection for an improved efficiency of sporulation and (b) selection for dispersal. The assumption which runs through our entire analysis is that spatially contiguous, genetically identical amoebae form the units on which selection can act. Bonner (1967) starts with the opposite assumption—that in nature cells of diverse genotypes commonly come together in an aggregate—and comes to quite different conclusions regarding the function of aggregation. One is that aggregation serves as a partial substitute for sexuality, because the nuclei of the many genotypes gathered together in one spore mass have the potential to be redistributed as new combinations. He also suggests that genetically diverse cells living in close proximity might have developed mutual deficiencies which could have been overcome by aggregation. There are hints from the literature that two other selective agencies, predation and the occurrence of symbiotic or commensal organisms, might favour aggregation and fruiting. Waddell (1982) has reported the isolation, from bat guano, of a species of predatory cellular slime

mold. When tested in combination with a number of other species, the predator is able to delay the morphogenesis and (very probably) consume the amoebae of the prey species. Ellison and Buss (1983) have found a case of synergism between field specimens of *D. mucoroides* (a species similar in many respects to *D. discoideum*) and the fungus *Mucor hiemalis*: the presence of the fungus induces stalk formation in *D. mucoroides* and fungal extracts advance rate of fruiting in this and other species (though not in a laboratory strain of *D. discoideum*, which conceivably had already been selected for very rapid development). The stalkless variant of *D. mucoroides*, which forms in the absence of the fungus, aggregates normally but neither forms a slug nor migrates. The aggregating mass rounds up and differentiates straightaway into a mixture of spores and dead amoebae. While it is not possible at present to seriously consider which features of communication in *D. discoideum* might have been selected as adaptations to predation (to discuss commensal living is even harder), we can imagine that anything which lowered the risk of predation must have been strongly favoured. So, for instance, both the tendency to form fruiting bodies as well as an increase in the overall rate of development would have helped (rate, because in a communication network the same set of events can have different effects on fitness if the temporal relationships of the events differ (Bonner 1982)). Both environmental conditions (Schindler and Sussman 1977) and the genotype (Kessin 1977) can influence the life cycle of *D. discoideum* by affecting the speed of development. Similarly, using a substance which was harmful to a predator as an agent of communication or using a misleading signal (imagine that cAMP is an alarm pheromone for some predator) would clearly improve the prospects of survival.

It is important to note that the speculations in this paper refer only to the first steps in the evolution of pathways of communication in *D. discoideum*; what one finds today must be the result of many further steps of refinement. The most important refinement was probably the origin of receptors (Newell 1977). Receptors would enable signals to work their effect without having to enter a cell, allowing for increased efficiency and specificity. Also, the same substance used as a signal could then serve different ends, depending on which subset of receptors it happened to interact with at any given time. Other refinements could result in the signal becoming ritualised as has happened in higher animals (particularly in the case of courtship signals; see Wilson 1975). The signalling pathway would pick up successively arbitrary modifications and develop into a link between source and receiver which is highly reliable and specific but displays few clues as to how it could have evolved. Whatever be the extent to which the primitive signal has become ritualised, if the view adopted here is correct it must follow that all the conjectured "signal substances" must be components of the cell's internal response to a deteriorating environment. Haldane (1955) has asserted as a general principle that a signal is always a sign of a physiological or psychological condition within the sender; what I am suggesting is that in the present context the signal is so to speak the condition itself. To take a specific example, the choice of cAMP as a chemoattractant would not be totally arbitrary (in the sense that human language is said to be), but would be related to a role played by cAMP in the internal metabolism of a starved cell, even if the role were that of a waste product to be discarded. This is a testable statement.

Cellular slime molds are social organisms, and the origin and continued evolution of sociality all the way to the extreme altruism displayed by stalk cells must surely be a consequence of, in part, the high degree of genetic relatedness, or even genetic identity, of the amoebae in an aggregate (Wilson 1975; Bonner 1982). Nevertheless, I believe the

term 'group selection' is better suited to describe the situation than 'kin selection'. Kin selection is usually invoked when an individual sacrifices part of its potential reproductive fitness for the benefit of another individual related to it by common descent (Hamilton 1964). In the slime mold case, leaving aside the suicide by presumptive stalk cells for the moment, each of the adaptations we have considered has the characteristic that it is adopted by every member of the group; therefore its cost or benefit is the same for every member. It is the group which must succeed or fail, in comparison with other groups, with these adaptations. Even if this is not true at any one time because an aggregate consists of more than one genotype, it must be a factor which comes into play once the less fit genotypes have been eliminated (we take it of course that the genotypes differ in respect of the adaptations referred to in this paper). An implicit assumption is that all pre-fruiting cells are functionally identical: if this were not so, 'kin selection' might well be an appropriate description. An important example of functional non-identity would be if, for example, only the future stalk cells were to release the chemoattractant.

What if a cell belonging to a cheater genotype fortuitously gets into an aggregate, a genotype which responds to external signals with the rest of the group but does not produce the signal itself? Armstrong (1984), in analysing the survival of "cheaters" which never form stalk cells, suggests that division of labour would not be an evolutionary stable strategy under conditions which favour such cheaters. I feel this side-steps the basic problem, which is to explain why division of labour is observed even though a "cheater" (of whichever sort) is always at an advantage whenever it arises. The correct answer, according to me, is that the frequency of the cheater genotype will increase from one generation to the next until an aggregate consists of so many cheaters that the strategy does not pay any more. If the cheater only responds to signals released by the wildtype but does not produce them itself, at some stage the signal strength will be so weak essentially everywhere except at the locations of the signalling cells that viable aggregation will simply not occur. If the cheater always differentiates into spores the final state in evolution will be an aggregate consisting only of mutant spores; in line with the assumption under which we have operated the spores will be unable to disperse and therefore to survive. The cheater genotype increases in fitness but eventually drives the group to extinction. Therefore the normal division of labour is best described as a case of group selection.

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Ground-feeding migratory songbirds as cellular slime mold distribution vectors

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A NATURALLY OCCURRING DEVELOPMENTAL SYNERGISM BETWEEN THE CELLULAR SLIME MOLD, DICTYOSTELIUM MUCOROIDES AND THE FUNGUS, MUCOR HIEMALIS[1]

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HETEROCYTOSIS IN CELLULAR SLIME MOLDS*

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Evidence for Mitochondrial DNA Polymorphism and Uniparental Inheritance in the Cellular Slime Mold *Polysphondylium pallidum*: Effect of Intraspecies Mating on Mitochondrial DNA Transmission

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A predatory slime mould

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Evolution

Somatic cell parasitism and the evolution of somatic tissue compatibility

(chimera/*Dictyostelium mucoroides*/frequency-dependent selection/fusion rejection/self/not self)

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EVOLUTIONARY STRATEGIES AND DEVELOPMENTAL CONSTRAINTS IN THE CELLULAR SLIME MOLDS

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Why Don't Cellular Slime Molds Cheat?

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The evolution of communication and social behaviour in *Dictyostelium discoideum*

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Altruism, selfishness, and heterocytosis in cellular slime molds

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Evolutionarily Stable Stalk to Spore Ratio in Cellular Slime Molds and the Law of Equalization in Net Incomes

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Cellular slime molds: why and how to become pluricellular?

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BEHAVIOURAL RHYTHMS AND THEIR MECHANISMS

BY

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Biological Rhythms and Their Mechanisms

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The subject that is concerned with the study of organisms in relation to their distribution and adjustments to space is called ecology. The subject that addresses itself to study of organismal adaptations to the rhythmic environment is now called Chronobiology. Unicellulars (except bacteria and blue green algae), plants, animals and humans expresss their adaptations to the periodic universal forces by means of the various biological rhtyhms we know.

Biological rhythms vary in period from a few milliseconds as in the firing of nerve cells of animals to an entire calendar year, as in flowering of some trees and plants, reproduction in animals etc. We shall consider only those biological rhythms which match (and are entrained by) environmental rhythms. Three major classes of biological rhythms are:

i) The daily 24 hour rhythms (circadian) (circa-about; dies - a day)

ii) The lunar daily 24.8 hours and lunar monthly 29 day rhythms

iii) Annual (circannual) rhythms

Circadian rhythms possess the following basic features:

1) The rhythm persists in LL or DD and constant temperature

2) In persisting, the period deviates from the strict 24 h periodicity of the environment.

3) The Q_{10} is close to 1 (unity). Many circadian rhythms have now been reported:

A few examples:

Fungus Neurospora crassa - Spore formation

Alga Chlamydomonas - phototaxis

169 Dinoflagellate Gonyaulax - bioluminescence

Fruitfly Drosophila - eclosion (emergence from puparia) rhythm

Bean plant Phaseolus - leaf movement

Touch-me-not plant Mimosa - leaf movement

Many birds and rodents - locomotor rhythms

Human beings - sleep-wakefulness and temperature rhythms:

Tidal rhythms

The tidal habitat differs from all others by changing rhythmically with the phases of the moon. The result of the moon's influence on the tides is that all costal areas include three rather different habitats. The important habitats are the lower zone almost fully terrestrial and there are animals that exploit both these features. A famous example is the grunion fish Leuresthes tenuis whose males and females swarm up Californian beeches to spawan, on the crest of high spring tides. There they first bury their eggs, leaving them to develop in the warm sand until the next high spring tides wash them out to hatch in the open sea.

There are several well documented 29 day rhythms. These are clearly coupled to the moon's phases. They are found among invertebrate organisms, not only in marine species but also in terrestrial species. For example, the emergence of some may flies occurs in a peak just after the full moon.

Annual rhythms

The ability to measure the duration of daylength is photoperiodism and it is certainly used by many organisms. For example, the carpet beetle Anthrenus verbasci shows a persistent circannual rhythm of adult emergence when kept for years in constant DD. Certainly species such as deer (antler growth) and many species of birds (migration, reproduction etc) exhibit circannual rhythmicity and respond to changes in daylength. The circannual rhythm presumably makes the physiology of the animal, such as its production of sex hormones, change at roughly the right time of year so that it can correct its seasonal response when the appropriate daylength arrives.

Mechanisms

Three possible theories have been proposed for how the basic oscillator might work. The first theory places the clock mechanism in the cell's nucleus. The theory proposes that the circadian period is measured out by continuous reading of the genetic code along a very long loop of DNA in a chromosome. This idea has several attractive features and is supported by some experimental evidences, but it also has some flaws.

The second theory assumes that the clock has its roots in the organism's oscillating biochemistry. The problem is that it is theoretically difficult to construct a 24 hour clock from the known biochemical oscillations because these all have a high frequency with the time-span of each cycle measured in seconds or, at best, in minutes. The theory thus proposes that circadian rhythmicity is generated by an interaction of many of these high frequency chemical oscillations in such a manner that one inhibits another to create a net slow output. As yet, however, there is no concrete physiological evidence that this actually occurs.

The third theory of the biological 'escapement device' envisages that the circadian oscillation occurs as a result of slow changes in the membranes within a cell. As a result of these changes, which affect the permeability of the membranes, ions such as potassium leak passively through a membrance from one part of a cell to another, and are then actively pumped back again in the reverse direction when a particular imbalance in their concentration is reached. Moreover, while most chemical treatments either have no effect on circadian clocks or put them permanently out of commission, chemicals such as alcohol and heavy water, which are known to alter the permeability of cell membrane actually slow down or phase shift circadian rhythms in both plants and animals. This implies that these substances are directly affecting the basic oscillators contained in the organism. So it looks as though the membrance clock does have a sound experimental basis.

The brain of an insect, such as housefly, is the largest nerve centre in its body. Groups of brain cells seem to act as circadian clocks, which in some insects have been found in the optic lobes on either side of the brain.

The pineal gland at the top of bird's brain is probably the location of the clock controlling the bird's circadian rhythms. This 'third eye' is not used for seeing but it, nevertheless, sensitive to light. Its removal makes the bird's behaviour

171 arrhythmic. On transplantation the recipient assumes the schedule of the donor. The pineal seems to be a circadian clock and also a rhythmic source of a behaviour regulating hormone (melatonin).

The daily activity rhythms of mammals and presumably, therefore, of man are driven by a clock in the hypothalamus-a key area of the mid-brain that controls body functions such as temperature, rate of metabolism, appetite and thirst. The actual clock cells are in two tiny groups called the suprachiasmatic nuclei.

In Drosophila a period mutant (per^{O}) has been reported. This involved a single locus on the chromosome undergoing mutation which resulted in the absence of the circadian rhythm in the locomotor activity. The mutations, depending on kind resulted also in longer (per^{l}) or shorter (per^{s}) periods. There is now a good case for the genetic basis for circadian rhythm.

Recent work based on DNA sequencing of the 7217 bases in the biologically active segment of per locus DNA that encodes for the 4.5 Kb RNA species, supports the notion of long transcript required for clock function.

DNA homologous to the per locus has been found in a number of vertebrates. Thus, the tandemly repeated sequence forming of portion of the 4.5 Kb per transcript was found to be strongly homologous to mouse DNA and to a lesser extent to DNA in chicken and man. Cloned DNA from mouse and Drosophila were related by long, tandem repetitions of the sequence ACNGGN (N-purine). This sequences at the per locus is predicted to code for poly (Thr-Gly) tracts as long as 48 aminoacids in length.

The field of chronobiology has been the interest of macro level studies from scientists working on animal behaviour. As seen above some work has gone on in understanding the molecular basis of the rhythmicity. However, in general there is a gap between genetics and biochemistry of circadian rhythm and the underrstanding of its dynamic functioning.

ESTIMATING ANIMAL ABUNDANCE BY LINE TRANSECTS

BY

ULLAS KARANTH

LINE TRANSECT METHOD OF CENSUSING ELEPHANTS IN NAGARHOLE NATIONAL PARK

K Ullas Karanth

My study on censusing of elephants, using the line transect method, was conducted in Nagarhole National Park in Karnataka state. This was part of a larger project on population structure, density and biomass of large herbivores and predator-prey relations.

Using available maps along with my own field surveys, I determined the extent and proportional availability of the three major habitat types (Fig-I). The habitat stratification and transect lengths sampled have been given in Table - I.

Line transect method was judged to be the most appropriate method since my objective was to derive estimates of absolute densities rather than density indices. The method followed was that of Burnham *et al.* (1980). The method generates reasonably unbiased and precise density estimates if certain underlying assumptions are satisfied.

My objective was to obtain density estimates in each major habitat type, and for the overall study area by pooling the data. The 8 permanently marked transects covered a total distance of 19.3 km.

Vegetation modifications on the transect was minimum to avoid attracting or repelling animals. The transects did not follow major topographic features, streams, or roads. Furthermore, the populations being sampled were motile. Thus the overall sampling system seemed to meet the stratified random sampling criteria as discussed by Eberhardt (1978) and Burnham *et al.*(1980).

Each transect was walked twice per month between July 1986 and July 1987. Uniformity of coverage was ensured among the 3 seasons by sampling each transect 8 times per season. Because the study species were most active in the mornings and evenings, the transects were walked in two time blocks, between 0600-0900 hr. and 1600-1900 hr. Each transect was sampled equally during mornings and evenings.

I walked the transect accompanied by another trained observer at a uniform pace of about 1.5 km/hr. For each animal group sighted I recorded the number, sighting distance and sighting angle. The distance and angle were measured to the estimated geometric centre of the animal group. Other auxiliary information such as time, age-sex composition of the group and location was also recorded.

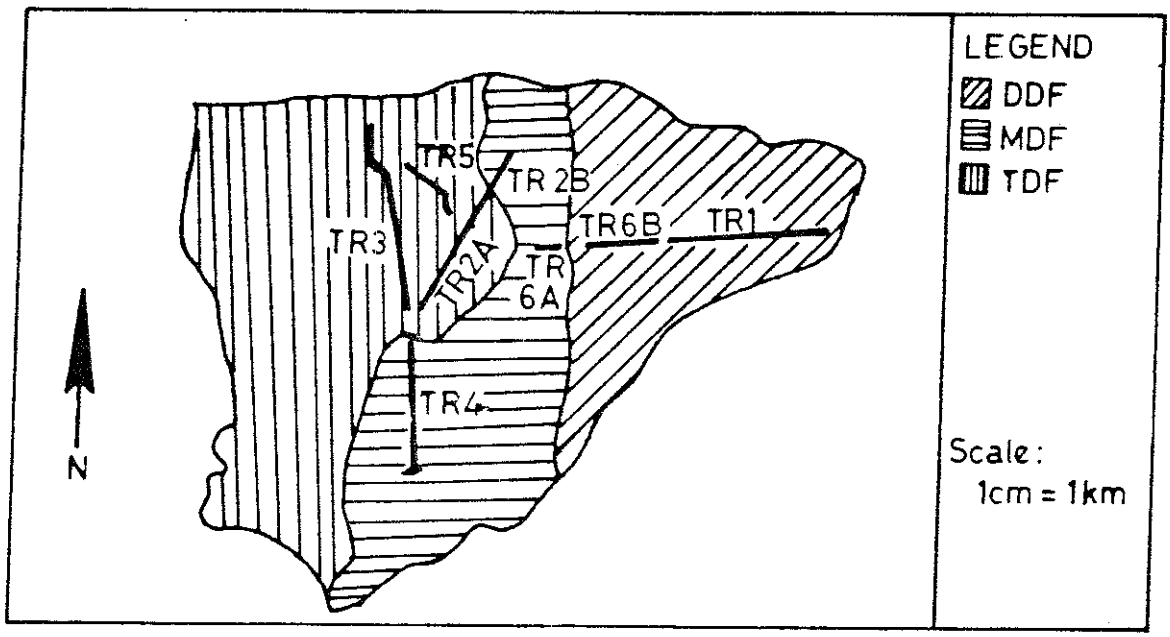
As suggested by Burnham *et al.* (1980) the sightings resulted from both active searching where we saw the animal first and passive detection when the animal flushed before we saw them. For passive detection I recorded measurements to the initial location of the animals, which could usually be judged from movement of the disturbed vegetation.

Undetected movement of animals away from the transect in response to the observer is considered to be the most serious field problem in applying the line transect models. I was interested in knowing if such movements caused serious underestimates of densities derived from my walking transects. To address this question, I also conducted some line transect sampling using a trained riding elephant as a mobile platform for 2 observers and myself. The study indicated that the species are less disturbed by elephants than by people on foot. Therefore, I assumed that if any serious bias from undetected movement occurred in my walking transect, the density estimates derived from them would be significant underestimates when compared to estimates from elephant back transects. The estimates of group densities derived from these elephant back sampling were compared with estimates from 27 walking replications on the same transect during the same months. No significant difference was found between the density estimates got from transects done on foot (1.79 ± 0.57) and the transects done on elephant back (1.97 ± 0.93).

The mean density of the population and its standard error were calculated using computer program TRANSECT (White 1987).

The results of this study have been summarized in Table-II.

Fig 1
Map of study site showing the transects numbered TR1 to TR6



DDF - Dry Decidous Forest
MDF - Moist Decidous Forest
TDF - Teak plantation Dominated Forest

Table 1

Habitat stratification and transect length sampled

Habitat type	Area sq. km.	%	Transect length (km)	%	Location, transect no.
DDF	31	31	129.6	28	TR 1, 6B
MDF	29	29	108.0	23	TR 2B, 4, 6A
TDF	40	40	225.5	49	TR 2A, 3, 5
Total	100	100	463.2	100	-

Table II

Density estimates of elephants in the different vegetation types

Parameter	Habitat type DDF	MDF	TDF	Overall
Number of groups sighted	9.00	9.00	28.00	46.00
Density of elephants (Groups/sq. km.)	0.49	1.32	1.18	0.92
Standard error of groups / sq. km	0.17	0.60	0.34	0.20
Mean group size	4.40	3.79	3.25	3.58
Density of individuals / sq. km.	2.16	5.00	3.83	3.29
Standard error of individuals/sq. km.	0.76	2.34	1.18	0.73
Coefficient of variation of indivdual density (%)	35.06	46.70	29.17	22 35
95% confidence limits	0.7-3.7	0.5-9.6	1.6-6.0	1.9-4.7

Note : The calculations were based on Fourier Series Analysis

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CENTRE FOR
ECOLOGICAL SCIENCES

BEHAVIOURAL ECOLOGY AS A BASIS FOR MANAGEMENT DECISIONS

BY

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The Management of Large Mammals in Relation to Male Strategies and Conflict with People

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ABSTRACT

Many large mammals such as elephant, rhino and tiger often come into conflict with people by destroying agricultural crops and even killing people thus providing a deterrent to conservation efforts. The males of these polygynous species have a greater variance in reproductive success than females, leading to selection pressures favouring a 'high risk–high gain' strategy for promoting reproductive success. This brings them into greater conflict with people. For instance, adult male elephants are far more prone than a member of a female-led family herd to raid agricultural crops and to kill people. In polygynous species, the removal of a certain proportion of 'surplus' adult males is not likely to affect the fertility and growth rate of the population. Hence, this could be a management tool which would effectively reduce animal–human conflict, and at the same time maintain the viability of the population. Selective removal of males would result in a skewed sex ratio. This would reduce the 'effective population size' (as opposed to the total population or census number), increase the rate of genetic drift and, in small populations, lead to inbreeding depression. Plans for managing destructive mammals through the culling of males will have to ensure that the appropriate minimum size in the populations is being maintained.

INTRODUCTION

Many large mammals such as the Asian elephant *Elephas maximus*, the African elephant *Loxodonta africana*, the Great Indian rhinoceros

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Rhinoceros unicornis and the tiger *Panthera tigris* come into conflict with people by destroying agricultural crops, domestic livestock and even killing people. This creates considerable antipathy among people living on the periphery of nature reserves and is a deterrent to conservation efforts.

The Asian elephant, for instance, is estimated to damage crops worth US$0·5 million and kill 30–50 people annually in southern India (Sukumar, 1985, 1989). In the Indian state of West Bengal a small population of about 150 elephants was responsible for killing nearly 50 people during 1988 alone and causing considerable damage to crops (D K. Lahiri Choudhury, pers. comm.). In peninsular Malaysia the economic loss to a single agency (Federal Land Development Authority) from destruction of oil palm and rubber plantations by elephants is estimated to be US$20 million per year (Blair *et al*., 1979). The African elephant similarly comes into conflict with agriculture (Allaway, 1979). The Indian rhino may damage the entire crop in some villages in the vicinity of Royal Chitwan National Park, Nepal (Mishra, 1982). In the Sundarbans mangrove region of India and Bangladesh, an average of 57 people were killed each year by tigers during 1975–84 (Khan, 1987; Sanyal, 1987).

Although it may be impossible to eliminate conflict totally, except by exterminating the offending animals, there is no doubt that this problem must be minimized if conservation efforts are to succeed in developing countries facing harsh socio-economic realities. Large, potentially destructive mammals need to be conserved by a combination of various management strategies. For instance, electrified human dummies have been used successfully in reducing the incidence of man-eating by tigers in recent years (Sanyal, 1987; Rishi, 1988) and high-voltage electric fences have reduced depredation of crops by elephants in peninsular Malaysia (Blair *et al*., 1979). In this paper, I outline another approach to reducing conflict, taking into consideration social organization, behavioural differences between the sexes and demographic processes of the species.

SOCIAL ORGANIZATION, BEHAVIOUR AND CONFLICT WITH PEOPLE

Many large mammals, including those mentioned above, are polygynous species with marked sexual dimorphism. The males attain a larger adult body size than the females and may have secondary sexual characters such as horns (Clutton-Brock *et al*., 1982). There is strong selection for these characters in the male since they enhance its ability to succeed in male–male competition for females. In polygynous species the males have a greater variance in reproductive success than females. It follows from this that

selection would favour a 'high risk–high gain' strategy which promotes reproductive success (Trivers, 1985). Differences in risk-taking behaviour between the sexes may become manifest at an early age, as in the elephant seal *Mirounga angustirostris* (Reiter *et al*., 1978).

This inherent risk-taking behaviour may also bring the male of the species into greater conflict with people. A study of the Asian elephant's interaction with people in the Chamarajanagar and Satyamangalam forests of southern India illustrates this point (Sukumar, 1985, 1989, 1990; Sukumar & Gadgil, 1988). Although both male and female elephants raid crops and the risk of death during a raid is the same for both sexes, an adult male elephant entered cultivation about six times more frequently (49 nights in a year on the average) than did a member of the female-led family herds (8 nights per year), obtaining a higher proportion (9·3%) of its total diet from crops compared to the latter (1·7%). Raiding itself is related to the higher palatability and nutritive value of cultivated crops compared to wild plants (Sukumar, 1989, 1990). Clearly the male elephant is more willing to take risks in obtaining the extra nutrition which could be translated into better growth, adult body size and a successful expression of musth (or rut), all of which may mean an enhanced reproductive success (Sukumar & Gadgil, 1988).

Not only does an adult male elephant raid six times more frequently, but each time it enters a cultivated area it consumes more than twice as much crop *per capita* than does a member of a family herd because of its larger body size and requirements. An adult bull weighs about 4000 kg compared to 1750 kg of an average herd member (Sukumar *et al*., 1988), and consumes on average 1848 kg (dry weight) of crop plants per year compared to only 139 kg by a herd member—or a level of damage 13·3 times higher (Fig. 1). Further, an adult male is more prone to damage crops such as coconut (they can push down large coconut trees more easily), which are economically more valuable than cereals or millet. The net result is that an adult male elephant damages crops worth about US$600–700 compared to only US$30–35 per year by a family herd member, a 20-fold difference in economic terms (Sukumar, 1989).

The relative proportion of total loss of crops due to adult males and herds would, of course, depend on the population structure or proportion of these categories. In the southern Indian study area, in which adult males (>15 years) constituted about 7% of the elephant population, the adult males caused 62% and herds 38% of the total economic loss during 1981 (Sukumar, 1989). Figure 2 depicts the relative loss due to adult males and herds for differing population structures with 20-, 10- and 5-fold differences in *per capita* damage.

A variety of mammals including primates, rhino, deer and wild pig are known to damage crops. Mohnot *et al*. (1981) observed that all-male bands

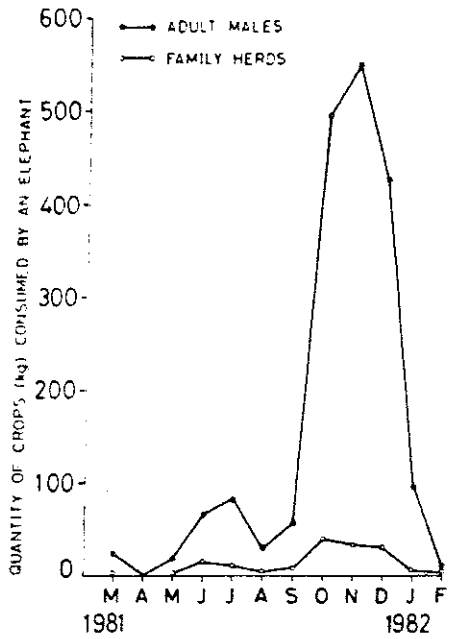

Fig. 1. Quantity of crops in kg (dry weight) consumed by an average adult male elephant or an average individual in a family herd during different months

of Hanuman langur *Presbytis entellus* may raid orchards and gardens more readily compared to the bisexual troops. I do not know of comparable observations of differences between the sexes of other species in raiding crops, but would predict a similar pattern of greater risk-taking by the male in polygynous species.

There may also be sex-biased patterns in manslaughter by animals. Records of manslaughter by elephants in southern India show that over 80% of the killings were by male elephants above 10 years in spite of the fact that they constitute less than 10% of the total population (Sukumar, 1989). Nearly half the incidents occurred inside cultivated areas when male elephants came to raid crops.

There may be some exceptions to this pattern. For instance, a few herds of elephants comprising some 40 individuals dispersed from their original habitat to a new area in southern India during the mid-1980s (Sivaganesan & Bhushan, 1986). These have been responsible for considerable damage to crops and over 30 human deaths, many of them due to the ignorance of local people unaccustomed to wild elephants. A similar situation has arisen in central India where about 60 dispersed elephants have been causing similar havoc to crop and human life (unpublished and newspaper reports).

Some observations on human killing by tigers also suggest that the male may be the worse offender, although the evidence is not that conclusive. Ten

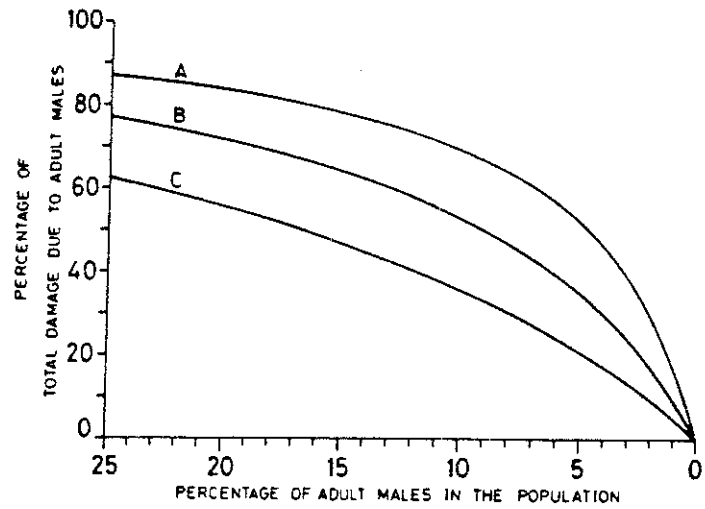

Fig. 2. Percentage of total economic loss to crops caused by adult male elephants as a function of differing percentages of males in the total population assuming (A) 20-, (B) 10- and (C) 5-fold difference in *per capita* damage by an adult male compared to an individual in a family herd

out of 13 man-eaters recorded by Hendrichs (1975) in the Sundarbans of Bangladesh were males and these accounted for 86% of the victims Similarly, most of the human kills in the Royal Chitwan National Park, Nepal, since 1980 could be attributed to three male tigers (McDougal, 1987). Apparently these male tigers were displaced from their former territories by rival males and hence moved to the periphery of the park where they claimed their human victims During an eight-year period (1980–87), however, four male and three female tigers were involved in man-eating or life-threatening situations in the region (Mishra *et al.*, 1987). Corbett (1944, 1954) describes six male and five female man-eating tigers When we consider the fact that in wild populations the adult sex ratio of male to female tigers is likely to be 1:3–4 (Sunquist, 1981), the above observations also seem to support the hypothesis that the male tiger is more likely to come into conflict with people The Champawat man-eater (Corbett, 1944)—which is reputed to have killed 436 people—was, however, a female

CULLING OF MALES, SKEWED SEX RATIOS AND DEMOGRAPHY

If the male of a polygynous species is involved in a more serious conflict with people than the female, one way of managing such potentially destructive species would be to selectively remove the offending males from the

population. This would have a significant effect in reducing conflict, while making the least impact on the population demography. Thus, culling an adult male elephant would be equivalent to removing a family herd of 20 elephants in terms of economics of crop damage. Additionally, the loss of a male in a polygynous species would make much less impact on the population fertility and growth rate than would the loss of a female.

The demography of a population depends essentially on the female population size and the female vital rates—age at first reproduction, size of litter, interval between births, age of reproductive senescence and mortality. In a polygynous species such as the elephant, the male merely contributes the sperm, expending no further energy towards rearing the offspring. In that sense, there are usually 'surplus' males which can be removed without affecting the fertility of the population, since the remaining males can usually ensure that all available females successfully conceive. Of course, if the sex ratio becomes too female-biased there would not be sufficient males for mating with available females, resulting in a decline in fertility.

At this time we do not have sufficient information on what the 'critical' adult sex ratio is for a polygynous species; this would vary from one species to another and among different populations of a species depending on spatial distribution, density, seasonality in breeding, duration and periodicity of oestrus in females, reproductive behaviour and so on. It may be possible, however, to give an upper limit to the sex ratio that should be maintained to ensure 'normal' fertility in a population. The elephant populations of southern India have the most skewed sex ratios in Asia, because of high male mortality from ivory poaching (Sukumar, 1986, 1989). In the southern Indian population studied in detail, the adult male-to-female ratio of 1:5 still ensured an inter-calving interval of 4·7 years (birth rate of 0·21/adult female/year) which compares favourably with the most fertile African elephant populations having a positive growth rate (Douglas-Hamilton, 1972; Laws *et al.*, 1975; Sukumar, 1989). The operational sex ratio in this population at a given time would have been less skewed, in the range of 1:2 to 1:3, since a certain proportion of female elephants would be pregnant or in lactational anoestrus.

Because poaching of male tuskers continued, their proportion in the population declined further, resulting in an adult male-to-female ratio of about 1:8 by 1987 (Sukumar, 1989). The consequences of this skewness on the demography will be known only during the coming years. Culling of male elephants as a management policy to reduce conflicts may not be justified in southern India, except in rare cases, because poaching has already taken a heavy toll on the males. In fact, this has already significantly reduced crop damage. Many of the villages in the Chamarajanagar and Satyamangalam region which suffered heavy damage to crops during 1981 reported a sharp decline in depredation by 1988 (personal observation).

However, most of the other Asian elephant populations can be expected to have a less skewed sex ratio. This would depend on the frequency of tuskers in the male segment of the population and the pressures of ivory poaching. Among Asian elephants only the males may possess tusks (unlike the African elephant in which both sexes have tusks). Here again, there is a wide range in the proportion of tuskers in the male segment of different populations. In southern India over 90% of the males are tuskers, in northeastern India tuskers and tuskless males are roughly in equal proportion, while in Sri Lanka less than 10% of the males possess tusks. Populations in which a large proportion of males are tuskless face little or no threat from ivory hunters. Consequently, the sex ratio in these is likely to be the least skewed, for instance one adult male for every two adult females, with adult males constituting 16–23% of the total population, as in some regions of Sri Lanka (McKay, 1973; Kurt, 1974). Culling of crop raiding or 'rogue' males from such populations can be an effective management measure to reduce conflict. The culling need not necessarily be killing of the males, at least in Asia, although this may have to be done in the case of extremely troublesome animals. Traditions of domesticating elephants are ancient in Asia. Some of the culling can simply be by capturing them, using chemical immobilization techniques, for domestication.

SEX RATIOS, EFFECTIVE POPULATION SIZE AND MANAGEMENT

There is one more aspect to be considered, that of the genetic consequences of a skewed sex ratio. If too few males do all the breeding, there could be problems of inbreeding depression, especially in small populations. The effective population size N_e (as opposed to the total population or census number N) is equal to $4N_mN_f/(N_m + N_f)$, where N_m and N_f are the number of breeding males and females respectively (Franklin, 1980; Frankel & Soulé, 1981). The more skewed the sex ratio the lower would be the effective population size. It has been suggested that inbreeding should be kept below 1% per generation, which means that an effective population size of at least 50 individuals should be maintained, for short-term viability of a population. For long-term viability, in terms of maintaining evolutionary potential, an effective population size of 500 has been suggested (Franklin, 1980; Frankel & Soulé, 1981).

Although these figures of 50 and 500 are still theoretical and may not apply to wild populations (Soulé, 1987), these are the best available estimates for maintaining genetic viability of a population. Management of destructive mammals through selective culling of males should ensure that an appropriate effective size is maintained in the population. This would

necessitate a knowledge of size and structure of the population to be managed. There are few Asian elephant populations which have effective population sizes of over 500 breeding individuals. Most of those in fragmented habitats may have to be managed only from a short-term perspective, or as metapopulations through exchange of individuals in order to maintain genetic variation (Santiapillai, 1987; Sukumar, 1989). Many African elephant populations, however, are still relatively large enough to allow a certain reduction of the male segment without any genetic problems arising (see Douglas-Hamilton, 1987, for population sizes) although the recent spate in ivory poaching may have considerably skewed the sex ratios (Poole & Thomsen, 1989).

In the case of endangered species such as the tiger, an effective population size of even 50 is doubtful in most populations. This would severely limit the manager's options in dealing with man-eaters, especially if these cannot be reliably identified. Rhino populations, both in Africa and in Asia, are even more endangered. Only two populations of the great Indian rhino, one of about 1000 at Kaziranga National Park in Assam and the other of about 300 at Royal Chitwan National Park in Nepal, are of viable size. Decisions of culling the males would be even more difficult to make for rhino populations, although capture for translocation to another area may be acceptable.

CONCLUSIONS

Management practice has not always been based on sound ecological principles. For example, the northeast Indian states of Assam and Meghalaya were permitted to capture 200 elephants, mostly as family herds, during the mid-1980s as a crop protection measure. The same results could have been achieved by capturing 10–15 male elephants, while at the same time ensuring a near-normal demographic growth of the population. The exception to selectively culling only males would obviously apply to stray, dispersed herds which may have to be removed.

Lest it be misunderstood that I am advocating the culling of mammals as a routine management policy, let me emphasize that culling should be the last resort of a manager. Often the choice may be between losing an entire population of a species in deference to the wishes of people who have suffered its depredation or reducing conflict through culling. Anti-conservation feelings run high among people in the periphery of many protected areas. Whether one likes it or not many elephants are being electrocuted or shot in defence of crops, and tigers poisoned. This is a reality that conservationists and managers have to keep in mind when dealing with

problem areas. If a decision to cull has been taken, it is usually better to selectively cull the male of the species

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BEHAVIORAL STUDIES AS A TOOL FOR VERTEBRATE CONSERVATION

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Key words: behavioral study, vertebrate, conservation, exploitation, preservation, captive breeding, hybridization, raising, pest control, diseases, habitat

INTRODUCTION

Can studies of animal behavior help solve conservation problems? Having been set this question by the organizers, I will draw upon case studies to answer, yes, there are many different categories of conservation problem to which behavioral ecology has contributed usefully. I define conservation problems as those where a biologist's expertise can help resolve difficulties at the often tumultuous interface between men, wildlife and the environment, and embracing everything from preservation to extermination. A subsidiary message of this paper is that there are plenty of academically exciting questions which have practically useful answers, but the marriage of theory and practice is all too often unfulfilled (Kareiva 1989; Macdonald and Smith 1991)

The following sections illustrate some of the categories of problem to which behavioral knowledge has proven helpful

Exploitation: Although no longer operational, the harvest of Southern Elephant Seal, *Mirounga leonina*, from South Georgia remains one of the best examples of rational and sustainable use of wildlife (reviewed by Bonner 1989) The breeding system of these seals facilitates harvest: a widely-spaced, feeding population aggregates on protected beaches to breed, females tightly packed in the harems of males Furthermore, in early spring breeding animals are rotund with the fat that made them valuable. In the 1950s, R. Laws contrasted the behavior of elephant seals in populations that were, or were not, harvested. His observation, shortly after the annual quota for South Georgia had been set at 9,000 males, demonstrated that: (i) the mean age of males in the culled population was 6.6 yr and none reached 10 yr, whereas elsewhere the mean age was 10 yr and some survived more than 20 yr, (ii) the age and thus size of breeding males affected the breeding system: younger males could not monopolize so many females, and (iii) age of first reproduction for females was 3 yr in culled population but 4–7 yr elsewhere, probably because of the males' competition for food with smaller females. Laws concluded that the harvested population was on the point of collapse, and used his observations to model the population characteristics that would give harvesters the Maximum Sustainable Yield: he suggested an annual harvest of 5,842, culling only males of >3 5 m, and sparing every tenth one to inseminate females This industry ended in 1964 (due to the collapse of the associated whaling industry from overexploitation), with Laws's prediction closely on target

Preservation: An important facet of preservation is captive breeding and reintroduction Case studies include the Golden lion tamarin, *Leontopithecus chrysomelas*, (Kleiman in press) and the classic case is the Arabian oryx, *Oryx leucoryx* (Stanley Price 1990). In 1959 there were 100–200 oryx in Saudi Arabia, and slightly more in Oman. By 1972, due to overhunting, they were extinct in the wild In 1976 the Sultan of Oman set up a captive breeding herd, and Stanley Price (*op. cit.*) describes how studies of their social behavior and movements (indicating the importance of local knowledge in finding flushes of grass produced by localized rainfall) underpined the strategy for reintroduction which culminated in the births of the

first wild calves in 1980

Dowell (1990) has recently demonstrated the behavioral complexities of captive breeding. In Great Britain, the husbandry of game birds has a major impact on the management of wildlife and habitat. In particular, the deaths of intensively-reared and released game birds, provoke hostile attitudes to predators. Dowell tackled the question: do the circumstances of their rearing affect the abilities of these birds to survive? He flew a hawk model over coups in which young grey partridges, *Perdix perdix* were observed. Each coup contained partridges reared either in incubators, or under a broody chicken or by their natural mother. Not surprisingly, the parent-reared partridges behaved most appropriately towards the hawk-model; they crouched cryptically until it had passed overhead. Unexpectedly, the chicken-reared partridges behaved even less appropriately than incubator-reared birds: when faced with the hawk-model either they showed no fear or they dashed for cover. The latter strategy might well have been adaptive for an ancestral jungle-dwelling chicken, but in the open-field habitat of partridges there is no cover. Dowell (pers. comm.) is now applying this discovery to the captive breeding of the endangered cheer pheasant, *Catreus wallichi*, of Pakistan, which is also an open-country species which was previously reared under chickens.

Ignorance of the behavioral requirements of rare species limits many captive breeding efforts. For example, Ginsberg and Macdonald (1990) note that while 32 of 36 canid species have been bred in captivity recently, 19 have bred on average in fewer than four collections per year and 80% of litters come from only six species. Only one of these six, the African wild dog, *Lycaon pictus*, is rare. In general, there was almost a linear decline in pup mortality with logarithmic increase in the number of litters bred of each species; that is, great increases in attempts to breed a canid species are required to effect a small reduction in pup mortality. The species of canid most endangered with extinction tend to breed most poorly in captivity. In this example, lots of practice makes perfect; a crucial ingredient is better knowledge of the species' behavior.

Uncovering Problems, Dispelling Myths and Raising Profile: Exploratory field studies of rare species often disclose unexpected threats. When Gottelli and Sillero-Zubiri (1990) began to study the endangered Simien jackal, *Canis simensis*, in Ethiopia they did not anticipate discovering that the immediate threat lay in hybridization with cowherds' dogs (see Ginsberg and Macdonald 1990). The same problem emerged as crucial in Boitani's (1982) study of wolves, *Canis lupus*, in Italy, which also illustrates a major, albeit indirect, contribution of behavioral research to conservation: by publicizing his fascinating findings, Boitani dispelled myths, raised the profile of wolves and engendered support for political action to conserve them (e.g. Macdonald and Boitani 1979).

All too often, the problem identified by behavioral ecologists has no immediate solution, but understanding remains a prerequisite to prudent management. For example, the greater horseshoe bat, *Rhinolophus ferrumequinum*, was previously distributed throughout the palaearctic, but has suffered a widespread and rapid decline. In the UK it declined by 98% in the 1970s and only six known breeding sites remain. Stebbings (1984) studied the behavior of these bats using radio-tracking. He found that they need a large number of widely-dispersed, secluded sleeping sites, with different sites for hibernation, for pregnant mothers and for rutting males. For example, in summer, pregnant females used to gather at maternity roosts in caves where the collective warmth of thousands of their bodies raised the temperature from c 10°C to the optimum for gestation at 28–30°C. Nowadays agro-chemicals and farming practices have so reduced the bats' food supply, decimating their numbers, that roosts comprise too few individuals to generate this heat. Instead, pregnant females often roost in the roofs of houses where the ambient temperature of c 30°C provides the energy for fetal growth, but where they are threatened by the toxic properties of timber preservatives. The fact that it is not yet obvious how to break this vicious circle does not diminish the importance of understanding it.

Pest Control: A prerequisite to managing a pest problem is describing it. For example, Sukumar (1990, 1991) assesses crop-raiding by elephants, *Elephas maximus*, and concludes the losses are significant but can be managed with attention to inter-sexual differences in behavior. In contrast, Hewson (1990) concludes the losses of lambs to foxes, *Vulpes vulpes*, are economically trivial. Two examples concerning squirrels show that behavioral research can fa-

cilitate not only predicting where pest control will be needed, but may also provide an elegant solution

In mid-summer, grey squirrels, *Sciurus carolinensis*, indulge in bark-stripping, which deforms and kills oak, sycamore and beech trees of 15–40 years old The motive for this behavior was mystifying until Kenward et al 's (1988) discovery that bark was stripped from individual trees in proportion to the abundance of phloem tissue beneath Phloem volume, itself a measure of sap volume, explains 56% of variation in the incidence of bark-stripping; sap volume provides a 75% prediction of the squirrel's sugar intake There was no year to year relationship between phloem volume of given trees, nor with the number of attacks per tree by the squirrels However, there was a relationship between the extent of damage in a woodland during one year and the percentage of trees attacked there the following year Kenward et al concluded that squirrels that had learned the idea of bark stripping in one year, sampled trees widely during the following year to find the good ones, on which they then concentrated their attacks This provides a basis for foresters to predict where to focus squirrel control effectively They also proposed a rather more esoteric idea to use genetic engineering to select trees with unpalatable phloem

The paradigmatic example of behavioral studies offering an ingenious solution to a wildlife problem is Hurley et al.'s (1987) work on the Canadian red squirrel, *Tamiasciurus hudsonicus* These squirrels eat up to 85% of the cone crop in seed orchards, and traditional control by killing them is ineffective due to the rate of immigration The squirrels pick cones in order to store them for use over the winter They cache some solitarily, but hoard others in stores of up to 2,000 cones, often hidden in piles of debris that form under the squirrel's favored eating place The squirrels also hide cones in artificial mounds of leaf litter Hurley demonstrated that it was more efficient for the foresters to use the squirrels' labor than to kill them: if the foresters provide the squirrels with piles of vegetation in which to hoard cones, these can then readily be harvested, whereupon the squirrels pick more which can in turn also be harvested The forester must then replace the stolen hoard with peanuts (much cheaper than cones) to sustain the squirrel over-winter (otherwise the starving squirrels will strip bark from the trees, leaving the forester with dead trees)

Wildlife Diseases: Behavioral studies are crucial to the understanding and control of wildlife diseases, e.g. bovine tuberculosis and badgers, *Meles meles*, (Cheeseman et al. 1989), Leishmaniasis and crab-eating foxes, *Cerdocyon thous* (Lainson et al 1990) and rabies and many carnivores (Macdonald and Voigt 1986).

Rabies is a viral disease, transmitted in the saliva when an infected animal bites a susceptible one Fox rabies in Europe is a huge and widespread problem: it has been tackled traditionally, but largely unsuccessfully, by trying to kill so many foxes that infectious individuals would run out of susceptibles to bite Studies of foxes indicated complicated interactions between habitat, population densities, spatial organization and reproductive biology in ways that affected ideas on rabies epidemiology A new approach, oral vaccination of wild foxes against rabies, takes into account many of these factors, leaving fox society undisturbed and arguably therefore not elevating contact between infected and susceptible survivors (Macdonald 1988) This approach is now well on the way to controlling wildlife rabies on Continental Europe (Kappeller 1988), although there is debate (again informed by behavioral research) as to whether it would work in the peculiar case of Great Britain with its large urban fox population (Harris and Smith 1990)

Behavior Tools for Research: Knowledge of animal behavior can provide a useful means to an end For example, faced with the task of designing a management plan for the spotted hyaena, *Crocuta crocuta*, of the Kruger National Park, Mills (1990) needed to know how many of them there were and what was their impact on prey He devised a census method of tape-recorded playbacks of calls recorded at kills The hyaenas responded by coming into the open to be counted They were attracted to the taped calls for a maximum of 3 5 km and took as long as 21 mins to arrive; the minimum distance at which they failed to react was 2 km Mills concluded that he was sampling 12 6 to 38 5 km^2, and that 6% of hyaenas were not attracted by the calls (floaters, seeking to avoid unpleasant encounters with residents) The result was an estimate of 1,269–3,886 hyaenas, with important variation in numbers between habitat types

Habitat-Oriented Problems: Conservation of habitats is clearly a prerequisite for conserving species. There are many notable studies directed at discovering how much space, and what type of habitats, species need (see discussion in Lovejoy et al. 1988; Pimm and Gilpin 1989). Important studies have focused on the conservation potential of fragmented forest blocks; for example 10 ha plots of Amazonian primary rain forest sustained populations of howler monkeys, *Alouatta* spp., but not saki monkeys, *Pithecia* spp. Fragmentation of habitats is a major conservation problem (Wilcox and Murphy 1985). Because of its spatial and temporal patchiness, farmland offers many opportunities to explore the principles affecting conservation in a fragmented landscape (Macdonald and Smith 1990, 1991). For example, the studies of Fahrig and Merriam (1985) on the importance of habitat corridors to rodent populations, and of Opdam et al. (1985) on the corollaries of woodland size on bird communities illustrate widely applicable concepts (Pimm and Gilpin 1989).

CONCLUSIONS

Finally, having illustrated some diverse contribution of behavioral studies to conservation (see also Metcalfe and Monaghan 1987), I will conclude by considering whether any particular research strategy is especially helpful. One sort of bigotry dismisses useful research as banal, another sort considers theoretical work irrelevant. In fact, the evidence is that the most interesting and the most useful research can stem from a mixture of theory and empiricism, a synergism which produces not only short-term answers but also long-term understanding (Macdonald and Smith 1991). I suggest that the ideal is to consider a practical problem within the framework of theory, and then to tackle it through hypothesis-testing empiricism based on sound knowledge of the relevant autecology. This approach often starts with a species and ends with a community. For example, grey partridge, *Perdix perdix*, in the south of England declined by 80% during 40 years. Studies of their diet selection by Southwood and Cross (1969) linked this decline to agricultural changes that diminished the supply of insect food eaten by partridge chicks. Green (1984) radio-tagged breeding partridges, and found that the parents led their chicks to the edges of fields where weeds and arthropods were most abundant. Next, Rands (1985) measured both the prey populations and the partridges' breeding success in a farm-scale experiment: 6 m wide strips were monitored around 37 fields in a replicated design where some were farmed normally, whereas some were spared from broad-leaved weed herbicides. In these unsprayed strips chick survival improved dramatically. Using these data, Potts (1986) has simulated the population dynamics of the partridge. From these studies, stimulated initially by the commercial importance of partridge-shooting, has come not only a practical solution to the problem, and much understanding of fundamental concepts, but also a plethora of studies on other components of the cereal ecosystem ranging from rare plants to butterflies (Sotherton et al. 1989).

A final point concerns an external constraint on progress. Because of career structure and funding policy, few projects are funded for more than three years. However, many of the questions crucial to conservation do not fit within these short-term opportunities. They may demand long-term work, sometimes against a background of continued monitoring. I conclude that the capacity of behavioral studies to underpin sound conservation is great and varied, but that capacity is easily frustrated by short-termism in research strategy.

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HOST-PARASITE STRATEGIES

BY

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HOST - PARASITE STRATEGIES

by

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Parasites are defined by Holmes and Price (1986) as 'Organisms living in or on other living organisms, obtaining from them part or all of their organic nutrients, commonly showing some degree of adaptive modification, and at least potentially causing some damage to their host.' For a distinction between parasitism and commencialism, the last part of the definition is important. It is unfortunately not always easy to define and demonstrate 'damage to the host'. For many organisms conventionally considered as parasites, the detrimental effects are yet to be demonstrated. Under certain conditions a parasite may even increase the fitness of the host (Moore 1987, Freeland 1986). The precise limits between parasitism, mutualism and commencialism are difficult to delineate. Further, practical complications arise when one species of a genus is demonstrably pathogenic while another is a commensal or even a mutualistic symbiont. I will therefore go by the imprecise but more practical definition of parasites as 'the taxa studied by parasitologists'.

Until about a decade ago, ecologists paid little attention to the role of parasites in ecological interactions. Since the late 1970s, a substantial body of theory developed regarding the potential role of parasites in the evolution and ecology of the hosts. There are however very few examples of good empirical data substantiating the theory.

Parasites in host population regulation:

Parasites responsible for devastating epidemics have resulted in severe reductions in host populations e.g. rinderpest in African ungulates (Sinclair 1979, Nawathe and Lamorde 1984) or myxomatosis in rabbits (Sumpton and Flowerdew 1985). It has been suggested, on the other hand, that maximum depression of population growth in the long run may be achieved by parasites of moderate to low pathogenicity (Anderson 1979, 1980). The nature of the effects of parasites on host population regulation is influenced by the degree of aggregation of parasites. If the distribution of parasites is random, parasite induced mortality leads to unstable oscillations of host populations. Most parasites are however aggregated and the effect of aggregation is stabilizing (Anderson 1991).

There are only a few empirical studies demonstrating population effects of parasites. The fluke *Gyrodactylus bullatarudis* was found to effectively regulate guppy population (Scott and Anderson 1984, Gregory and Keymer 1989) while the nematode *Heligmosomoides polygyrus* heavily reduced mice populations (Scott 1987) in experimental systems. Perhaps the only well studied example of population regulation by parasites in field conditions is that of the red grouse *Lagopus scoticus* in England, parasitized by the nematode *Trichostrongylus tenuis* (Potts, Tapper and Hudson 1984, Hudson *et al* 1985, Gregary and Keymer 1989) In this case an inverse relationship between parasite loads and breeding success was shown. The predators

selectively took grouse with higher worm burdens (Hudson *et al* 1992). The cyclic fluctuations in grouse numbers also matched well with the oscillations predicted by Anderson and May (1978) (Hudson, Dobson and Newborn 1985).

Host competition and Coexistence:

In north America the white tailed deer carries the meningeal worm *Parelaphostrongylus tenuis* which is fatal to moose and caribou. In areas where moose and white tailed deer coexist, moose numbers are inversely related to the prevalence of meningeal worm in deer. Attempts to reintroduce moose and caribou into areas occupied by the white tailed deer have failed apparently because of the parasite (Anderson 1972, Gregory and Keymer 1989, Moore 1987). Introduction of avian malaria in Hawaii brought about the extinction of many native bird species. The surviving native bird species now occupy the higher altitudes where the mosquito vectors are rare, while the lowlands are dominated by the introduced species. Schall (1992) demonstrated that the competitive coexistance of two species of lizards, *Anolis gingivanus* and *Anolis wattsi* was mediated by the parasite *Plasmodium azurophilum*. *A. gingivalis* was a stronger competitor and where malaria was absent only this species existed. However, in presence of the parasite, both species coexisted owing to greater susceptibility of *A. gingivalis* to malaria than *A. wattsi*.

Price *et al* (1988) predicted and showed in a few examples that in parasite mediated host competition, a species with a

wider geographic distribution is more likely to be a winner. Also if the body sizes are different, the smaller species is more likely to replace the larger species. This is because the number of parasite species per host increases with host range, thereby increasing the probability that one or more of its parasites can be advantageous in competition. A large range also reduces the probability of exposure to novel parasite species, and the host resistance is usually high to a wide range of parasite species. Small host size on the other hand correlates well with higher densities, higher reproductive rates and thereby accommodation of more parasite species.

Predator-prey dynamics:

Parasites can modify the predator prey dynamics by increasing the susceptibility of the prey towards predation (Hudson *et al* 1992, Temple 1987). Parasites having the prey species as intermediate host and the predator as a definitive host may be benefitted by the altered predator prey dynamics. As a result of parasite induced susceptibility to predation, the threshold density to sustain the parasite is reduced considerably and parasites can survive at very low densities of the definitive hosts (Dobson 1988, 1989). Freedman (1990) modelled the predator-prey-parasite dynamics giving conditions for stability. He further suggested that, a 'paradoxical' mutualistic association between the predator and the parasite may exist. It is not clear, however, how and under what conditions such a mutualism can evolve. Several examples of parasite induced susceptibility have been reviewed by Holmes and Bethel (1972) who classify them into

four mechanisms --- reduced stamina, increased conspicuousness, disorientation and altered responses.

It has also been suggested that the parasite related susceptibility to predation may also increase the host's inclusive fitness in at least a few invertebrate host-parasite systems. This adaptive suicidal behaviour of the host (Smith Trail 1980) has been debated (Moore 1984, Gotelli and Moore 1992).

Reproductive isolation and speciation:

It has been shown in the case of two species of parasitic wasps of the genus *Nasonia* that cytoplasmic microorganisms prevent hybrid offsprings. Elimination of microorganisms by antibiotic treatment allows hybrid formation (Breeuwer and Werren 1990). Reproductive isolation caused by microorganisms can lead to rapid speciation and therefore play an important role in evolution of diversity. It is not known, however, how common such phenomena are.

In the case of *Mus musculus* and *Mus domesticus*, two species of mice, the hybrids are more susceptible to helminth parasites and thus presumably have reduced fitness. This has resulted in preventing geographical range overlap as well as maintaining reproductive isolation. Hybrid mice occur only in a 20 km wide belt where the geographic ranges of the two species meet (Sage *et al* 1986).

Host defences and immune system:

The evolution of the entire immune system is no doubt a direct response to the continued selection pressure exerted by micro and macroparasites. The parasites in turn have evolved mechanisms to counter host defences (Freeland 1986, Hayunga 1989). As opposed to popular belief the complete elimination of all parasites may not always be advantageous to the host. Instead it might be better in some cases to harbour a parasite which can competitively exclude or reduce the chances of colonization by other parasites of higher virulence (Freeland 1986).

Sex and sexual selection:

Hamilton (1980, 1982) and Hamilton *et al* (1990) suggested that sexual reproduction evolved as an adaptation to resist parasites. Since parasites have considerably shorter generation times than their hosts, they can evolve much faster and overcome host resistance mechanisms. This hypothesis views sex as an adaptation enabling long-lived organisms to counter the faster evolution of parasites, by producing new recombinant genotypes in each generation. The parent to offspring transmission of parasites in particular can be a strong selective pressure favouring sex (Rice 1983). Lively (1992) demonstrated in snails that sexual females outcompeted parthenogenetic ones in presence of parasites. The frequencies of producing males was positively correlated with prevalence of a trematode parasite. Moritz *et al* (1991) provided further evidence for this hypothesis by showing that parthenogenetic lizards were more susceptible to parasites than the sexual ones. Since sex is an important process defining and

underlying speciation, parasites can be considered as a major force generating biodiversity.

One of the most debated hypotheses has been the role of parasites in sexual selection. Freeland (1976) suggested that mate choice by females may be related to parasites and pathogens carried by males. Hamilton and Zuk (1982) further developed the concept that host parasite coevolutionary cycles might drive the evolution of female preferences for extreme male displays. Males carrying resistance genes will be healthier and in a better condition to grow plumage or perform strenuous displays. Females by preferring these males ensure 'good genes' for their offsprings. However unlike other good gene hypotheses, the resistance genes will be constantly changing since the parasites are also evolving, and thus the system remains dynamic maintaining the importance of the female choice.

Many negative correlations between the male displays and their parasite loads have been shown (listed by Howard and Minchella 1990). These correlations, however, can have alternative explanations not involving coevolutionary cycles (Atkinson 1991). Also as pointed out by Atkinson (1991), only certain types of parasites can be involved in coevolutionary cycles leading to sexual showiness, but most studies have looked at any or all types of parasites without analysing whether they satisfy the necessary conditions.

Parasites ideally suited for coevolutionary cycles are of medium virulence, chronic type which may cause high infant

mortality but chronically survive in adults, and which are likely to produce coevolutionary cycles long enough to create average positive parent-offspring fitness correlations. Too short a cycle may produce negative correlations (Hamilton and Zuk 1982). Parasites that can multiply within a host individual will probably evolve too fast and may not be suitable for this model. The external lifecycle parasites such as the visceral helminths, on the other hand, must have life cycle stages outside the host, which will not necessarily invade the same host individual again. For such parasites, selective pressures will operate to overcome not the genotype of an individual host but the most prevalent genotype in the host population. These are the parasites expected to have cycles of appropriate duration. However, most studies have ignored this group of parasites.

Parasites and host behaviour:

Freeland (1976) suggested that many aspects of primate social behaviour may have evolved due to parasite-mediated selection. Social integrity, xenophobia and sexual fidelity serve to avoid new pathogens. Stressful relationships with a new member joining a group may lead to stress-related expression of latent infections. Female-induced stress in males during courtship may also serve the same purpose and thus help in choosing a relatively parasite free male. Maintenance of a territory may itself be a disease-avoiding mechanism. The movement pattern of a troop may be influenced by the risk of acquiring parasites. The extent of allomothering or infant handling by other members may

be determined by the chances of pathogen transmission to the infant. The size of the sleeping groups may be influenced by the rates of attracting haematophagous insects.

Some of these predictions have been empirically tested for some species. The daily movements of Mangabeys seemed to be more related to the risk of acquiring parasites than to food availability or any other ecological factors (Freeland 1980). Hourly grouping tendencies were shown to correlate best with activities of biting insects. (Freeland 1977). Apart from these few exceptions, empirical studies on the role of parasites in shaping host behaviour are conspicuously absent.

There can be many other ways in which parasites can influence the behaviour, ecology or evolution of the host. Parasites can influence the foraging strategies of the host (Milinski 1984, Lozano 1991). The role of parasites in mating system of social insects is recognized recently (Shykoff and Schmidt-Hempel 1991, Gadagkar 1992). Species differ in the time, preferred places and the manner of defaecation. These behavioural patterns are likely to be shaped by parasites. Allogrooming might have evolved initially as a 'vaccination behaviour'. Seasonality in breeding of many species may have been selected by seasonal variation in parasite abundances.

Conservation and management of wildlife:

The study of parasites and parasitic diseases is important for management and conservation of wildlife. Although the importance of diseases such as rinderpest, foot and mouth

disease, anthrax and rabies is recognized, it is difficult to decide when and whether control measures are necessary, possible and feasible and what are the best methods of disease management (Wobeser 1989). The importance of chronic parasitic diseases which do not cause devastating epidemics, on the other hand, is usually not recognized at all. In order to answer the question when the wildlife managers should intervene in the disease process and when they should not, one needs adequate data on parasites and diseases of apparently healthy and normal wild populations. Such data are scanty throughout the tropics and practically nonexistent in India.

It is important to realize that the ecological effects of parasites and diseases are not restricted to their host species. Epidemics of fatal diseases can disturb the highly interlinked trophic interactions. Thus, rinderpest in wild ungulates has lead to man-eating by lions (Sinclair 1979) and myxomatosis in rabbits has lead to local extinction of the large blue butterfly (Sumpton and Flowerdew 1985). Rabbit myxomatosis also resulted in changes in host parasite relationships of other host species. Large scale deaths of rabbits led to an increase in *Echinococcus granulosus* infection in foxes which relied on scavenging on sheep carcasses. Rabbits harboured the stomach-worm *Graphidium strigosum*, the bacterium *Pasteurella pseudotuberculosis* and coccidians which were more pathogenic to the European hare. Reduction in rabbits resulted in reduction of these parasites, so that the hare population increased and their range expanded (Sumpton and Flowerdew 1985). It has been suggested that in Isle

Royale, the survival of the wolf may depend, at least in part on the parasites which make moose susceptible to predation (Freedman 1990). It is therefore important for wildlife managers to know the role of parasites in the population ecology of important protected species in order to take decisions about control measures if and when necessary.

Transmission of diseases and parasites between wild animals and domestic animals is possible and wild animals can act as reservoirs of parasites for domestic animals and vice-versa (McKenzie and Davidson 1989, Arora and Ramaswamy 1990, Jhala et al 1990). Parasite transmission to humans is also possible (Nelson 1972, Rao and Acharjyo 1990) and therefore a study of parasites of wild animals is important from the public health point of view as well.

Parasite community ecology:

Throughout the discussion above, we have focussed on how parasites are likely to affect the ecology, evolution and conservation of their hosts. Considerable interest has been generated recently in the parasite communities themselves. A recent book edited by Esch et al (1990) summarizes the work done in this field so far. The first book on this subject, which the editors call a 'primer' concludes with a note,

> 'We envy the authors of final chapters of other books which usually conclude with definitive statements. In comparison the present effort may appear a rather weak commentary with it's 'maybe it is maybe it's not, it could be --- it's probably not' conclusions, particularly to a book which attempts to synthesise information on a central theme.'

This effectively summarizes the state of knowledge in this field. Although the book makes certain generalizations and successfully demonstrates certain interesting patterns, they remain tentative and ask for much more quantitative empirical work. A major issue in the last decade has been the role of competition and other interactions among parasites. Relatively less importance has been given to host ecology. However, since trophic systems are 'driven from below' and the host forms the resource base for parasites, parasite communities must be 'host driven' (Price 1990). One should therefore look at ecological parameters of the host that may shape parasite communities. Published work on this aspect is only recent (e.g. Bell and Burt 1991, Dobson *et al* 1992a).

This completes a full circle of arguments. We started with the number of ways in which the parasite communities can affect host ecology and ended with a note that host ecology should be held largely responsible for shaping parasite communities. I have tried to examine several aspects of these interactions, using the wild mammals of the Mudumalai Wildlife Sanctuary and their faecally dispersed helminth and protozoan parasites as the study system.

Choice of the host parasite system:

Mammals usually receive the highest priority in conservation efforts (Dobson and May 1988) for reasons beyond the scope of the present discussion. Studying mammals of conservation priority therefore can be an obvious starting point. To study parasites in

relation to host ecology, a good prior knowledge of host ecology in the selected study area is necessary. Since the establishment of a field research centre of the Centre for Ecological Sciences, I.I.Sc. in Mudumalai Wildlife Sanctuary in 1987, substantial basic population data on large mammals have been gathered. Research on elephants in the same region by the Bombay Natural History Society also provides some of the necessary ecological data on this species.

Most studies on parasite communities come from fishes, amphibians and reptiles where the common method is to catch and kill sufficient number of sample individuals. This method not being possible and feasible for mammals in a wildlife sanctuary, the most practical alternative was to study parasite propagules in faecal output. This approach gives substantial information per unit effort. The host group and the study area were thus a careful choice while the parasite group more of a default.

Since not many studies of this kind in tropical forest mammals are available, I have tried to look at as many questions as possible being well aware that this puts constraints on the depth to which any one problem can be pursued. I justify this 'exploratory' approach since in a relatively unexplored field one has to identify the relevant problems first before examining any one in detail. Secondly, I have adopted a 'black-box' or a 'descriptive holistic' approach in the sense of Wilson (1988). I have looked at parasite propagule outputs from individual hosts without looking at what goes on inside the host or without

studying in detail the life-cycle of any parasite species. This was necessitated by the scanty prior information, limitations of the methods of study and a compromise between the breadth and depth of a study. Futures studies could address these aspects in greater details.

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CENTRE FOR
ECOLOGICAL SCIENCES

CHEMICALLY MEDIATED ANIMAL BEHAVIOUR

BY

MEENA HARIBAL

Animal Behaviour Ecology

Chemicals involved in Animal behavio

Secondary chemicals or metabolites are compounds of small molecular weight and present in plants as well as animals. Initially these were considered to be waste product of the plant or animals. But as early as 1956 Frankel put forward the theory that they are not simply waste products but have been synthesised and accumulated for specific purposes by these organism. In last 15 to 20 years more than 10000 papers have been published where specific roles of these chemicals have been identified. Chemicals are involved - may be as a odoriferous substance in many aspects of animals life: scent marking, territorial marking, sexual recognition, mating, sexual attraction, physiological status, alarm, predatory-prey interactions defense, reproductive isolation, feeding, in recognition of kin, caste, age social status, physiological status and even individuals. Over 25 years ago Karlson & Lushaher proposed the term Pheromone (Pherein - to carry, hormono - to stimulate in Greek) which is substance secreted or produced by an animal to the outside and causes a specific reaction in an individual or organism.

Further these have been classified as <u>release pheromones</u> (such as involved in alarm, territorial, trail, social status, sexual attract, etc.) - if the stimulus triggers an immediate behavioral response in receiving organism. <u>Primer pheromones</u> (such as involved in puberty acceleration - pregnancy block, estrus synchronisation, etc.) - if the response is a long lasting one.

Allelochemics are substances involved in interspecific communications.

<u>Allomones</u> are those chemical substance which are produced or acquired by an organism, which when in contact with an individual of another species in the natural context evoke in the receipent

organism behavioural or physiological reaction adaptively favourable to the emitter.

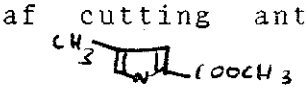
Kairamones are chemical messengers the adaptive benefit of which falls on the receiver rather than the emitter.

Semiochemicals (Semion - Mark) are chemicals that devilers any message to any organism.

Origin: Many types of glands are involved in the production and/or emission of semiochemicals; labial, mandibular, Dufour, hindgut, poison, pygidial, sternal, anal, supraanal, cephalic, tibial, epidermal, salivary, cibarial in insects and tarsal, inguinal, chin, orbital, frontal and caudal glands in mammals. Phemomone may be synthesised or may be directly obtained from the plants on which it feeds or may be partially converted. Environmental and physiological factors control the production and emission of pheromones. Light intensity, temp, host habitat and air velocity are environmental factors and physiological are time of day, age, previous experience, population density, diet, hormones and seasonal rythms. In some cases micro-organisms in the gut or body are capable of converting substances from the food plants into chemicals which can be used as pheromones. For example the microorganisms are involved in the production of the wolf's anal sac secretion, if it is treated with the antibiotics production decreases.

Semiochemicals may be a multicomponent system or may be single compound. As many as 33 compounds have been separated from the hairpencils of *D. Plexippus*. Mandibular gland of bee *Andrena haemorroha* consists of 40 substances consisting of spiroacetals, straight chain fatty acids derivatives (of sec alcohols, acetates, methyl ketones, primary and secondary alcohols and hydrocarbon) and isoprenoids .

Perception depends on the substance, emitter and receiver. Mathematically depends on (1) Rate of molecular emission, (2) diffusion co-efficient of the substance, (3) the distance from the source and (4) time from initiation of the emission.

Insects can detect surprisingly small amounts. Male *Bombyx mori* can react to the air containing as little as 100 moles of female sex pheromone per cc. The trail pheromone of leaf cutting ant *Atta texana*, Methyl 4-methyl pyrrol 2-carboxylate  is perceived at a concentration of 0.08 pg/cm^3, i.e. 3.48 molecules/cc. Almost same amount has been recorded for trail pheromone of *Reticulitermes virginicus* termite workers. Pheramones could be detected from as far as 1 to 2 km from the source. Examples of lime and Red Pierrot, can detect the food plants by chemical cues.

Insects perceive them by means of organs located in antennae, tips of maxillary and labial palps, in buccal cavity, epipharnyx etc. by means of sensilla. Sensillas are hairs perforated by large number of pores through which the pheromone molecules diffuse after being adsorbed on the surface. The binding of the molecules to the acceptor sites relies on the stercochemical shape of the pheromone & of the receptor.

Following types of sensilla are olfactory in nature.

(1) Sensilla trichodea (in Lep.)
(2) Sensilla basionica (in Lep. Diptera, Coleoptera and Hymenoptera)
(3) Sensilla placodea (in Hymenoptera)
(4) Sensilla coelonica (in Orthoptera)

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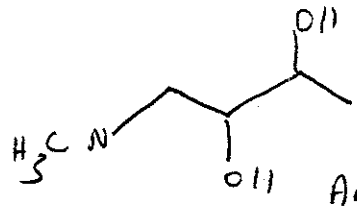
Chemical communication in marine animals :

The sex attractant secreted by female zebra fish is a mixture of estradiol and testosterone glucuronides. Introduction of water from a tank containing male *B. rerio* induced ovulation in an isolated female. The chemical substances effect both group and spawning behaviour. An interesting interaction between sea anemone and predator mollusk



Anthopleurine.

Anthopleurine is realised by an injured member of colonial sea anemone which evokes alarm in other members. After nudibranch eats sea anemone the mollusk for at least five days after ingestion evoke alarm response in sea anemone. This suggests that predator helps in transmission of the alarm pheromone which may reduce the predation of the sea anemone.

Relation between two organism (a) Young fish *Abudefduf leucogaster* and alcyonarian *Lithophyton virdis* has been described. *L. Virdis* produces a toxic chemical rendering it unpalatable to large fishes. The toxin effects *A. leucogaster* very slowly hence they remain together in coral and benefit indirectly. Chemical signals are also involved in fish migration. Juvenile salmons get impregnated with the unique chemical odor of the natal stream.

Paralytic shellfish poisons (PSP)

PSP are the toxins responsible for acute and often fatal poisonings caused by the consumption of certain shell fish. Dinoflagellates are the primary sources of the toxins discovered in shell fish, *Gonyaulax catenella, Gitamarensis, Pyrodinium*

bahamense and also fresh water blue-green alga *Aphanizomenon flos-aquae*. The accumulation of the toxins in the shell fish is the result of filter feeding of these organisms especially during the outbreak of blooms (red tides). PSP toxins are also found in certain species of crabs and carnivorous snails probably as a result of secondary toxin transfer in the food chain. The toxicity of shell fish is normally transitory and gradually diminished as the causative organisms disappear from water except in Alaska butter clam. *Saxidomus giganteus* which tends to retain toxicity in the siphon for a length of time.

Chemicals and social insects.

Almost all activities of social insects depend on the chemical signals. They are involved in sex attraction, reproductive isolation, recruitment, nest defense, nest building, predation, territoriality, kin recognition.

Ants and termites have basically following social structure: (1) Care for young, (2) Division of labour in reproduction, (3) Two generations contribute to assist parents.

Ants and termites have three classes: Reproductive, Workers and soldiers. In termites workers may be male but in ants males have no role in nest tending.

Methyl salicylate, 2,4 - dimethyl hexenoic acid and methyl anthranilate are secreted from the mandibular glands of *Componotus* species females and workers. The secretion initiates the activity of the females before swarming and is used to scent area near the nest entrance and to induce the female to swarm from the nest when the male flight is at a maximum.

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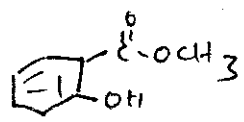
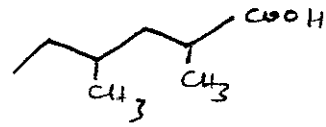
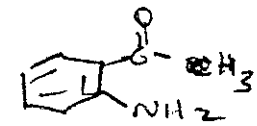
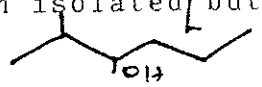
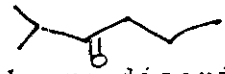




Different secretions are released by workers, females and queens from the *Tetramopium caspitum* 4-methyl, 3-hexanol and its ketone has been isolated from females but workers had only alcohol.

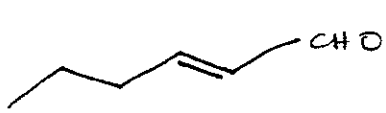
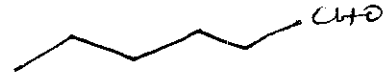



Guard bees *Lasioglossum zephyrum* discriminate - residents and non-residents by odor.

Chemical attraction of kleptoparasitic flies to heteropteron insects caught by orb-web weaving spiders.

It had been observed by the group of Aldrich and co-workers that the stink bugs and squash bugs when they spray to repel spiders etc. attract flies. When a spider has caught prey it takes sometimes hours to eat this prey. They drench their prey in the digestive fluid and suck up its liquefied contents. During this time many species of kleptoparasatic flies of the family Cecidomiidae, Phoridae, Chloropidae, and Milchiidae visit the spiders prey and run away with tit bits of food.

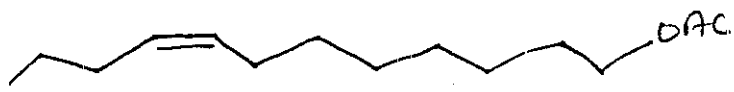
Now it has been proved that the flies are attracted here by chemical means. Studies by Eisner and his group have shown that when the stink bug is caught it emits secretions consisting of low molecular weight carbon comp of which trans 2-hexenal and hexanal are major components. Milichiids have been proved to be attracted to these compounds.

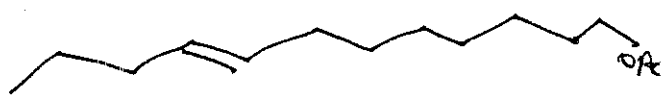
Scout ants lay down trail pheromene to attract nest mates to predation sites. When the thief ants arrive in the prey colony they release from the poison gland a repellent trans 2-buty 1,5-heptyl-pyrrolidine - which prevents brood tending ants from defending their larvae.

Role of pheromone in reproductive isolation of insects :

Pheromones may be stimulus during mating behaviour and also may be an important barrier to interspecific mating. For example in the family of Tortricidae (Lep.) *Grapolita prunivora* and *G. packardii* have same type of life style but the pheromone released have **E & Z** configuration. The cis 8-dodecenyl acetate acts as pheromone to *G. prunivora* and trans isomer to *G. packardii*.



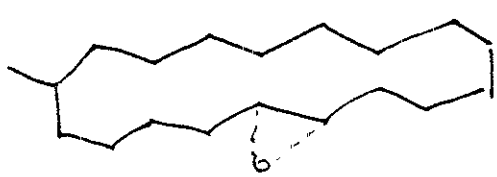
Cis-8-Dodecenyl acetate



Trans-8-Dodecenyl acetate

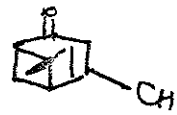
If more than one attractants are present then there may be variation in concentration.

Different circadia mating rythms provide another means of reproductive isolation. Cis 7,8-epoxy 2-methyl cyclooctadecane is attractant to both moths *Parthetria dispar* and *Lymanthria monacha* which are spread from Europe to Japan. *L. monacha* mates between 6.00 p.m. and 1.00 a.m. and *P. dispar* is diurnal.

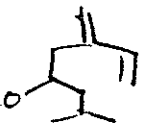


Cis 7,8-epoxy 2-methyl cyclooctadecane.

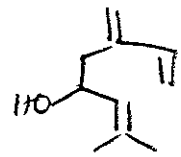
Aggregation pheromone of *I. paraconfuscus* consist of mixture of 3 cis-verbenone, ispenol, ispendienol. Although compound S(-)isomer of ispenol is an attractant R(+)isomer is an inhibitor.



cis-Verbenone



ispenol



ispendienol

Danainae butterflies
Cardiac glycosides, Pyrrolizidone alkaloids and their feeding behaviour

Predator-prey interactions :

This has been observed by Swiss entomologist Hubner in 1810 among the slave-maker ants of the species belonging to *Formica ruf escens*. They raid on the another related species by means of a trail pheromone which guides worker to the target area, where they kill or repel defending workers after which they penetrate into the nest and carry pupae and larvae to their own colonies. When the pupae develop into adults they accept the slave makers as nest makers and assist them in the task of the colony.

Longhurst observed that the ants preying on termites emit a non-repellent aliphatic alcohol as a major components of the secretion from their mandibular glands. Non-specialised ants produce aldehydes and ketones.

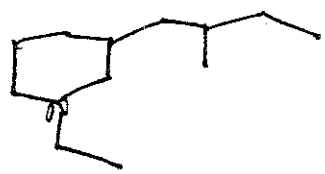
Theif ants *Fugax* and *Nomada* bees have developed a method to steal. S. Fugax steal brood from nearby nests and other ant colonies by building a system of subteranean tunnels which lead to the nest of their prey.

Defensive secretions

The secretions may kill the predator as in example when HCN is discharged by *Geophitus vittatus* or it may repel as in larval secretion emitted by *Papilio machon* which contains isobutryic

acid and α-methyl isobytric acid and in aristolochie feeding butterflies aristolochich acids are present.

An interesting defense behaviour is exhibited by an aquatic beetle *Stenus comma*. The beetle lies on the water surface near river bank and in case of danger it jets towards the banks, safely at a speed of 45-75 cm/s without using its legs. The beetle immerses the tip of abdomen into the water and emits from two pairs of pygidial glands a secretion of that stenusin which depresses the surface tension of water thus helps it in propelling itself forward on the water. Stenudin been isolated as the propelling agent.

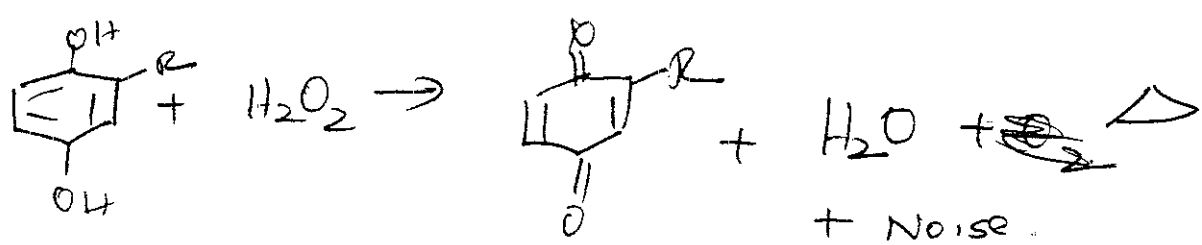


Stenusin.

Defense secretion of Bombardier Beetle (Eisner 1991).

Beetles have perfected chemical reactions. The reaction vessels consists of two chambers and they open adjacently on the tip itself. One contains oxidising agent H_2O_2 and the other contains hydro-quinols. When both come in contact they react violently and produce heat upto 100°c and oxidise quinols to quinones.

These beetles are sluggish creatures. When evoked they discharge spray along with audible detonations. Second discharge is coloured and it takes long time to evaporate.



R = H, CH_3, C_2H_5

FORAGING DECISION IN ARBOREAL HERBIVORES – THE DIMENSIONS OF TIME & SPACE

BY

RENEE BORGES

FORAGING DECISIONS IN ARBOREAL MAMMALIAN HERBIVORES -- THE DIMENSIONS OF SPACE AND TIME

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Foraging is a complex process which is greatly influenced by the spatial and temporal availability of food resources.

See Figure.

In order to solve foraging problems, the animal needs to possess certain knowledge. It needs to know (a) the type of resources available at any given moment in time. (b) the **abundance** of available resources in both the area over which it is currently foraging and over the range as a whole. (c) the **spatial distribution** of available resources. (d) the **location** of available resources.

The animal also needs to store this "information" in short or long-term memory and to selectively "unlearn" any ad-hoc "rules of thumb" that may be undergoing rapid change.

Based on these fundamental knowledge components (and in order to test if the animal does possess this knowledge), specific questions need to be asked eg. 1) Does diet diversity decrease when availability of food items declines? 2) Does the animal allocate more time to foraging when resources are scarce? 3) Does an uneven spatial distribution of resources result in an uneven/patchy use of space? 4) Does habitat sampling (searching) occur in months when resources are patchily distributed in space?

Many of the above predictions (based on the questions) have been found to be true in different animals yet the proximate mechanisms by which the knowledge is attained are still not yet completely known e.g. the presence or number of coconsumers at feeding source may indicate the location and abundance of the resource but may also indicate that the resource is likely to be rapidly depleted.

The resource-scape for arboreal herbivores varies greatly in space and time. Climatic seasonality interacts with geology and past/ongoing herbivore pressures to produce a variety of phenological patterns and spatial distributions of tree species,

coupled with a variable chemical/nutrient profile for each type of resource.

Examples

Bats: Fleming and Heithaus (1986) studied *Carollia perspicillata* in Guanacaste province of Costa Rica (Santa Rosa N P) which is a dry deciduous forest containing a mosaic of forest patches of various successional stages and patches of riverine forest. Using radio telemetry, they asked the following broad questions among others 1) Are there qualitative/quantitative seasonal differences in foraging behaviour. 2) What is the relative importance of food distribution in affecting foraging behaviour? Based on a knowledge of seasonal changes in abundance and distribution of food patches, they predicted that in the dry season. 1) Bats should forage further away from the roost. 2) they should visit more feeding areas per night. 3) they should concentrate feeding activity in a narrower range of habitats. 4) they should change locations of feeding areas more frequently.

Predictions 1, 3 and 4 were borne out, presumably in response to higher rate of food species turnover per month in the dry season. However 2 features did not change seasonally. 1) Number of feeding areas an individual visits/night. 2) High night to night consistency with which bats visit a given set of feeding areas.

According to Fleming and Heithaus, this indicates that individuals are using the same qualitative strategy all year-round -- this consists of concentrating on fruit species of low nightly density but high *spatiotemporal predictability* whenever possible to minimise the energetic costs of commuting in search of food. A similar strategy is used by *Phyllostomus hastatus* on Trinidad whereas the larger *Artibeus jamaicensis* concentrates on ephemeral but abundant fruit species (eg. figs.) on Barro Colorado Island, Panama.

Primates and prosimians

1. Theat-tailed dwarf lemur *Cheirogaleus medius* hibernates 6-8 months in the dry season when fruit, insects and nectar are scarce. When these resources are abundant, it accumulates fat under the skin in the tail which it uses as a resource during "aestivation" (Petter).

2. Gibbons in Malaya (Raemaekers 1980) reduce energy expenditure as abundance of preferred foods decline. They then exhibit diminished selectivity (reduced diet diversity) and travel less each day by concentrating on less ephemeral resources such as leaves. This phenomenon of "cutting losses" is shown by a number of primate species during crunches of preferred resources.

3. In Sri Lanka, Hladik studied of 3 sympatric primates. a) *Presbytis senex* follows strategy of minimal energy expenditure with exploitation of lower quality resources. It feeds on small number of plant species, lives in groups of 4-7 members with a small home range (approx. 4 ha). Key resources utilised are *Adina cordifolia* and *Schleichera oleosa* which are evenly distributed throughout each home range. b) *Presbytis entellus* feeds on a larger variety of species, forms larger groups (2--30 members) and use ranges of 10-15 ha. (more energy expenditure and exploitation of broader resource base). c) *Macaca sinica* (toque macaque) has 12 members per group and range = 30-50 ha; diet includes animal prey also.

Group size is a compromise between efficient food location, size of resource base (can it be shared?) and protection from predators.

Polyspecific associations are often to increase the efficiency of foraging (eg. Spider monkeys and Capuchin monkeys) as is thought to be the case with mixed-hunting parties in birds.

Giant Squirrels

The Malabar Giant squirrel *Ratufa indica* is a large territorial tree squirrel, each individual possessing an independent territory. The preferred foods are seeds and ephemeral items such as flowers and young leaves. There is considerable variation between individuals in the consumption of preferred food especially fruit. This is due to a social structure in which some individuals have restricted access to food species either because of the spatial dispersion of these species relative to the location of their feeding ranges or due to territorial exclusions which deny access to the preferred resources or a combination of both factors. Like the earlier examples, Giant squirrels cut their losses when preferred foods

are unavailable. At such times their feeding ranges shrink and they concentrate on non-ephemeral foods such as mature leaves and bark. Active territorial defense is not a frequent activity of territory owners. However, levels of aggression increase in the fruiting season when territorial incursions occur. Squirrels also use time-sharing mechanism of resource utilisation besides other avoidance tactics to prevent aggressive encounters. They achieve this by 1) territorial advertisement calls and movement/contact calls and 2) Scent marking of food resource trees. Scent marking is absent in the monsoon probably due to the negative effect of rain on the longevity of the signal.

Owing to its large body size, *Ratufa* is a relatively K-selected species. It produces a single pup per year; females may not breed every year. Weaning occurs after 5 months. Pups are dependent on mothers for long periods. Squirrels are also sensitive to extremes of temperature and may retire to their nests during such extremes or during rain. This limits the total available diurnal feeding time. Each squirrel may build 8-10 nests per territory. Nest building is also a major time consuming activity. Given the size-related reproductive strategies and aspects of its nesting biology as well as the patchy distribution of preferred fruit sources, *Ratufa* is non-migratory and territorial. Large body size in Ratufa can also provide insurance against periods of low-fruit availability because it provides the potential to expand dietary diversity to include low profit fibre-rich foods (in this case via an enlarged caecum). Large body size and its attendant dietary flexibility enable each individual to switch from a predominantly fruit diet to a predominantly leaf or bark diet depending on its own unique level of spatio - temporal fruit resource availability. Since fasting endurance scales allometrically with body size, severe restrictions (lasting for a period of hours or days) on feeding time imposed by climatic conditions (such as monsoonal rain, extremes of temperature) can be endured.

Concept of short-term v/s long-term foraging "optimization"

Should conclusions be drawn from short-term studies? What if an animal is behaving optimally in the long-term sense? eg. male squirrel monkeys store fat prior to the breeding season and then virtually starve during the period of mate acquisition. Which animals may be more suited for short-term v/s long-term studies? These are some important questions which need to be addressed.

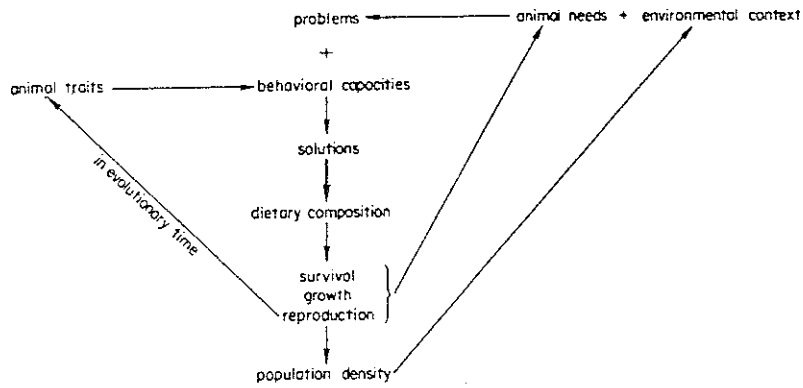

Figure 11.1. A model of the foraging process. Arrows indicate deterministic relations between classes of variables

Table 11.1. Some Components of the Foraging Universe

I Environmental Factors
- Climate
- Physical structure of habitat
- Predators
- Co-consumers
- Spatiotemporal distribution of food patches
- Patch size
- Arrangement of foods within patch
- Physical characteristics of food items
- Constituents of food items

II Foraging Problems
- When to forage
- How to locate a food patch
- What food patch to enter
- How to move within a food patch
- How to acquire food items
- How to ready items for ingestion
- When to leave a patch
- How to travel between patches

III Animal Traits
- Morphological
  - Body size and proportions
  - Tissue proportions (skin, fat muscle, skeleton, gut, etc.)
  - Musculoskeletal structure of limbs, trunk, jaw, neck, and face
  - Dentition
  - Digestive tract structure and volume
  - Brain size and structure
  - Sense organ structure
- Physiological
  - Contraction rates and fatigue resistance of muscle fibers
  - Metabolic pathways
  - Rates of metabolism
  - Digestive processes
  - Neurophysiological function

IV Behavioral Capacities
- Cognitive and perceptual
  - Learning and problem-solving abilities
  - Abilities to respond to sensory stimuli
- Travel
  - Locomotor abilities
  - Thermoregulatory abilities
- Feeding
  - Postural abilities
  - Manipulatory abilities
  - Masticatory abilities
  - Digestive abilities

VOLES AND CYCLES

BY

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CENTRE FOR
ECOLOGICAL SCIENCES

VOLES AND CYCLES

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1.Introduction:

Among the most remarkable ecological phenomena are the 10 year and 4 year cycles of small mammals, the former apparently seen only in the northern coniferous forests of North America, and the latter in the arctic tundra of both North America and Eurasia. Why these cycles occur is the topic of today's talk. The answer is not known as present. Most of this talk will consist of a review of theoretical attempts to understand these cycles, that is, attempts at model-building. Ultimately, a fully successful theory of these cycles would have to address the following facts:

(i) These cycles seem to occur only in the northern hemisphere;

(ii) They only occur in the extreme north, that is, no such cycles have so far been reported in tropical regions;

(iii) The 10 year cycle is even further restricted only to the northern coniferous forests of North America;

(iv) For some species, such as *Lynx canadensis*, the cycles seem to be *synchronized* over all the regions of North America where they occur;

(v) The 4 year and 10 year periods are the only ones seen over a wide variety of species (see below);

(vi) Within the areas of their occurrence, the same periods are seen over wide differences of habitat and geographical areas.

Given the state of confusion in the field, a model that explains at least the occurrence of these cycles and the periodicity of 4 or 10 would be remarkable advance at present.

2.Evidence

The evidence for cycles of small mammal populations before 20th century professional ecology comes primarily from fur returns and hunting-bill estimates. These records provide direct estimates only if the animal in question was killed for fur or for hunting. Even in these circumstances, many factors can bias these estimates. For fur return statistics, economic considerations, which do not remain constant over long time periods, obviously influence the numbers. An additional source of difficulty is that there is a curious kind of density-dependence that only affects the peak of a cycle. When the population number and, therefore, the density is high, the number

of animals killed by trappers and hunters is disproportionately high not only because it becomes economically desirable to prey on these animals but also because, due to hunger, animals are more likely to enter traps. Hunting statistics can be even more biased since they are also subject to fashion and local hunting regulations. Moreover, for animals such as lemmings, and voles which are neither valuable for their fur nor usually hunted, population data are based on anecdotal evidence or from data on their predators. Such data is subject to even more bias than direct records.

Nevertheless, these sources of bias are unlikely to introduce a cycle where there was none. Moreover, they would not affect the *periodicity* of a cycle when one is recorded, that is, peaks would remain peaks and troughs would continue to be troughs. However, they show that the *intensities*, measured by the height of peaks or depth of troughs, cannot be very reliably estimated from such data.

An additional source of difficulty comes from the fact that any population is subject to random fluctuations which can go upward or downward even if there is no true cycle. It is important to be able to distinguish these fluctuations from cycles. The problem is non-trivial. Suppose that we are given n random numbers, $x_1, x_2 \ldots\ldots x_n$ that are all distinct. A peak can be defined as any number x_i, such that $x_i > x_{i-1}$ and $x_i > x_{i+1}$. There are 6 permutations of 3 numbers, and 2 of these will show a peak. Thus, starting with random numbers, the probability of finding a peak is 1/3. If there are n random numbers, there are $(n-2)$ successive groups of 3. Therefore, the average number of peaks is $1/3\ (n-2)$. There will, therefore, be $1/3\ (n-2) - 1 = (n-5)/3$ cycles on the average. The average length of a cycle will be the length of the series divided by the average number of cycles, that is, $n/((n/5)-3) = 3n/(n-5)$. Consequently, if only averages are calculated, and this is all that is usually possible, one can obtain spurious cycles even from random data. Moreover, if n is large, the average length of the cycle becomes 3. It is possible to go even further: by choosing only "dominant" peaks, that is, peaks which are higher than their adjacent ones (on either side), one can generate an average cycle length of 9. 3 and 9 are surprisingly close to 4 and 10. Therefore, it appears that the observed cycles of small mammals are artifacts: the underlying data could well be random and subject to ordinary fluctuations.

This possibility is easily removed but the procedure requires some relatively sophisticated statistical analysis, introduced in the 1950s. The basic intuition is that cycles have to be regular - no one is likely to claim the existence of a cycle only on the basis of an ability to calculate mean "cyclic" lengths. With this in mind, the identification of a cycle is based on the satisfaction of three criteria : (i) there is a series of events consisting of a peak (increase above the mean) followed by a decrease to a trough (decrease below the mean) followed by a return to the mean; (ii) this series of events must

be repeated; and (iii) the repetition must occur at relatively regular intervals. The satisfaction of these criteria is judged using a statistical technique called *autocorrelation analysis*: it measures the goodness of fit between a series starting at some point, t, and the same series, now starting after an interval δ, that is, at $t + \delta$. The autocorrelation function, which depends on δ, will oscillate between +1 and -1 if a series is cyclic. For random noise the autocorrelation function will show no such periodicity. Further refinement is obtained by performing a *spectral analysis* on the autocorrelation function. This is based on the fact that any finite series can be represented as the sum of sine and cosine terms which is called its Fourier expansion. If the series is cyclic, then a particular sine or cosine term will be the only large term in the Fourier expansion, and the period (or the frequency) of the series can be estimated from this dominant term. Spectral analysis on an apparently periodic autocorrelation function provides further evidence of the existence of a cycle.

When both these techniques are applied to the data, the llowing cycles emerges. This table is by no means complete:

Four Year Cycles			Ten Year Cycles		
ecies	Common Name	Distribution	Species	Common Name	Distribution
mmus *lemmus*	Brown lemming	Norway	*Lepus americanus*	Snowshoe hare	Canada, Alaska
mmus *imucronatus*	Brown lemming	Canada, Alaska	*Lynx canadensis*	lynx	Canada
ctrostonyx *endlandicus*	Collared lemming	Canada	*Vupes fulva*	red fox	Canada
ctrostonyx *dsonius*	Collared lemmig	USA	*Martes americana*(?)	pine marten	Canada
opex *lagopus*	arctic fox	Canada, Alaska	*Martes pennauti*	fisher	Canada, USA
pes *vupes*	red fox	Scandinavia	*Gulo luscus*	wolvesine	Canada, USA
pes *fulva*	red fox	Canada	*Memphitis memphitis*	striped skunk	Canada, USA
crotus *'estis*	vole	USA	*Ondatra zibethicus*	muskrat	Alaska, Canada, USA
crotus *insylvanicus*	vole	USA	*Mustela vison*	mink	Canada
crotus *lifornicus*	vole	USA	*Canis lupus*	wolf	Canada
crotus *vnsendii*	vole	USA	*Canis latrans*	coyote	Canada
crotus *irogaster*	vole	USA			

3. Models

The existence of these cycles has long been recognized as a puzzle that ecological theory should be able to resolve. Now two aspects of these cycles should be distinguished. First, there is the period of the cycle: approximately 4 - 10 years. Second, there is the intensity. As noted before, many factors can bias the intensity. Autocorrelation and spectral analyses, moreover, only provide data on the period. Therefore, any model that can account for the period of these cycles would be satisfactory irrespective of whether or not it also accounts for the intensity, as long as the latter remains within plausible limits (in the model). Consequently, all the models that will be discussed below have been constructed - and are judged - with periodicity in mind.

Moreover, there is a deeper philosophical reason for concentrating on periods and not on intensities. Ecological systems are overwhelmingly complex, and this complexity routinely precludes the possibility of constructing tractable quantitative models that take into account all the interactions within a system. Often, what can only be achieved, and what is most interesting, is the *type* of behaviour predicted by a model. This is called *qualitative modelling* but "qualitative" here should not connote any lack of rigor. Qualitative behaviour can occur in a system at different levels of detail. In the systems described here, at the lowest level is the qualitative behavior that these systems have cycles. At the next level of detail is the behavior that the periods of these cycles are always 4 or 10. There does not appear to be any other qualitative behavior that is quite as puzzling as these two. Compared to them, the actual intensities of the cycles pale in interest.

Because of the interest in the problem, the general complexity of ecological systems, and the long period during which this problem has remained unsolved, a bewildering variety of models have been offered as purported solutions. Not all of these have been presented with mathematical rigor. Some have been merely verbal, and part of the task of theoretical research in this field consists of constructing exact versions of verbal models. The models presented below have been classified into three categories: (i) "external" models; (ii) interacting species models; and (iii) single species models. This classification is only for convenience. It is not the only one possible and, indeed, is not as conceptually clarifying as a good classification should be. There is as yet no standard classification of models in this field. The names given to the models have also been selected for convenience; here, too, there is no extant standard.

(i) "External " Models:

These models are "external" in the sense that the crucial factors responsible for the cyclic phenomena in these models would conventionally be considered as "external" to the ecosystem

and often be lumped together in the heterogeneous category of "environment".

(a) Weather models

The motivation behind looking at weather as a critical factor is the observation that cycles can sometimes be synchronized over large areas (e.g. *Lynx canadensis* over N. America). It is obvious that weather can influence population members. If there is a cyclic pattern in the weather, this could potentially induce a population cycle. There is little evidence for this periodicity in weather in the time-scale relevant to these cycles.

(b) Sunspot and Lunar Cycle Models.

The 11.2 year sunspot cycle has been suggested as a source of the 10 year cycle but its period is too long for it to have a direct effect on that cycle. Because of the 10.9 day difference between the solar and lunar years, it is possible that 29.5 day lunar cycle is involved in the generation of both the 10 year and the 4 year cycles. If there is a fixed "critical period" such as the beginning of breeding in spring during which some event such as a new moon could affect fitness, cycles would result: the new moon in spring would generate a 9.6 year cycle if the critical period is 1 day long. If it is 6 days long, the 4 year cycle could result. There are many other such models that can be constructed based on various planetary cycles but these are probably best left for a future sub-discipline of astrological ecology.

(ii) Interacting Species Models:

These models assume that cycles arise because of an interaction between two (or more) species, usually a prey and a predator.

a) Lotka-Volterra Models:

The classical example of the interaction between a predator and a prey species is the Lotka-Volterra model:

$$\frac{dx}{dt} = ax - bx^2 - cxy$$

$$\frac{dx}{dt} = -ey + c'xy$$

where x is the density of the prey species, y the density of the predator species, and a, b, c, c', and e are rate constants. Note that in the absence of predation, that is $y = 0$,

$$\frac{dx}{dt} = ax - bx^2 = ax(1-b/a\ x)$$

Which is the logistic equation with a as the intrinsic growth rate and a/b as the carrying capacity. As stated, this system of equations does not give rise to cycles.

If however, the prey species grows exponentially in the absence of predation, that is, $b = 0$, these equations become:

$$\frac{dx}{dt} = ax - cxy$$

$$\frac{dx}{dt} = - ey + c'xy$$

and stable cycles can be formed. However, the period of the cycle depends on all the parameters and the initial population densities. It would be miraculous if these were all coordinated in such a way that the same period is obtained for a variety of species across a wide diversity of habitats. More sophisticated models of the predator-prey cycle (including stochastic versions of the Volterra equations) fare no better in explaining the ubiquity of the 4 year and 10 year cycles.

(b) Cyclic Prey Driven Models:

One popular idea is that at least cycles in predators can be explained by the predator population tracking a cyclic prey population. This has often been suggested for the *Lynx (Lynx canadensis)* - snowshoe hare (*Lepus americanus*) system and the fisher (*Martes pennanti*) - snow shoe hare systems. Moreover, cycles of the striped skunk (*Memphitis memphitis*) and musk rat (*Ondatra zibethicus*) have also sometimes been explained on the basis of their being alternative prey to normally snow shoe hare predators. But perhaps the most convincing evidence comes from the colored fox, *Vulpes fulva* which has a 4-year cycle on the Labrador coast where its chief food is the lemming and other microtines, and a 10- year cycle elsewhere in Canada.

It should be emphasized that such a model does not explain the cycles of the underlying prey species and so, at most, it can only provide a partial explanation of the general cycle problem. However, does the model even do what it is supposed to, that is, predict robust predator cycles from the prey cycle ? It is easy enough to write down equations for the process :

$$\frac{dx}{dt} = aw \cos(wt + a) - cxy$$

$$\frac{dy}{dt} = -ey + c'xy$$

As far as I know, this model has never been analyzed. It is likely that is has non-trivial dynamics.

(c) Cyclic Predator Driven Models :

Alternatively, could intruisic cycles in predators drive cycles in prey ? Two models can immediately be written down:

$$\frac{dx}{dt} = ax - bx^2 - cxy$$

$$\frac{dy}{dt} = ew \cos(wt + a) + c'xy$$

if the independent growth of the prey is represented by a logistic equation; or

$$\frac{dx}{dt} = ax - cxy$$

$$\frac{dy}{dt} = ew \cos(wt + a) + c'xy$$

if the independent growth of the prey is exponential. As far as I know, these models, too, have never been analyzed.

(iii) Single Species Models:

These models look for characteristics of a cyclic species itself in order to try to account for those cycles. Among the main reasons for concentrating on these is the apparent failure of finding the desired periodicity (4 or 10) in environmental factors and the interacting species models. Surprising many of these single species models display a tremendous amount of complexity in their behaviour, and many of them are very poorly understood at present.

(a) Stress Models:

The basic idea is that animals are under stress at high densities because of a lack of food or cover, leading to intraspecific conflict or increased predation pressure. The hormonal response to this could include increased exertion of the adrenal and pituitary glands which can decrease viability by producing exhaustion and low resistance to disease and other mortality factors. There is little evidence in support of this model which, in any case, has never been exactly formulated. Intuitively, it is hard to say why this sort of stress, even if it exists, should lead to cycles (especially with the ubiquitous 4 year and 10 year period).

(b) Delay Models:

Perhaps the most interesting models in population dynamics are those which attempt to incorporate delays: there's a 4-6 week gestation period for fertilization before a Vole (*Microtus pennsylvanicus*) becomes an adult (reproductively capable) member of the population; changing reproductive rates, etc. One way in which this has been modelled is to introduce the delay-differential equation for logistic growth :

$$\frac{dN}{dt} = \frac{rN\,(1 - N_{(t-\delta)})}{k}$$

if $r\delta > \pi/2$, this equation gives rise to stable oscillations for large t. The period of the oscillations remains roughly 4 δ, over intensity (amplitude) changes by 2 orders of magnitude. δ-1 would give the 4 year cycle. However, the natural interpretation of , at least for Voles, is 4 -6 weeks that is $\delta < 0.16$ and this does not give the appropriate periodicity.

(c) Behaviour/Genetic Polymorphism Models

Among the most interesting models that have been proposed for the origin of cycles are those that assume that there are behavioural differences among the individuals in a population which lead to cyclic behaviour of that population. Different behaviours can become dominant at different stages of the cycle and the behaviours may be under genetic control. In particular, it has been sugsted that dispersal from a population, even before it has reached saturation, is the critical necessary behaviour for cycles to occur. One model for this process assumes that such behaviour is genetic, and selection favors large aggressive animals with low fertility at high densities, possibly leading to dispersal, and smaller docile animals with high fertility at low densities.

A quantitative model incorporating this hypothesis is easily constructed. Let aggressive behaviour be controlled by 1 locus with 2 alleles; let the aggressive allele, a, be recessive. Let

x_1, x_2, x_3 be the numbers of *aa*, *Aa* and *AA* respectively. Let the number of females be equal to the number of males. Then:

$$\frac{dx_1}{dt} = (b_1x_1 + b_2x_2/2)p - d_1x_1 - ex_1$$

$$\frac{dx_2}{dt} = b_1x_2\beta + b_2x_2/2 + b_3x_3p - dx_2$$

$$\frac{dx_3}{dt} = (b_3x_3 + b_2x_2/2)\beta - d_3x_3$$

where $p = \frac{x_1 + x_2/2}{x_1 + x_2 + x_3}$ is the frequency of *a* and $\beta = 1-p$ is the frequency of *A* and (b_1, b_2, b_3) and (d_1, d_2, d_3) are respectively the birth and death rates of *aa*, *Aa* and *AA* and are frequency dependent. e is the rate of immigration of aa. If e = 0 and selection is slow, then it is easy to show that cycles exist, but are probably not stable. That is as far as the analysis has been taken so far.

OPTIMIZATION OF FREQUENCY DISTRIBUTIONS OF SEEDS PER FRUIT IN PLANTS

BY

UMA SHAANKER

OPTIMIZATION OF FREQUENCY DISTRIBUTION OF SEED NUMBER PER FRUIT IN PLANTS

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Starting from an otherwise normal distribution of ovule number per ovary in multi-ovulated species, plants exhibit distinct patterns of distribution of seed number per fruit. These distributions range from highly positively skewed to negatively skewed and ocassionally "disturbed" or multi-modal. In this lecture, I seek to discuss whether these represent optimal distributions. I do this by using specific cases of plant systems studied at our centre.

Case (A) : Negatively skewed distribution of seeds per pod

This distribution is characterised by a long tail to the left, with most fruits having many seeds and a few with less. Typical examples of this distribution is found in Leguminous pods (eg. cowpea, Bauhinia, Leucaena etc.). In these species, the pods at maturity dehisce and release the seeds. As such therefore, the pod coat merely serves as a protective organ. Consider that the maternal parent invests

certain energy (cost) in packing the seeds as given by

$$TC = FC + VC * n ,$$

where,

FC = fixed cost of packing seeds in fruits (in structures such as peduncle),

VC = variable cost (in pod coat elongation) and

n = seed number per fruit

The cost of packing per seed is therefore

$$TC/n = 1/n*(FC) + VC$$

In otherwords, the packing cost per seed decreases with the seed number. Thus selection to minimize the cost of packing per seed should favour packing as many seeds as possible. We examined this prediction in Leucaena. The negatively skewed distribution of seeds per pod conforms to that expected on the basis of minimizing the cost of packing per seed.

Case (B) : Positively skewed distribution of seeds per fruit

Clearly, the positively skewed distribution of seeds per pod with a long tail to the right cannot be explained (and hence cannot be regarded optimal) when compared with that expected on minimizing the cost of packing. Ganeshaiah and Uma Shaanker (1988) argued that it is possible to view these distributions as a response to selection for enhancing the dispersal efficiency of fruits through wind, water or animals. In Dalbergia sissoo, the entire fruit is dispersed as a unit through wind. The dispersal efficieny of an object

in air is inversely proportional to its wing-loading (weight to surface area). This is because, objects with low wing-loading when released from a height, settle slowly (and hence have a greater probability of being swept away by wind currents) compared to those with high wing loading. In Dalbergia sissoo, wing loading of fruits increases with seed number and hence fruits with few seeds are likely to be dispersed to farther distances than those with many. In otherwords, if dispersal is advantageous, selection should favour packing few seeds in the fruits though this involves a high cost of packing per seed. Infact, positively skewed distribution is common pattern in species whose fruits are dispersed by wind, water and in some instances by animals.

Case (C): Normal distribution of seeds per fruit:

In the skewed distributions, the disadvantages associated with the region of the skew had to be demonstrated before an inference on the optimality or otherwise of the distribution could be made. The task of drawing such a conclusion on the optimality of a normally distributed frequency of seeds per fruit is doubly difficult because one has to demonstrate the negative selection on two parts of the curve, the left and the right tail.

In Solanum pubescens, a bird dispersed secies, the frequency distribution of seeds per fruit is normally distributed. We asked if this distribution is infact shaped by the differential preference of birds for fruits of

varying size classes (and hence seed number). Both in situ data on the removal rates of fruits of different size classes and in vitro feeding trials with the dispersers, red vented bulbuls, indicated that birds prefer medium to large size fruits than small and very large fruits. In otherwords selection for increasing the probability of dispersal in Solanum should favour medium to large size fruits. Indeed the observed frequency distribution of seed number per fruit closely compares with the one suggested based on the preference data.

Case (D) : Disturbed/multi-modal distribution of seeds per fruit:

These distributions are not very common and are yet to to be satisfactorily expalined. For example, Caesalpinia pulcherrima, exhibits a distinct bimodal distribution of seeds per pod. Though the right mode is explicable as a response to selection to reduce packing cost per seed the left mode is not.

In summary, an attempt has been made to identify the selective forces that might explain the observed frequency distribution patterns in plants. That the observed compares well (on gross scale) with that expected on the basis of the various selective forces may be taken as an indication that the observed distribution pattern of seed number per fruit in plants are indeed optimal. However, a few questions remain at large, for example : do these selective forces

explain the tails of the distribution ? when more than one selective forces operate - what are the weights to be attached to each of the factors ?

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PLAUSIBLE ECOLOGICAL DETERMINANTS OF SIZE & MATING SYSTEMS IN THE DHOLE CUON APLINUS

BY

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PLAUSIBLE ECOLOGICAL DETERMINANTS OF GROUP SIZE AND MATING SYSTEMS IN THE DHOLE *CUON ALPINUS*

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The order Carnivora displays a remarkable array of social systems ranging from highly solitary species to obligate social species exhibiting high levels of cooperative hunting and breeding. Cooperative hunting has been well documented in Lions (*Panthera leo*) (Packer *et al*, 1990), African hunting dogs (*Lycaon pictus*) (Malcom and Marten, 1982) and Dholes (*Cuon alpinus*) (Johnsingh, 1982). Cooperative breeding is exemplified in highly social canids such as Wolves (*Canis lupus*) (Harrington and Mech, 1981), African hunting dogs (Malcom and Marten, 1982) and Dholes (Johnsingh, 1982). Ecological factors are thought to play a significant role in moulding carnivore society. The resource dispersion hypothesis (Macdonald, 1985) stands out as an elegant explanation for grouping in carnivores which rely on resource patches whose richness varies both temporally and spatially. Explanations for mating systems and cooperative behaviour observed below suit from this hypothesis.

Two packs of dholes in the Mudumalai Wild Life Sanctuary which have been monitored extensively for the last three years may provide a useful model for testing this hypothesis. Their principal prey species, Chital (*Axis axis*) live in large herds, which may be thought of as patches, whose richness varies both temporally and spatially. Data will be presented on the nature

of such patches and the manner in which dholes may be utilizing such patches to try and suggest why grouping in dholes may fit the explanations offered by the resource dispersion hypothesis. Home territories encompassing such patches may be rare causing ecological constraints to dispersal. Consequently the mating system may be influenced by such forced building up of groups. Preliminary information will be provided on the dominance hierarchy observed and how this could comply with the hypothesized mating system. Finally the implications of such a mating system on the prevalence of the high levels of cooperative behaviour will be inferred.

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BIOLOGY AND BEHAVIOUR OF BATS

BY

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Biology and Behaviour of Bats

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Bats are the only flying mammals that mastered flight much before man's own lineage began. Today they form the second largest group of mammals in their number of species and the most abundant. Almost a thousand species are distributed around the world varying from the tropical "flying fox" which weighs about one kilogram to the tiny Kitti's hog-nosed bat of southeast Asia that weighs about two grams.

Bats belong to the order Chiroptera which means hand-winged. They fly with their fingers connected to one another by a web-like membrane and they crawl by their thumbs. The order Chiroptera is divided into two suborders - microchiroptera and megachiroptera - and they roost in different kinds of habitats such as caves, caverns, crevices, cellars, branches of trees, hollow-trees, culverts, the underside of bridges, temples, ruins and attics. Interestingly, a few species of bats modify large palm leaves by biting a series of holes across the centre of the leaf so that the leaf hangs like a tent; the bats then roost inside.

The feeding habits of bats show remarkable dietary variations. The megachiropterans feed upon fruits and nectar and most of the microchiropterans prey mainly on insects. However, there are bats belonging to the latter which favour additional food such as frogs, mice, fish, the blood of cattle and even smaller bats.

The activity pattern of bats remarkably synchronizes with the environmental factors especially to the light-dark cycles. The timings of daily onset and end of activity have been studied for several bat colonies. During late afternoon the bats exhibit arousal activity by showing increasing restlessness and begin to make circling flights in the large chambers or corridors of caves. The endogenous regulator acts as a 'wake-up timer' to insure the arousal of bats and 'turning on' the nervous system to regain the full sensory capacities before trying to perceive

the external environment. The circling flights around the cave mouth may allow the members of a colony to check their endogenous clock against the light-dark cycles over the seasons and to assess the light conditions. This is known as 'light sampling' behaviour. When the darkness advances, the bats set out for foraging and leave the cave in groups. This emergence by coup is probably valuable to confuse the predators (eg. owls) that usually wait at the cave mouth during evening hours. The time of outflying of the first bat indicates the onset of activity for the colony. Similarly the time at which the last bat returns to the cave during pre-dawn hours indicates the end of activity. The onset and end of activity go parallel with the timings of sunset and sunrise over the seasons. The time interval between the onset and end of activity represents the duration of activity of the colony and it shows a positive correlation with the duration of night.

It can be a great fun to follow the bats during nights in the field and thus gaining an intimate picture of their foraging activity. By marking the bats with visual marker tags or chemiluminescent tags it might be possible to follow the bats in the open area. However one has to visually locate the tagged individuals while using this light - emitters. Instead, in this age of electronic gadgets, radio tracking is a seductive technique to make a systematic study on the foraging behaviour of shy or elusive animals like bats. It needs a set of expensive equipment - transmitters and receivers. By means of radio tracking, it is possible to find out the direction and approximate distance covered by the bats and to quantify the duration spent in flight and rest through out the nights for about two weeks.

Bats fascinate us because they "see" with their ears, hang upside-down to sleep by day, and can catch insects while flying even on the darkest of nights. Bats can thread their way dexterously through hill and dale and thickets and bushes in total darkness. They do it with a kind of sonar that challenges our highest technology. While flying they emit a series of ultrashort pulses of patterned, high-frequency, high-intensity sounds through the nose or mouth, and adroitly pinpoint the exact location of obstacles and of the smallest prey with the aid of the echoes coming back from them.

The discovery of this phenomenon is rather recent. In 1794 the Italian scientist Lazzaro Spallanzani demonstrated that bats can fly even when blinded. In Geneva, Ludwig Jurine added the significant discovery that bats could no longer perceive

obstacles once their ears were tightly plugged with wax or other materials. In 1920 the English physiologist H Hartridge hypothesised that bats emit high-frequency sounds, above the range of human hearing, and use their echoes for orientation. In 1938 the American biologist Donald R Griffin used instruments designed by G W Pierce and demonstrated that bats emit ultrasonic sounds with a frequency of more than 20,000 cycles/sec (inaudible to the human ear) and utilise the reflected echoes to detect obstacles and to navigate in their environment.

Echolocatory navigation is restricted only to microchiropteran bats. The megachiropterans have prominent eyes, depend on vision to reach feeding areas and on the sense of smell to locate ripe fruits. It is thus clear that the microchiropteran bats are very efficient gatherers of insects such as moths, beetles, crickets and grasshoppers. A single bat may snatch two insects out of the air in less than five seconds and as many as 500 insects in an hour. However, some of the insects have ear-like structures sensitive to ultrasounds and are able to protect themselves from the marauding bats. When bats approach, noctuid moths, which are serious agricultural pests, take evasive action by making a variety of flight patterns, loops, spirals and changes in both speed and direction or they simply fold their wings and drop like pebbles. Arctiid moths have been found to emit trains of ultrasonic clicks to which are ascribed a variety of functions ranging from jamming the echolocatory system of bats, to stratling them, to conveying a warning that they are distasteful.

A few species of bats switch off their echolocatory apparatus to circumvent insect defenses and rely on other cues. The fringe-lipped bats (Trachops cirrhosus) use the sounds produced by their prey-frogs, while the Indian false vampire bats (Megaderma lyra) use the rustling movement of mice, the jumping of frogs, and the running of spiders and geckoes. Since they passively listen to the noise associated with the movement of the prey, it is known as passive method of prey detection. Nevertheless a few individuals of M. lyra skim at the surface of the pond in darkness for a few minutes, apparently detect a stationary frog and in a dart the bat captures a frog in its mouth. While skimming at the water surface the bat emits ultrasounds and thus actively uses its echolocatory system. We call this method as active acoustic localization of prey in water. The returning echoes from protruding targets (head of a frog) in the water should be easily distinguished from echoes returning from the smooth water surface which acts as an acoustic mirror. Interestingly the bats are not able to detect a freshly killed frog if its head is immersed just below the water surface.

Being mammals, bats carry their young in the womb until they are ready to be born. The gestation periods range from six weeks to eight months. Pregnancy does not begin soon after mating. A few hibernating bats living in temperate areas mate before the onset of hibernation and the females store the sperm during the period of hibernation (about four months). Fertilisation occurs after the termination of hibernation. No other mammals stores sperm for such long periods as do these species of female bats.

Each female gives birth to a single young and the newborn babies are hairless, sightless and flightless - but with claws to grip for precious life. Mothers lavish meticulous care upon their babies and carry the latter with them in the abdomen while flying night after night, outmanoevering hundreds or even thousands of insects. The babies tenaciously cling to the body of their mothers on such wild rides. Sometimes, to lighten the load, mothers leave their young at home. The youngsters wait for their mothers to return with teats full of warm milk. Remarkably each mother is able to identify her own baby in the prevailing darkness, by the baby's sound and scent. The adult bats of the hipposiderid bats (Hipposideros speoris) emit constant frequency (CF) sounds at 135 kHz with a frequency modulated (FM) tail with no harmonics. But at the early stages of life especially the newborn babies emit multiharmonic sounds with a combination of FM - CF - FM pattern. At prevolant and volant stages (about 30 days of age) most of the energy is concentrated in the second harmonic which is elevated to the frequency range of adults' CF - FM pattern at the age of about 6 weeks. However the young bats wean after 3 months, begin to operate their sonar system and become independent.

Although bats are known to host a variety of microbial organisms, disease transmission to man is rare. According to Merlin D Tuttle, who has studied bats for the past 20 years in various parts of the world and examined their impact on their native environment, parasites of bats are not significant to human health and even the danger of rabies "has been vastly exaggerated". Rabies infection in bats is rare in Asia, Africa and Europe and unknown in Australia. The US reported a total of nine cases of human rabies from bats in more than 30 years and only a single case is known in Canada.

Bats are highly beneficial in that the insectivorous kind control insect pests, and the fruit-eating kind help in tropical reforestation by defecating seeds of the fruits they consume as they fly over barren areas. Nectar bats are the sole pollinators of several valuable species of trees and plants such as peaches,

bananas, mangoes, guavas, figs, cashews and cloves. They also produce hundreds of thousands of tons of guano which is a major source of fertiliser. However most people do not realise the beneficial role of bats and destroy them in thousands each year.

Bats are legally protected in the Soviet Union and in all European countries. In a few areas of India they are considered sacred. However, unawareness and ignorance of the beneficiality of fruit bats coupled with misconceptions and unjust persecution as crop pests, have resulted in their categorisation as vermin in Schedule V of the Indian Wildlife Protection Act 1972. Tuttle recently formed Bat Conservation International (BCI) based at Austin, Texas, USA to disseminate information about bats to conservationists, health officials, educators and the news media. M K Chandrashekaran, Professor in the Department of Animal Behaviour, Madurai Kamaraj University, Madurai is a member in the scientific advisory committee of the BCI, from India. The purpose of BCI is to prevent the extinction of bats, to ensure the survival of viable bat populations and to inform the public of their value.

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COST OF INCREASING HOST DIVERSITY IN POLYPHAGOUS MITES

BY

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Cost of switching hosts in Tetranychus urticae (Acari) - a case study

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As opposed to monophagy polyphagous animals should not experience host scarcity, even if some host species in their diet breadth are rare. Hence being polyphagous helps a species in continuously feeding and breeding. But every time a host species is switched it involves some cost. The costs involved are mortality, fecundity and survival of offsprings of individuals arriving on the new host in addition to finding the host.

Tetranychus urticae is a phytophagous mite with wide distribution and over 25 plants recorded as hosts. This was cultured in the laboratory for over 35 generations on mulberry. For studying the effect of changing hosts the mites were shifted to three different hosts, viz., French beans, brinjal and chow-chow. The table below shows that when the mites are transferred to a host like French beans, fecundity, developmental time, adult mortality and juvenile survival are unaffected whereas when it is shifted to a host like chow-chow, its fecundity and juvenile survival are lowered, but not as drastically as would happen when it is shifted to brinjal.

This indicates that, as long as T. urticae is able to find an equally favourable host like French beans it is

cost-effective to switch, but in the process if it encounters hosts like brinjal it will be very detrimental.

	Fecundity per female	Days to develop (egg to adult)	Adult survival (days to 50 % mortality)	Juvenile survival (%)
Mulberry	61.74	11.304	14.4	96.75
Beans	58.16	11.88	14.8	90.9
Chow-chow	37.02	11.77	16.2	86.32
Brinjal	20.11	13.50	15.4	74.14

INSECT – PLANT INTERACTIONS : THE GALL FACTOR

BY

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Insect - Plant Interactions: The Gall Factor

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Introduction

Galls induced by insects have fascinated naturalists from the time of Hippocrates [c. 350 B.C.]. Although the intricacy of this relationship involving two unrelated genomes is not yet clearly known, it is now generally accepted that galls arise on plant organs as a result of feeding or oviposition activity of certain groups of insects. The insect is not only highly specific in its host plant and organ selection, but also has profound control over the shape, structure, colour, and dehiscence of the gall. Generally an insect accomplishes this by imparting a wound-like stimulus on the host tissues that are at a particular stage of development. This association, in principle, benefits the insect by providing shelter and food and protecting it from predatory and parasitic organisms.

Evolution of the Gall-Forming Guild

Gall insects are specialized herbivores and are generally restricted to seven orders. Because these insects have different non-cecidogenous ancestors, they should have evolved along parallel lines. Given that detritus-feeding [saprophagy,

..2.

scavenging] is the most-primitive of trophic types in insects, feeding on living plant and animal substrates evolved later in geological history and therefore it is considered derived. Herbivory, per se, appears to have evolved in the Cretaceous particularly because of the radiation of Angiosperms in that period. Spore feeders and later pollen feeders, followed by plant-sap feeders represent anciently-derived trophic types, whereas stem-borers, foliage feeders, and leaf miners represent recently-derived types. Within various arthropod families, major and minor groups of gall inducers can be recognized. Most members of a major group [a family or a subfamily] generally are gall formers and usually they occur on a variety of higher plants. Major groups of gall inducers are supposed to have evolved from an ancestor that already possessed gall-forming ability in an early period of Angiosperm radiation.

Minor groups of gall inducers among Curculionidae, Tenthredinidae, Gelechiidae, Tephritidae, and Agromyzidae have remained exceptions within their families where recently-derived types of phytophages are dominant. Host plant ranges are narrow becauee radiation appears to have occurred only in particular gall-making genera. However, compared with other herbivores, gall inducers are of recent origin.

Cecidogenetic Patterns

One of the striking aspects of galls is the rich diversity of shapes, colours, and sizes. Some appear like fruits and seeds,

and membranous bags or hard swellings. It is, however, important to note that each gall insect species evokes a specific type of a host response developing into a gall.

The following are the general rules of cecidogenesis: [a] Development of most of the insect galls synchronizes with the active growth period of the host plant. [b] Meristematic host tissues respond intensely to the gall insect's action by developing into a gall (Exceptions: Aphid stem mothers, Diaphorina truncata [Psylloidea]). [c] Gall development can be recognized into [i] initiation, [ii] growth and differentiation, [iii] maturation, and [iv] dehiscence. [d] Host tissues respond through hypertrophy and hyperplasia, controlled essentially by the gall insect.

Gall initiation process involves a clear recognition of the host plant and a suitable site on it by the gravid female in some (thrips, aphids, psyllids, and coccids) or by the first instar larva in others (gall midges). When the gall is initited by the first instar larva, feeding activity triggers gall development. If the gall is initiated by a gravid female, feeding activity as in many species of gall thrips [Thysanoptera] or oviposition activity as in many cynipids and sawflies [Hymenoptera] initiates gall development.

Cecidogenesis, in principle, does not involve mechanisms that are unknown in normal plant morphogenesis. However, morphogenetic events often overlap or manifest in combination

and so are often difficult to differentiate and analyze. Gall tissues act as physiological sinks as the wounded plant tissues do, draining photoassimilates from other parts of the plant. These sinks occur close to the insect as a result of insect's continuous feeding and the consequent wounding stimulus and cell proliferation, mobilizing a variety of metabolites.

Gall-inducing factor varies with insect groups: among thrips wounding and salivary secretions play a vital role, among sawflies, plant wounding and ovipositional fluids are important, among cynipids eggs and young larvae have a strong lytic action; in gall midges, light mechanical wounding and salivary enzymes appear vital. Insects with primitive mandibulate mouth parts [sawflies, moths, beetles] induce simple galls, while gall midges and cynipids with suctorial mouth parts induce complex gall types.

In short, the gall insects modify specific areas of their host plants by provoking unusual morphogenetic expressions in such a way that new subcellular, cellular, tissue, and organ changes get expressed. The insect, thus, is able to open and provide opportunities for new developmental activities in the host plant which were initially directed against it, but later these changes become useful to the insect.

Nutrition of Gall Insects

Gall formation represents one of the most elaborately evolved and complex aspects in insect - plant relationships. Among the

several dimensions of dependences identified, nutrition of the gall insect is a key factor. Each type of gall insect obtains its nutrition in a particular way and the plant tissues respond corresponding to the insect stimulus [mode of action of the mouth parts and salivary secretions]. Feeding mechanism of the gall insect can be grouped according to the family and they range in complexity from simple punch and suck activity of thrips to subtle sucking of gall midges that occurs without puncturing the host cells.

The nutritive cells show specialized features such as [i] hypertrophied and highly lobed nuclei, [ii] hypertrophied and often vacuolate nucleoli, [iii] abundant cytoplasmic ribosomes generally grouped into polysomes, [iv] numerous, poorly developed plastids and mitochondria, clustered around the nucleus, and [v] abundant autophagic vacuoles [the last being particularly characteristic of old nutritive cells]. The nutritive tissue is an adaptational modification of the existing plant tissue developed by the the insect's feeding stimulus and it extends towards outside from the locus of larval incidence. The few layers of cells that usually lie close to the insect are the "typical nutritive tissue" while those that occur along the periphery are the "storage nutritive tissue".

Interactional Dynamics of the Gall Insect and their Host Plants: Some Case Studies

[a] Multiple Gall Insects and Host Plant Accommodation [The

Phragmites communis and Gall Midges Model]

Growth in temperate common reed [*P. communis*] essentially involves 2 distinct phases: elongation of the earlier developed tissue and production of new internodes. Four gall midges, *Giraudiella inclusa*, *Lasioptera hungarica*, *Prolasioptera arundinis*, and *Microlasioptera flexuosa* [Diptera: Cecidomyiidae] attack *P. communis* at different times of plant growth on different plant organs. Under natural conditions, a mutual relationship exists between the plant and midges. *G. inclusa* and *L. hungarica* attack the main stem and they show a simple relationship. Larvae of *L. arundinis* develop on the lateral shoots and a complex relationship exists between the plant and this midge. Contemporary attack of lateral shoots by *L. arundinis* and the second generation offspring of *G. inclusa* demonstrates a more complex relationship with the plant.

[b] *Evolutionary Relationships between Gall Insects and their Host Plants* [The Sawflies and *Salix lasiopsis* Model]

The evolution of leaf-folding and gall-inducing species of sawflies can be traced by a comparative analysis of nematine sawflies [Tenthredinidae: Nematinae: Nematini] that occur on the shoots of *Salix lasiopsis* [Salicaceae]: [i] *Nematus* sp. in leaf holes made by some other external feeder, [ii] *Phyllocolpa excavata* inducing leaf folds, [iii] *Pontania pacifica* inducing leaf galls, [iv] *Euura* sp. inducing petiole galls, [v] *Euura lasiopsis* inducing stem galls, and [vi] *Euura macronata* inducing

bud galls. Among this set of cecidogenous organisms, species of Nematus oviposit below the leaf epidermis and the larvae feed externally on a leaf hole made by another arthropod and continue feeding towards the leaf edge. Clearly, this is the progenitor from which the galling species are derived. Phyllocolpa oviposit along the leaf edge and cause a leaf fold and the larva feeds within the fold. Once this ability to alter leaf development had evolved, a slight shift in the oviposition site in the lamina, as in P. proxima might lead to the initiation of galling. Another small shift in the midrib would result in the characteristic gall position of Pontania. A slight shift in the oviposition site to lower portions of the midrib could have given rise to petiole galls typical of Euura, and even lower oviposition on the petiole would produce stem galls as in the other species of Euura. Thus divergence of sawfly species from a Nematus-type onto different parts of the host plant may have resulted in oviposition behaviour leading to speciation. Interestingly, this evolutionary prediction is also supported by the characters of the saw of the sawflies in terms of the ovipositor length, increasing narrowness of the saw, and increasing number of the annuli - all related to the deepening oviposition into plant tissues.

[c] Host Plant Quality and Gall Insect Behaviour [Sawfly and Gall Aphid Models]

Mortality of larvae and embryos within eggs are frequent during

the development of cecidogenous Euura lasiopsis . Assessment of mortality rates over a 4-year period [1979-1982] indicates that this is strongly related to the host plant [Salix lasiopsis] quality. In three out of the four clones [MNA-2, MNA-4, NF-8, and NP-9] examined each year, the rate of abortions increased, suggesting that Salix plants were becoming increasingly resistant to sawfly attack. This pattern was correlatable to the reduced summer and winter rainfall, that caused reduced plant growth and eventually a reduced gall growth. In general, a change in host plant quality was obvious in relation to water availability which in turn altered gall insect survival.

At least with regard to the temperate species of gall aphids [Pemphigus sp.], large host leaves of Populus were more favoured than small leaves. Larger leaf area necessarily offered larger photo-synthetic surface area and therefore, greater productivity was obvious. In Populus, large leaves occur in the terminal regions of shoots, the sites of active growth and represent natural sinks of plant metabolites. Large leaves of Populus are also less defended phytochemically from gall aphids. Preference of Pemphigus betae for large leaves of Populus angustifolia has been negatively correlated with the concentration of phenolics. Smaller leaves avoided by the stem mothers have higher concentrations of phenolics than the preferred large leaves. Further, the large leaves on which the gall aphids feed have less susceptibility to wounding and

consequent blocking of phloem.

[d] Insect Life Cycles and Host Plant Modifications [Subtropical and Temperate Homopteran Gall Models]

Mangalorea hopeae [Coccoidea: Beesoniidae] induces sea-urchin like galls at the vegetative axillary angles of Hopea ponga [Dipterocarpaceae]. Immediately after the monsoon rains, freshly-emerged female larvae of M. hopeae invade the axillary angles of the vegetative buds of H. ponga, exploiting nutritionally the space created by the extraaxillary position of the buds. Feeding action of these larvae [one larva per vegetative axillary bud] activate the buds to develop into galls with an eccentrically grown massive columella that arches over the coccoid which never moves. The epidermal and subepidermal cells of the modified bud develop into hard, multicellular appendages. In the gaps between two neighbouring appendages, one male nymph occurs with its head end pointing towards the central core. During gall development, two life stages of the coccoid participate actively in Hopea gall system: [1] A single female I larva initiates the gall and it grows with the gall. [2] A progeny of males developed from the female that initiated the gall crawl out of the gall cavity of the mother and occupy spaces between the appendages; by their feeding action they alter the gall's physiology which results in the drying of galls enabling the escape of mature males.

In the galls of Trioza jambolanae [Psylloidea: Triozidae] on

the leaves of Syzygium cumini [Myrtaceae], development occurs over a period of 40 days, involving 6-8 generations per year. Shifts in feeding sites within galls synchronized with the growth of the stylet bundles and maturation of larvae prepare the mature gall to dehisce through a specific physiological change. This involves a differential synthesis of starch and polyphenolic materials in particular patterns in the tissues of gall wall. Cells that contain starch and polyphenolic materials become sclereids during later stages of cecidogenesis. Sclereids occur as linear files alternating with rows of parenchyma. These functionally antagonistic tisues act in coordination with water deficit enabling the dehiscence of the gall from a weak point in the gall roof.

Colonizing stem mothers of Pemphigus emerge from eggs that overwintered in the deep tissues of the primary host Populus, and migrate en masse to developing leaves. Although stem mothers are wingless, their migration is fast with as much as 83% of a population arriving at the developing leaves in a 3-day period after bud burst. With repeated probing behaviour, the stem mothers select a suitable host site and begin to induce a gall. Within the gall, the stem mother [fundatrix] produces nearly 300 or more offspring, parthenogenetically and viviparously. With the dehiscence of the gall of stem mother in midsummer, the progeny migrates to a herbaceous secondary host where they go underground and feed on roots. Interestingly, these gallicolae

are not specific to their hosts. On the secondary host, a wingless generation is produced which returns to the primary host [Populus] and continue their life cycles.

[e] Gall Communities

Many of the insect galls display the participation of a great variety of insects within them. Although the gall is initiated and sustained by one species [the gall maker], subsequent development of the gall allows migration of a range of other arthropods that coinhabit the gall facility. Indeed, some of these coinhabitants do modify the structure of the gall. For example, an American cynipoid gall supports nearly 14 species of insects besides its gall inducer [Diastrophus kincaidii], while a British oak gall houses as many as 22 species of insects and other arthropods. As with all phytophagous communities, the host plant is central to gall communities too. Curiously, gall communities are remarkably consistent across the range of gall-inducing species. The trophic structure of the inhabitants of a gall ranges from herbivory to super parasitism and super predation, in addition to casual visitors. Inquilines that share herbivory with the gall inducer, parasites, and predators regulate the gall inducer populations substantially.

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LEARNING IN HONEY BEES UNDER DIFFERENT BEHAVIOURAL CONTEXTS – A CASE STUDY

BY

K. CHANDRASHEKARA

LEARNING IN HONEY BEES UNDER DIFFERENT BEHAVIOURAL CONTEXTS: A CASE STUDY

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Early ethology began as an attempt to explain the behaviour of animals based on the nature of 'sensory information' acquired in their natural surroundings. While the 'behaviourists' sought to explain species specific patterns in behaviour as arising out of responses to environmental stimuli, the ethologists argued that much of the 'sensory information' for some behaviours at least is inborn requiring little or no conditioning and therefore 'instinctive'. Traditionally the behaviours were thus pigeon-holed as either being 'innate' or 'learnt'. Innate behaviours were assumed to be completely genetically determined and learnt behavriours were moulded (largely or completely) by enironmental factors. The terms 'innate' and 'learnt' have been loosely used in literatrue and often led to acrimonius debate on whether or not these are determined solely by either genes or environment (Alcock 1984).

In early studies the important role instinct plays in the lives of insects and lower vertebrates like fishes and birds was convincingly demonstrated (Gould 1982). However, the ethologists also underscored the importance of learning under specific ecological and behavioural contexts. The digger wasp which hunts for bees to provision its nest need not learn to recognise its prey, the search image of what a bee looks like is inborn. The same wasp has to however learn the location of her nest each time she flies out!

Insects have been described as mere robots, programmed to behave in a certain manner with little or no scope for deviation. There is however an increasing realisation that insects are not creatures of instinct alone and that learning plays a crucial role in the lives of several insects, particularly the social hymenopterans, this is strikingly illustrated by the honey bee. It would be advantageous for a bee not only to perceive the signals given by a flower but also to 'know' in advance what a potential food source looks and smells like. In other words the bees may have an 'innate search image' for flowers, which can be later on perfected as 'learned search image' through experience. However, too strong or a specific search image would preclude the bees from using potentially better sources of nectar and pollen. The bees therefore should 'know' that flowers are a source of food even without any experience *and* also be able to quickly learn the specific features of a particular flower enabling them to assess their profitability and make the choice accordingly (Menzel 1985).

Do bees preferentially choose certain stimuli when searching for food? Are certain stimuli learnt faster than others? If there are such 'prepared' stimuli, are they used differently under different behavioural context? One can for example ask whether food signals can be used as signals for the hive entrance? It has often been argued that bees pay greater attention to spatial cues at the hive entrance than colour and are more sensitive to floral odour and colours while foraging. Using *Apis cerana* we decided to investigate whether the bees can be trained to use colour to find access to the hive as well as to a feeder. Methodology used in these simple experiments and some preliminary results will be discussed.

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MOLECULAR GENETICS OF SOCIAL WASPS – A CASE STUDY

BY

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Molecular Genetics and Behavioural Ecology

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In recent years, the technique of protein and nucleic acid electrophoresis has been increasingly used to provide useful information in a wide range of biological and medical situations. One major area has been its use as a tool for genetic analysis, using enzymatic proteins as markers of variation in the underlying genes (allozyme electrophoresis). Such genetic markers are useful not only for population structure analysis, but also for the identification of individuals, the delineation of species boundaries and phylogenetic reconstruction.

The *phenotype* of an individual consists of the observable physical or behavioural attributes of that individual. The phenotype is the result of the interaction, especially during development, of the *environment* and the *genotype* of that particular organism. The genotype consists of information biochemically coded in the form of a sequence of bases of deoxyribose nucleic acid (*DNA*). This sequence codes for the information needed to produce a very large number of different kinds of protein molecules, some of which are used in maintaining the structure of the organism while others catalyse particular chemical reactions (*enzymes*). Each kind of enzyme catalyses a quite specific reaction. There may however be more than one genetically-determined protein catalysing a particular reaction. For example, there are three different genes encoding mammalian lactate dehydrogenase and hence three different forms of the protein. The DNA sequence of any gene, again, may be altered by a *mutation*. This may result in there being more than one form of the sequence available for a particular locus within a species, *i.e.* the gene is *polymorphic*. Each of these alternative forms is called an *allele*. Different allelic forms of an enzymatic protein often vary in their molecular weight, shape and residual charge on the basis of their constituent amino-acids. This usually results in differential mobility of the different allelic forms of the protein on electrophoresis.

Genetic studies of diploid organisms using allozyme electrophoresis produce data that are normally based on *co-dominant* alleles at an autosomal locus. In this situation, the relationship between the observed phenotype and the underlying genotype is simple, and genetic analysis of the data collected can be carried out without difficulty. For example, 20 animals of phenotype A (genotype AA), 50 animals of phenotype AB (genotype AB) and 30 animals of phenotype B (genotype BB) may have been sampled and typed. From these data the frequency of each allele in the sample can be calculated. As there are two copies of each

gene in every individual, the number of genes sampled is twice the number of individuals sampled. In the above example there are (2 X 20 + 50) = 90 A alleles and (50 + 2 X 30) = 110 B alleles in a total sample of 200 genes. The resulting relative allele frequencies (p and q, where p + q = 1) are p = 90/200 = 0.45 and q = 110/200 = 0.55. Similar calculations can be used to determine the *allele frequency* of any number of alleles in a *sample set*. The allele, or 'gene', frequencies of this sample set can be used as estimates of the allele frequencies in the *population* sampled.

A clear distinction should be made between allele frequencies and *genotype frequencies*. As indicated above, the allele frequencies are the relative frequencies of the various alleles (two, A and B, in the example above) at a particular locus. Genotype frequencies are the proportions of the various genotypes (three genotypes, AA, AB and BB, in the example) in the population.

A *population* consists of individuals scattered, at various densisties, throughout the range of the species. These individuals are not independent but interact in various ways with the environment and with one another. Most importantly, interactions between individuals produce the next generation, which is, as a result, the product of historical events occurring before as well as after its initiation. Some of these events affect the genetic structure of the population, and such facts can be used to develop or test ideas about the structure of a population, notably the relationship between groups of individuals in different parts of the range of the species.

Population structure has been traditionally studied by using mark-release-recapture methods. Recently, however, there has been increasing interest in using genetic approaches to the analysis of populations. The use of genetic data to study population structure is based on the premise that population structure will affect all loci in a similar fashion, while locus-specific effects will differ from locus to locus. Genetic methods have some major advantages over the mark-release-recapture approach:

1. They can be used to study the population structure of animals too small to be marked.

2. They can be used to study the population structure of animals with a very high population density, where the probability of recapturing marked individuals is low.

3. They are relatively inexpensive compared to traditional mark-release-recapture approaches.

4. Useful results can be obtained in a short time span.

5. The estimate of population structure is often more appropriate to the question at hand than an estimate derived from mark-release-recapture studies.

There are, however, several points that need to be remembered when planning sampling programmes:

1. Many polymorphic loci (usually a minimum of six) must be used if any confidence is to be placed in the results to separate population-specific and locus-specific phenomena. Again, to be usefully polymorphic, the most common allele should have a frequency of less than 0.9.

2. Sample sets should be taken from the smallest, most homogeneous population units possible to reduce mixing in 'primary' sample sets.

3. Replicate sampling on the smallest geographical scale possible is needed in at least some samples to detect within-sample phenomena.

4. Sample sets need to be taken at varying geographical distances to detect between-sample phenomena and to discriminate between different population models.

5. Sampling at the geographic extremes of the species range and detailed replicate sampling across genetic discontinuities usually give information aiding interpretation.

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FORAGING PATTERNS OF BIRD PESTS OF CROP PLANTS

BY

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FEEDING PATTERN IN CERTAIN BIRD PESTS OF FIELD CROPS

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Several species of birds have turned into pests of field crops and often cause intense grain predation. Unlike in the natural habitats, where resource is patchily distributed and its availability is unpredictable in time, in agro-ecosystems resources are generally predictable both in time and space. Further,because of the monoculture cropping pattern,in agro-ecosystems resources for granivores are super-abundant.

In such a 'super abundant' and predictable resource habitat, the pattern of grain predation by bird pests showed 'between fields' and 'within field' variations. Two systems namely, Rice -- munia/Baya and Sunflower -- Parakeet systems were studied to understand these variations.

In the Rice -- munia/Baya system the 'between field' variation in grain predation by birds was closely linked with the movement and feeding activity of birds within the rice growing area. The feeding activity of munias (*Lonchura* spp.) and Bayas (*Ploceus philippinus*) was concentrated around a centrally located main roost site and was dependent on the distance of the feeding sites from the main roost. A field closest to the main roost had the highest concentration of birds, while the one farthest had the least number of birds. Interestingly, the selection of a specific feeding site was more dependent on the vegetation (trees or shrubs of > 1.5m height) complexity rather than the resource status (mature crop) of the patch.

Within the selected feeding area, a strong vegetation-cover dependent foraging by bird pests was observed. Nearly 76% of the feeding-birds were concentrated within 10m from the vegetation cover and decreased non-linearly with increase in distance. Further, certain structural features like plant stature and earhead characteristics of rice plants predisposed the rice crop to intense grain predation by birds.

In the Sunflower -- Parakeet (*Psittacula krameri*) system, within field variation in grain predation was dependent on the foraging pattern of parakeets. This was influenced by certain structural features of the plants, but not the resource load (capitulum size) on each plant. Analysis of feeding time budget of parakeets revealed that, selective feeding upon certain plants by birds was aimed at enhancing the predator vigilance. Parakeets spent a greater proportion of their time on feeding on plants that offered a better view of the surroundings.

From the Rice -- munia/Baya and Sunflower -- parakeet systems it appears that the feeding pattern of bird pests is more dependent by the selection for better vigilance and safety from predators than the availability of resource per se. This

behaviour might appear to be skewed when compared to that prevailing in natural situation where it is likely that both due to increased predation risk owing to the openness of the habitat and reduced probability of finding resources, birds should indulge in a trade off between the two. Agro-ecosystems offer a good control in this respect to study the differences in foraging behaviour of birds.

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SOCIAL SYNCHRONIZATION OF BIOLOGICAL CLOCKS

BY

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Social cues and circadian rhythms in bats, mice and humans

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I shall be summarising in this lecture the research findings made by me and my students in the course of the last 12-13 years at the School of Biological Sciences, Madurai Kamaraj University at Madurai.

We have been working on the behavioural expressions of circadian rhythms in bats, mice, squirrels, birds and humans for several years. We have in particular concentrated on the entrainment, freerunning and phase-shifting properties of the circadian rhythmic systems in the context of social factors. The light-darkness (LD) cycles generated by sunrise/sunset are the ubiquitous entraining or synchronizing agents (zeitgebers) for circadian rhythms from unicelluars right upto humans. LD entrainment of circadian (24 hourly) rhythms has been literally experimentally demonstrated for 100 years now. LD cycles and circadian rhythms are in fact so closely associated that the subject of chronobiology appeared to have become a branch of photobiology. It is against this backdrop that the series of experiments were started in Madurai to investigate the role of

social cues as zeitgebers to circadian rhythms. We speculate that a new branch of chronobiology called "social chronobiology" may well be launched in the not too distant future.

Circadian rhythms occur in all eucaryotic organisms, in other words only bacteria have not been shown to possess circadian rhythms. All genuine circadian rhythms have the following diagnostic characteristics.

1. Persistence in LL or DD and constant temperature
2. In so persisting expression of periods close to but never exactly 24 hr (circa) (free run)
3. Compensation of the period for temperature i.e. showing Q_{10} values close to unity.
4. Resettability of the rhythm by light and/or temperature perturbations.
5. Have a genetic basis, often clock control being effected by a single locus clock gene.

The role of social interaction in synchronizing activity/rest patterns of several species of birds and mammals seems only all too clear from the great synchrony with which flocks of animals leave their roosting sites to forage and return later to roost. In literature such social interactions in the cotext of the activity rhythms have been accorded only cursory attention. This is surprising in view of the fact that such social cues that help to entrain the individual clocks or animals and bring about a

synchrony during, for instance, the beginning of activity of the colony, are of vital importance to the very survival of the species. Novick called the synchronized emergence "emergence by coup" and considers such behaviour as aiding in confounding predators.

From our experiments conducted at Madurai with bats both in the field and in the laboratory, we have evidence that the onset, end and amount of activity and rest are all under control of the circadian clock. Experimental proof of the value of social cues in tuning circadian clocks in the individuals of a colony and/or species have been few and far in between.

BATS

Bats of the species Hipposideros speoris living 40 m inside a narrow and contorted cave where the darkness is absolute, temperature and humidity constant still wake up around 6 p.m. which is atleast one hour before sunset and their flying out. This they may do with the aid of a circadian clock. The bats animatedly fly around in a chamber very close to the cave-mouth "sampling light" and the entire colony exits the cave like a cloud-burst soon after sunset. We asked ourselves if each bat had to sample light for itself to know that it is dark outside too or is their a social communication of information of sunset.

Three captive bats held 40 m into the cave showed clear-cut entrained activity patterns and flew inside the flight activity cages at the same time as their free-flying conspecifics. In contrast to this the flight/rest activity of a solitary male Hipposideros speoris bat studied inside another adjacent cave without any bats, freeran. No social informers no entrainment.

Hipposideros speoris is silent to human hearing and emits ultrasonics of 1,34,00 cps. Into this cave we introduced an alien bat Taphozous kachhensis, who emits in the range of ca 80,000 cps, and studied its activity/rest. The bats rhythm was not entrained by the activity/rest of the colony of 600 Hipposideros speoris sp bats, and it freeran. Neurophysiological studies made on the 'best hearing frequencies' and the audiograms in the inferior colliculus of these two spp. indicated that the 'alien' could not even 'hear' the resident bats. We called this in publication a "communication gap". This striking social synchronization is abolished by artificially created LL of ca 10 lx. We do not know the active social agent that entrains; it could be 1) the general bustle and wing beat 2) pheromone or 3) acoustic communication.

MICE

We have also reported a "behavioural maternal entrainment" of the circadian rhythms of activity/rest of the pups for the field

mouse Mus booduga. In experiments performed in DD in the laboratory the mother was presented and absented to pups 12:12 h respectively. We call this presence:absence or PA cycles. The pups interpret the presence of the mother to mean subjective day and the absence of the mother to mean subjective night. Entrainment is possible to PA cycles of 11.5:11.5 h (T=23), 12:12 h (T=24) and 12.5:12.5 h (T=25) but not to cycles shorter or longer. The limits of maternal entrainment are 23 to 25 h. Mother must be present for atleast 1/3 the cycle (8:16) but not beyond 2/3 the cycle (16:8) for successful entrainment. This impressive maternal entrainment is again abolished by LL of ca 10-20 lx. Reasons are not known.

HUMANS

We have investigated the circadian rhythms in bodily functions of human subjects since November 1987 in a specially constructed and equipped human isolation facility for periods of 15-35 days. The social and temporal isolation of the subjects was total and rigorous. So far experiments have been completed on 8 human subjects (6 men and 2 women) in 9 experiments between the ages of 24 and 35 years.

We investigated the circadian rhythm in sleep-wakefulness (SW rhythm) and in the rectal-temperature profile (Temp rhythm) of a 24-year-old female subject under conditions of social and

temporal isolation. The subject stayed in the isolation facility, fitted with basic living amenities but devoid of time cues, for 35 days. In isolation the Temp rhythm of the subject freeran with a period of 25.1 ± 0.8 h, but her SW rhythm freeran with a period of 45.9 ± 2.1 h (circabidian), resulting in desynchronization of the two rhythms. In 35 calender days the subject experienced only 22 subjective, sleep-wakefulness days. Interestingly the menstrual cycle of this subject was normal, i.e. two episodes of onset of menses occurred 28 calendar days apart. We conclude in this first report on the subject that the menstrual cycle in the human female may not be coupled to the circadian rhythm underlying sleep-wakefulness while under social and temporal isolation.

In another series of experiments we investigated how human subjects living in our isolation facility estimated 2 h intervals without the aid of watches or clocks. We discovered a direct correlation between the circadian sleep-wakefulness rhythm and time estimation in humans under prolonged isolation. The estimates of 2 h time intervals were strongly coupled to the number of hours humans stay awake. Their sense of time seems to contract and dilate as a function of hours of wakefulness. Further experiments on human circadian rhythms are in progress in our laboratory.

PRUDENCE AND PROFLIGANCY : BEHAVIOURAL ECOLOGY OF HUMAN RESOURCE USE

BY

MADHAV GADGIL

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PRUDENCE AND PROFLIGACY : BEHAVIOURAL ECOLOGY OF HUMAN RESOURCE USE

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- Can predators be prudent ?

- No, they will refrain from harvesting a resource only if harvesting some other element yields higher levels of net benefits.

- But human resource harvesting behaviour is far more complex

Repertoire size	Harvesting regime: Prudent	Harvesting regime: Profligate
Limited	Equilibrium at high densities of prefered species	Equilibrium at low densities of prefered species
Open ended	-	No equilibrium, Sequential exhaustion

- Because,

(a) People can build models of how nature functions, and how they impinge on it

(b) Reciprocity including material, informational exchanges central to human social life

(c) Group level interactions (including violent conflicts) are important in evolution of cultural traits.

Human History as a story of prudence and profligacy

- Over much of their evolutionary history, humans behaved as profligate predators

(a) Era	Prior to 10,000 ybp
(b) Society	Hunter-gatherers in contact with only hunting-gathering societies
(c) Relationship with other societies	Occasional territoreal conflicts
(d) Significance of natural biological populations to society	All important, the mainstay of subsistence
(e) Extent of resource catchment	Restricted, a few hundred km2 at a time
(f) Permanance of resource catchment	Often shifting over a terrain of a few thousand km2
(g) Exclusiveness of resource catchment	Slight
(h) Resource type substitutability	Very limited
(i) Resource acquisition patterns	Optimal foraging
(j) Sustainability of resource use	Incidental, a result of low population size and modest resource demands

- Around 10,000 ybp humans began switching to more intensive utilization of resources over more restricted terrain.

- A social species, humans go in for unrestrained, violent conflict.

- A K-selected species, humans cannot quickly convert resources into additional people

- Maintaining the health of resource base of a limited group territory may be critical to cultural survival of a group

- This might lead to group selection effectively favouring ecological prudence

(a) Era	10,000 to 500 ybp
(b) Society	Subsistence agriculturists extensively dependent on hunting-gathering in contact with similar peoples
(c) Relationship with other societies	Acute territoreal conflicts
(d) Significance of natural biological populations to society	Extensive
(e) Extent of resource catchment	Very restricted, of a few hundred km2
(f) Permanance of resource catchment	Largely permanent, shifting within narrow limits
(g) Exclusiveness of resource catchment	Very high
(h) Resource type substitutability	Very limited
(i) Resource acquisition patterns	Incorporating restraints on harvest methods, seasons, localities and species
(j) Sustainability of resource use	Considerable, as a consequence of restraints on resource harvests

- "Ecosystem people"

- Restraints grounded in viewing resource elements as fellow members of a reciprocating community of beings

- Restraints in the form of a series of rules of thumb
(a) Complete protection to representative biological communities
(b) Complete protection to certain species, including keystone resources
(c) Complete protection to certain life history stages
(d) Complete protection over to certain time intervals (rotation)
(e) Ban on certain methods of harvesting
(f) Harvest - quotas
(g) Reduction in harvest rates in response to resource depletion

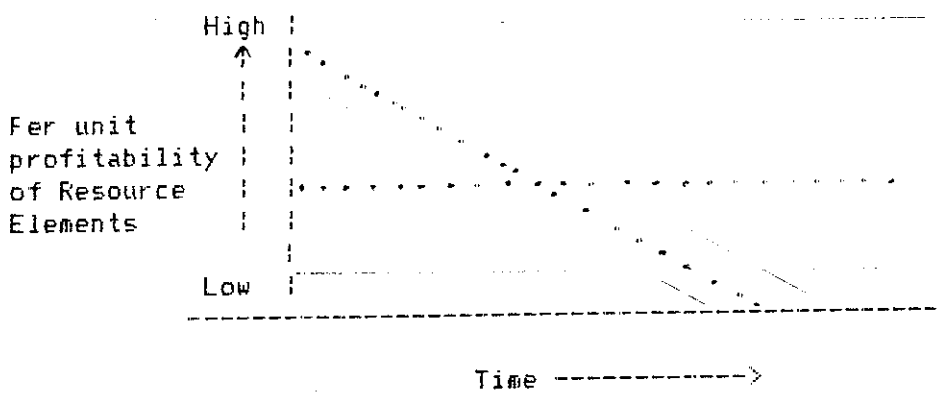
- Such restraints conditional on exclusiveness of access to a well defined, restricted locality

(a) Era	10,000 ybp to present
(b) Society	Agricultural colonisers with an edge over indigenous gatherers/cultivators
(c) Relationship with other societies	Violent conflict leading to displacement of indigenous peoples
(d) Significance of natural biological populations to society	Moderate
(e) Extent of resource catchment	Restricted at any time to a few hundred km2
(f) Permanance of resource catchment	Continually shifting over potentially unlimited terrain
(g) Exclusiveness of resource catchment	Slight
(h) Resource type substitutability	Limited
(i) Resource acquisition patterns	Optimal foraging, sometimes deliberately destructive
(j) Sustainability of resource use	Very low or absent

- Beginning 500 ybp, newly developed ability to accumulate information rapidly opened up immense possibilities of resource substitution, in kind as well as in space

- "Biosphere people"

(a) Era	250 ybp to present
(b) Society	Industrial societies able to easily acquire biological resources of agricultural societies on terms highly favourable to themselves
(c) Relationship with other societies	Periodic acute conflicts relating to control over resources with other industrial societies as well as with agricultural societies
(d) Significance of natural biological populations to society	Considerable
(e) Extent of resource catchment	Huge, potentially the entire global surface
(f) Permanance of resource catchment	Limited, with continual shifts in areas that are a focus of resource extraction
(g) Exclusiveness of resource catchment	Limited, with shifting claims by many parties
(h) Resource type substitutability	Very high, grounded in technological abilities
(i) Resource acquisition patterns	Resource exhaustion in a sequence in terms of resource types and localities
(j) Sustainability of resource use	Altogether absent in peripheral areas, considerable, as a result of deliberately imposed restraints in central areas



- Restraints imposed in central areas little more informed than rules of thumb of ecosystem people

- Marginalised ecosystem people

(a) Era	250 ybp to present
(b) Society	Subsistence agriculturists in peripheral parts of resource catchments of industrial societies
(c) Relationship with other societies	Dominated by industrial societies
(d) Significance of natural biological populations to society	Extensive, but continually diminishing
(e) Extent of resource catchment	Very limited
(f) Permanance of resource catchment	Considerable
(g) Exclusiveness of resource catchment	Very weak
(h) Resource type substitutability	Limited
(i) Resource acquisition patterns	Resource exhaustion in a sequence of resource types and localities, although on a scale much more limited in comparison with industrial societies
(j) Sustainability of resource use	Very low or absent

- Ability to accumulate information has now rendered possible extensive tinkering with life forms themselves

- To "biosphere people" turned "biomanipulators" natural biological populations appear suddenly of considerable economic value

(a) Era	Since mid 1980's
(b) Society	Industrial societies on the threshold of the biotechnology revolution
(c) Relationship with other societies	Continuing acute conflicts relating to control over resources with other industrial and agricultural societies
(d) Significance of natural biological populations to society	Very high
(e) Extent of resource catchment	Huge, potentially the entire global surface
(f) Permanance of resource catchment	Limited, with many shifts in areas that are focus of resource extraction
(g) Exclusiveness of resource catchment	Limited, with shifting claims by many parties
(h) Resource type substitutability	Very high, but currently limited by the fact that relevant technologies are just emerging
(i) Resource acquisition patterns	Currently very cautious extension of control over biodiversity
(j) Sustainability of resource use	Very limited, just beginning to be considered

- Sudden spurt of interest in knowledge and practices of ecosystem people.

So much for history, if you would permit me to extrapolate the trends that have prevailed till now, then the most likely scenario :

- Most likely scenario :

(a) Era	21st century
(b) Society	Industrial society that has successfully completed the biotechnology revolution and established a monopoly over biodiversity in ex-situ storages
(c) Relationship with other societies	Continuing conflicts amongst industrial nations, complete subjugation of agricultural societies
(d) Significance of natural biological populations to society	Little, except as a potential threat to maintenance of a monopoly over biodiversity
(e) Extent of resource catchment	Huge, potentially the entire global surface
(f) Permanance of resource catchment	Limited, with shifting focus
(g) Exclusiveness of resource catchment	Limited, with shifting claims by many parties
(h) Resource type substitutability	Tremendous, enhanced through advances in biotechnology
(i) Resource acquisition patterns	Complete elimination of natural biological populations
(j) Sustainability of resource use	Irrelevant

FROM ANIMALS TO HUMAN BEHAVIOUR

BY

M. D. PARTHASARATHY

CLUES TO HUMAN BEHAVIOUR

Prof.M.D.Parthasarathy

ABSTRACT:

The clue to social behaviour can be found in the evolutionary development of body parts and the brain. Man is considered unique because of his many characteristics, which are thought to have their phylogenetic homologues in infra-human primates. There has been a gradient of plasticity in behaviour among animals from low to high culminating in man. Non-human primates being the most evolved order are endowed with a great deal of genetic information. Ecology, the habitats and niches of primates are highly complex and diverse which makes their behaviour very interesting. However various alternative path ways of behaviour development is possible for them. The most important advancement in the case of primates including man is the involvement of subjectivity in social adaptations and levels of consciousness or awareness. In the past few years accounts of primate and other animal behaviour are used as source material to understand human behaviour. As early as 1932, Zuckerman observed a colony of Baboons kept in the London Zoo. In such cramped conditions the Baboons behaved with great ferocity. However few years later when the same species were observed in nature in Africa, they were found to be highly peaceable and even co-operative. Even in our own Bonnet Monkey it is seen they are much less combative when they live independently in jungle instead of our villages and towns under unnatural conditions. Each animal species is seen as adapted to a range of habitats

from an ecological point of view.

We find in animal societies the phenomena of cooperation and conflict. Examples of intolerant behaviour are very common. Some times animals kill or injured members of their own species. In Hanuman Langur the dominant male when it takes over a common group commits infanticide. (Parthasarathy, M.D., 1969).

Human behaviour is distinguished from all other species by the greater variability; hence it is less predictable than that of our cousin, the apes and monkeys. Much of human behaviour is culturally determined. Hence ontogenetic behaviour of development becomes important. This is reflected in studies of a human child's behaviour, starting from its very first year. The development of language as a mode of communication has assumed the greatest significance in all spheres of human activity.

From a socio biological point of view some types of behaviour among humans like altruism, selfishness and spite have created a lot of controversy. These behaviours are based upon kin selection and inclusive fitness. As far as Altruism is concerned reciprocal Altruism appears to have a lot of sway. Pure altruism has altogether disappeared. Selfishness is more common and spite no less. However spite does not seem to have evolved among animals. Spite is "all too human".

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SIBLING COMPETITION AND PARENT OFFSPRING INTERACTIONS IN PLANTS

BY

R. VASUDEV

Sibling Competition and Parent Offspring Interactions in Plants.

R. Vasudeva

LECTURE NOTES

Trivers (1974) noticed that in several species, parents and their offspring exhibit conflict in different ways. For instance when he was in India during 1972, he noticed dramatic cases of such conflict in langurs durirng the weaning period. Typically, towards the end of the weaning period, the mother would tend to neglect the young while the latter beg milk by uttering piercing cries and may even retaliate fiercely when rebuffed by the mother. Mothers are forced to concede to the demands by the infants; otherwise the infant calls may attract the predators threatening the safety of the whole family. Based on these observations Trivers (1974) proposed the concept of parent-offspring conflict (POC).

POC implies that while parents are selected to invest resources equally among all the offspring, the latter would be selected to demand more in order to increase their own individual fitness. Thus in situations where several offspring are synchronously developing as in a clutch of birds, they compete severely for maternal resources often leading to siblicide. In raptors, such competition is manifested in an extreame form, where the elder invariably kills the younger chick reducing the brood size; this might cost to the fitness of the mother results in POC over resources and brood size.

Ganeshaiah and Uma Shaanker (1988), Uma Shaanker et. al. (1988) and Bawa et. al. (1989) have suggested that fruits in plants, in

which several developing embryos compete for the common pool of maternal resource, constitute a potential scenerio for sibling rivalry and POC. In friuts with several seeds developing simultaneously, each seed can be expected to draw resources more than the mother is selected to offer. In extreame situation this might results in intense sibling rivalry leading to abortion of the weaker seeds (Fratricide). However, the intensity with which such fratricide is exhibited would depend on the genetic relatedness among seeds. The fratricide would be expected only if the developing seeds in a pod are genetically heterogenous and not when they are genetically homogenous (and similar). We have investigated the existance of such process in a couple of plant species.

Sibling aggression (fratricide) and hence POC would be more intense in multiovulated species where pod is the unit dispersal (i.e.in case of wind, water or animal dispersed species). In these species by resorting to fratricide, the surviving offspring gains additional dispersal advantage because of the reduced seediness of the fruits. This is substanciated by the fact that a large number of species which have pod as the unit of dispersal, produce more ovules than mature in to seeds. Increased dispersal advantage of few seeded fruits is also accrued to the maternal parent through the seeds surviving in such fruits. If this gain more than compensates for the loss due to seed abortion, maternal parent also may favour the seed abortion. Therefore it is likely that seed abortion could infact be a maternal strategy (infanticide) than a consequence of

sibling rivalry (fratricide). In a wind dispersed tree species (Dalbergia sissoo) Ganeshaiah and Uma Shannker (1988) have tested these alternatives and shown that the abortion in this species is a case of fratricide.

If sibling rivalry causes loss in the fitness of the mother, the latter can be expected to develop strategies that prevent such losses. Plants have developed such mechanisms. Selective elimination of few seeded fruits that are formed because of intense sibling rivalry could be one such strategy. Polyembrony, a condition where an additional embryo (mostly from nucellar tissue) is formed along with the zygotic embryo, as been argued (Ganeshaiah et. al. 1991) to be another maternal strategy to compensate for the loss in her fitness due to seed abortion caused by the sibling rivalry. It also proposed that evolution of carpels in fruits is to compartmentalise the developing sibs within a fruit in order to dilute the intensity of sibling rivalry.

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INTERSPECIFIC ASSOCIATIONS AND FLOCKING IN BIRDS : BENEFITS & COSTS

BY

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Association of drongos with myna flocks: Are drongos benefitted?

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Abstract Common myna (*Acridotheres tristis*) and jungle myna (*Acridotheres fuscus*) forage in pure and mixed flocks of various sizes in fallow lands. These flocks were often found associated with drongos that forage individually on the insects herded out by the movements of the flocking myna. We report here the benefits and costs of such association to drongos and mynas. Drongos had a tendency to associate with larger (>21) than smaller (<20) flocks irrespective of the species composition of the flocks. Drongos associated with larger flocks showed increased foraging trips and harvested more insects in a given time than those that were either isolated or were associated with small flocks. The food range of drongos and mynas differed significantly indicating that they do not compete with each other. Thus our results indicate that drongos are benefitted by this association; however this association neither benefits nor costs to the mynas. The association between the drongos and mynas therefore appears to be commensalistic.

Keywords Drongo; myna; flocking; commensalism

1. Introduction

Flocking behaviour of birds has been viewed both as a strategy of sharing vigilance time against predators (Kittie 1980) and as passive aggregation using cues about availability of food (Pulliam 1973; Merritt 1980). Flocking might occur among the members of same (pure) species (Powell 1974; Barnard 1980) or of different (mixed) species (Morse 1970; Thompson and Barnard 1983; Barnard and Stephens 1983; Williamson 1971). Members of different species constituting mixed flocks are also shown to share the same benefits as those that forage in pure flocks (Barnard and Stephens 1983; Thompson and Barnard 1983; Williamson 1971).

Often, solitary foraging birds of certain species are found associated with flock forming birds. Such solitary birds do not actively participate in flocking; rather they are attracted to the already formed flocks and forage along with or around them (Williamson 1971; Vijayan L, Joshi N V and Gadgil M, personal communication). Benefits derived by these solitary birds from such association are not clear. However, several passive outcomes of flocking such as cues about predators, food availability and herding of insects induced by the flock movements might be exploited by such non-flocking sympatric species.

In this paper, we document one such association between a solitary foraging species the drongo and flocking mynas and demonstrate that the former derives benefits by foraging on the insects herded out due to flock movement. Identifying the cost and benefit of such association to both the species, we argue that this association between drongo and myna flocks could represent a commensalistic relation.

2 Materials and methods

2.1 *System*

This study was conducted in open fields of the Main Research Station, University of Agricultural Sciences, Hebbal, Bangalore, during September to December, 1990. Two species of mynas *viz.* jungle mynas (*Acridotherus fuscus*) and common mynas (*Acridotherus tristis*) were found foraging in pure and/or mixed flocks in these fields.

When a few birds of any one of the two species started foraging on the ground, other birds of both the species joined them to form flocks. This process continues for some time, when the flock may instantaneously break, only to be reconstituted with members of different or the same flock. We found that any two mynas within a distance of 2 m behaved as if they belonged to a flock: for instance they responded simultaneously to external disturbances and gathered cues about the food availability from each other while foraging. Therefore we defined the flock as a group of birds wherein the distance between any two nearest members was <2 meters. These flocks were found to frequently attract drongos (*Dicrurus adsimilis*) foraging in the neighbourhood. The drongos thus attracted to the flocks perched at a height of 0.5 to 3 m above ground on stubbles, mounds or bunds located within or at the periphery at a distance of less than 3 m from the flocks. They foraged actively as long as the flock feeds in a particular patch. When the foraging flock abandoned the patch, drongos also left the patch and followed the flock.

The drongo is an aerial predator and exhibits sit and wait foraging strategy; it watches vigilantly for flying insects (*e.g.* grass hoppers, winged termites, moths, flies etc.), pounces upon and carries them off (Ali 1979; Khan 1990; Sharma 1991). We observed that it made frequent swoops (hereafter referred as foraging trips) over the myna flocks to harvest insects.

2.2 *Recording the observations*

2.2a *Flock size and composition*: Myna flocks are found in farm fields during the morning (7 to 10.30 h) and evening (16.00 to 18.30 h) hours on bright sunny days and throughout the day on cloudy days. During these periods random searches were made by walking along fields of 2–3 ha. During such scans, flocks ($N=177$) were identified and their flock size (number of birds flock), and species composition (common or jungle myna in the flocks) were recorded. Simultaneously, we also recorded the presence or absence of any drongo perching within a distance of 3 m from any foraging flock.

2.2b *Drongo foraging*: Any drongo associated with a myna flock generally does not tolerate other drongos joining the same flock and maintained a temporary territory by aggressively chasing any intruders. Consequently, in the study area there were always two kinds of drongos *viz.* (i) 'isolated drongos' foraging at a distance more than 10 m from the myna flocks and (ii) 'associated drongos' foraging along with or within a distance of about 3 m from the flock. Often however, a few large myna flocks had more than one drongo associated with them. We recorded the following observations on both 'isolated' ($N=35$) and 'associated' ($N=79$) drongos.

(i) *Foraging trips*: Number of foraging trips by the drongos were recorded in randomly chosen time windows of a minimum of 30 s for a total duration of 35 min and expressed as number per 30 s.

(ii) *Success rate*: This indicates the proportion of foraging trips that ended up in successfully harvesting prey. A trip was recorded as successful when we clearly saw an insect between in beaks of the drongos after the trip: we also confirmed this by observing through binoculars, the handling of the prey caught after the drongo returned to the perch. From this data we computed the success rate as percentage of trips that were successful (it is likely that our data is an underestimate of the success rate as we might have missed few instances of success that were not clearly visible).

(iii) *Food overlap*: Drongos were found foraging on the insects flying 15 cm to 60 cm above the ground, while mynas pecked at grains and insects on the ground. The food overlap between two groups was analysed as follows:

Six grids of 5 × 5 m were randomly marked in the foraging patches and insects were collected for 1·5 h each on 3 days as follows during the foraging hours of mynas.

(i) Insects were herded out by disturbing the area with a stick and caught by sweeping insect nets one foot above the ground. This represents predominantly the resource used by the drongos.

(ii) From the same grids insects caught on the sticky traps and those found on the ground were collected. This represents predominantly the resource range of mynas.

The body lengths and fresh weights of the insects were recorded and frequency distributions of size classes was constructed.

3. Results

3.1 *Flock size*

Common myna formed smaller flocks (2·65 ± 1·56) than jungle myna (11·86 ± 9·56). However, common and jungle myna frequently flocked together while foraging, and the size of such mixed flocks was generally larger (16·92 ± 10·16; table 1).

Table 1 Pure and mixed flock sizes of different species of mynas with and without drongos

	With drongo			Without drongo				Pooled		
Flock type	*N*	Mean	SD	*N*	Mean	SD	*t* test	*N*	Mean	SD
Pure flocks of common myna	8	4·13	2·80	46	2·39	1·09	$P<0.01$	54	2·65	1·56
Pure flocks of jungle myna	21	17·33	10·47	13	6·38	4·14	$P<0.01$	34	11·86	9·56
Mixed flocks of common and jungle myna	70	19·31	9·83	19	8·11	5·51	$P<0.01$	89	16·92	10·16
Total	99	17·67	10·39	78	4·63	4·15	$P<0.01$	177	11·61	10·39

3.2 *Association of drongo*

Drongos were associated with 56% of the myna flocks observed in the field; their association was least with the common myna flocks (15%) and highest with mixed flocks (79%; table 1). Drongo's association with flocks appeared to be influenced more by the flock size than the species of myna. This is further evident from the following:

(i) For each species, the size of the flock with which drongo was associated was significantly ($P<0.01$) larger than that of flocks without it (table 1). The size of the common myna flock with drongo was 4.13 ± 2.80, while the size of that without it was 2.39 ± 1.09. Jungle myna flock size associated with drongo (17.33 ± 10.47) was almost three times larger than the size of flocks without drongos (6.38 ± 4.14). Similarly the size of mixed flocks with drongo was also higher (19.31 ± 9.83) than the size of those without drongo (8.11 ± 5.51; table 1).

(ii) When the flocks of pure and mixed types were pooled, the per cent flocks with which drongo was associated, increased with the size of the flock (figure 1; table 2). Infact, by the time a flock grew to a size of 20 it was certain to have one or two drongos associated with it (figure 1; table 2).

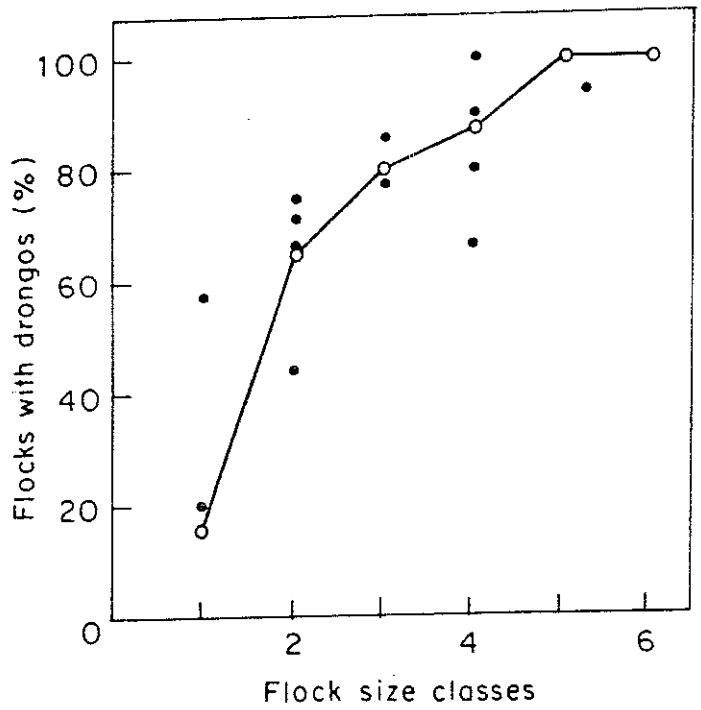

Figure 1. Per cent of various flock sizes associated with drongos. See table 2 for flock size ranges of different size class.

(iii) The number of drongos associated with flocks also increased with the size of the flock. Flocks with >25 birds, had an average of two drongos with them (table 2).

(iv) In the study area, in addition to myna, some other ground foraging bird species also formed flocks, though not as frequently as mynas (table 3). Their flock

Table 2 Per cent of flocks of various sizes associated with drongos

	Flocks with drongos (%)		Number of drongos/flock	
Flock size	*N*	Mean	Mean	SD
1–5	76	15·43	0·164	0·40
6–10	27	69·48	0·650	0·66
11—15	19	78·37	1·190	0·83
16–20	12	79·33	1·130	0·74
21–25	2	100·00	1·500	0·93
26–30	10	100·00	2·280	0·76
>31	15	100·00	1·780	0·71

Table 3 Association of Drongos with flocks of different species

	Flock size			Flocks with
Species	*N*	Mean	SD	drongos (%)
Common myna	54	2·65	1·56	14·81
Jungle myna	34	11·86	9·56	61·76
Spotted dove	20	1·90	0·21	5·00
White-headed babbler	17	4·35	0·57	11·76
Blue rock pigeon	4	4·00	1·73	–

sizes differed considerably and they also often had drongos associated with them. Correlation between the mean flock size of these bird species and the percentage of the flocks with drongos indicated a strong tendency ($r = 0{\cdot}9283$; $P < 0{\cdot}01$) of drongos to be associated with larger flock sizes. Thus drongos seems to prefer larger flocks of ground foragers irrespective of the species.

3.3 *Benefits to drongo*

The number of foraging trips of drongos in a span of 30 s was significantly ($P < 0{\cdot}01$) higher when they were associated with myna flocks ($2{\cdot}0 \pm 1{\cdot}91$) compared to when they were isolated ($0{\cdot}62 \pm 1{\cdot}08$; table 4a). Further, percentage of foraging trips that eventually ended up in catching an insect was very high when they were associated ($25{\cdot}99 \pm 36{\cdot}17$) compared to when they were isolated ($2{\cdot}93 \pm 8{\cdot}41$; table 4a). As shown in table 4b, drongos associated with myna flocks succeeded in catching insects more frequently than expected, while isolated drongos succeeded less frequently than expected ($\chi^2 = 8{\cdot}71$; $P < 0{\cdot}01$). Thus it appears that drongos gain considerably (in terms of their foraging success) by being associated with flocks. The gain in foraging seems to increase with flock size (table 5). The number of foraging trips per 30 s was significantly ($P < 0{\cdot}01$) higher for drongos associated with medium and large flocks than for those that were either isolated or associated with smaller flocks (table 5). The foraging trips and the success rate of drongos decreased slightly

Table 4a. Foraging trips and the success rate of drongos in the presence (associated) and absence of (isolated) of myna flocks

		Associated	Isolated	't' test
Foraging trips 30 s	*N*	79	35	
	mean	2·04	0·62	
	SD	1·91	1·08	$P<0·01$
Success rate (%)	*N*	75	25	
	mean	25·99	2·93	
	SD	17	8·41	$P<0·01$

Table 4b. Two way contingency table showing the number of successful and unsuccessful trips by associated' and isolated' drongos

	Associated	Isolated
Successful trips	21 (15)	1 (7)
Unsuccessful trips	58 (64)	34 (28)

$\chi^2 = 9·38$; df = 1; $P<0·01$

Values in parantheses indicate the expected values

Table 5 Foraging trips and the success rate of drongos associated with flocks of different sizes

	Foraging trips			
Drongos	*N*	Mean	SD	Success rate (%)
Isolated	51	0·28[a]	±0·47	2·38
Associated with				
Small flocks (1–10)	34	0·43[a]	±0·42	14·28
Medium flocks (11–20)	32	1·14[b]	±0·73	30·36
Large flocks (>20)	25	0·94[b]	±0·81	16·00

Values with same superscripts do not differ significantly

when they were associated with large flocks (>20) than medium flocks (11–20; table 5). This may be because drongos associated with larger flocks spent part of their time in aggressive interaction against other invading drongos (figure 3); the mean number of drongos associated with larger flocks is high and consequently they tend to chase other drongos in trying to defend their territories leading to reduced number of foraging trips. Thus increased number of drongos might lead to reduced success rate due to interference by other drongos

3.4 *Cost to the mynas?*

Drongos feed upon insects that are flushed out by the movement of flocks. The size of the insects collected from the ground where mynas peck (for grains and insects) and at a height of one foot above ground (where drongos usually forage) showed considerable non-overlap (figure 2; KS test-D max $= 0.7034$; $P < 0.01$). The insects on the ground had significantly ($P < 0.01$) larger body size ($0.15\ g \pm 0.11$) compared to those collected from a height of one foot above the ground ($0.05\ g \pm 0.05$; table 6). Thus drongos did not seem to compete with the resource pool of the mynas. In other words, presence of drongos does not seem to be a cost to the mynas.

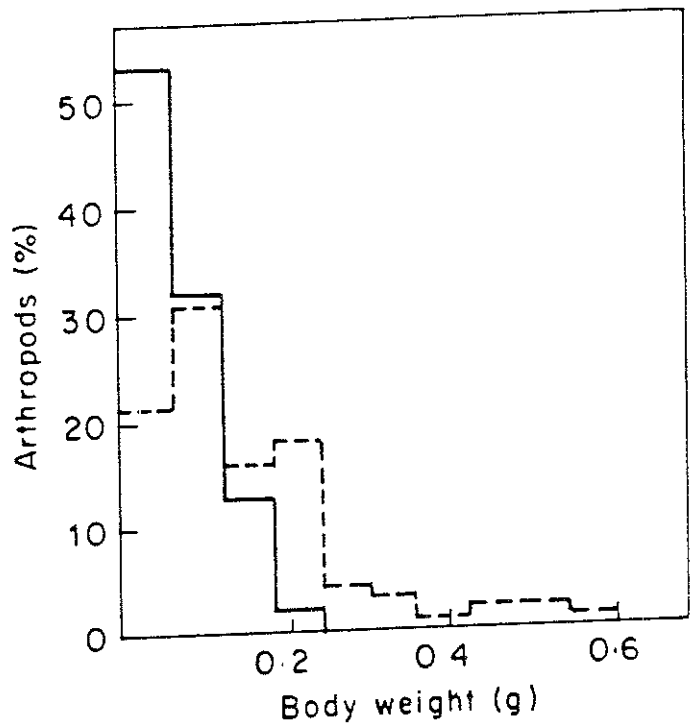

Figure 2. Frequency distribution of body weights of insects of aerial and ground strata.

4. Discussion

Solitary foraging birds are known to be associated with other foraging species in several unique ways. In Africa, Honey Guides (*Indicator indicator*) are known to mutualistically guide tribal people in locating honey combs and in turn harvest what is left by the honey gatherers (Conradson and Raistrick 1989). Cattle Egrets show commensalistic associations with foraging ungulates. However, association of solitary birds with other group foraging birds has rarely been reported (Vijayan L, Joshi N V and Gadgil M, personal communication). Our study demonstrates such an association of drongos with myna flocks.

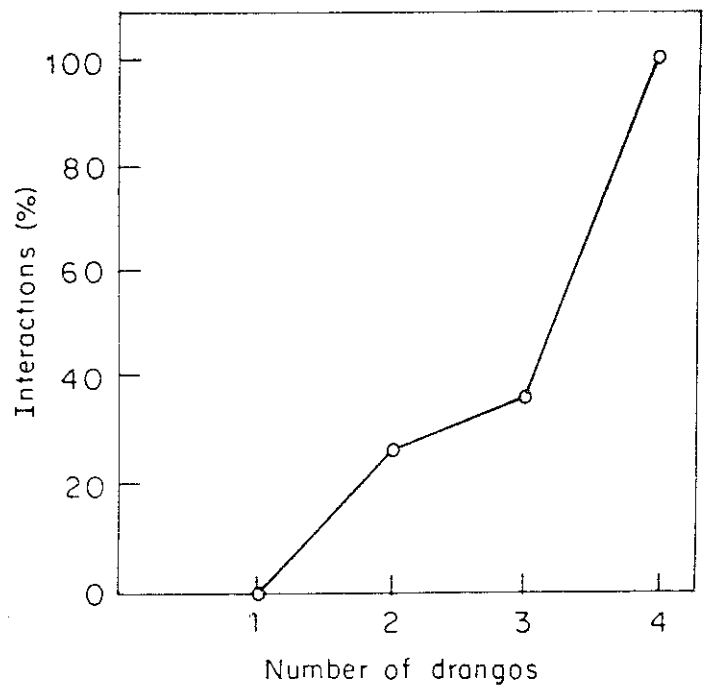

Figure 3. Per cent of the foraging trips of drongos ended up in aggressive interactions with other drongos. The interactions refer to the chases around the flocks.

Table 6. Body weights of insects collected at different strata.

	Body weight (g)		
	Aerial	Ground	*t* test
N	95	94	
Mean	0·05	0·15	$P<0.01$
SD	0·05	0·11	

Our results indicate that drongos gain by such association by feeding on the insects flushed out by the movement of ground foraging mynas. Their gain was clear both in terms of increased frequency of foraging trips and the probability of capturing insects in each foraging trip, compared to when they were isolated in the same foraging patch. There does not seem to be any additional cost to the drongo in being associated with myna flocks.

Mynas seem to neither incur any cost nor gain by such an association. Since, drongos perch at a height of 2 to 3 feet above ground and feed on air borne insects, they are physically separated from the ground habitat on which mynas feed. Further, the food range of mynas and drongos were overlapping only 50·48% (figure 2) suggesting that they might not intensely compete for resources. This is also substantiated by the fact that mynas tolerated the presence of drongos and never exhibited any aggressive interaction towards drongos; instead we observed aggressive

interaction among drongos to occupy perches in and around myna flocks (figure 3) There could however be some benefit to the mynas by the association of drongos Drongos perching at a height might sight predators more easily than mynas on the ground and might alert the myna flocks But we did not see any such behaviour in drongos; though Shikra. the potential predator of myna was sighted atleast 5 times during the study period, drongos did not exhibit any altered behaviour Indeed, mynas after hearing the call of the Shikra abandoned the patch immediately.

Mynas are not the only birds that drongos were associated with; they were found perching around the flocks of other bird species in the study area (table 3) Drongos appear to be associated with larger flocks of any ground foraging birds rather than with any particular species Thus the drongo seems to be an opportunist rather than an obligate member of this association

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MODERN APPROACHES IN POLLINATION BIOLOGY

BY

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Factors affecting pollination activity of *Megachile lanata* lepel

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Abstract. Foraging activity of *Megachile lanata* on *Crotalaria juncea* L. flowers occurred only when minimum threshold of environmental factors was surpassed while the cessation of activities was governed mainly by the fast decline in values of light intensity and solar radiation. Between the initiation and cessation of field activity, foraging population showed a positive correlation with air temperature, light intensity, solar radiation and nectar-sugar concentration fluctuations, but was negatively correlated with relative humidity, soil temperature and wind velocity. The path coefficient analysis revealed that direct effect of solar radiation and light intensity on foraging population were much pronounced and positive while the effects of other factors were of very low magnitude negative or negligible. However, their interrelationships caused accentuation of the overall effects of air temperature, relative humidity and nectar-sugar concentration. The resultant correlation with bee activity were strengthened through their favourable or unfavourable interaction with other factors.

Keywords. Environmental factors; *Megachile lanata*; *Crotalaria juncea*; pollination; path analysis

1. Introduction

The pollinating effectiveness of bees depends upon their foraging population in the field and their behaviour on a crop. Since the field population as well as individual's foraging behaviour result from their innate and unavoidable responses to various environmental stimuli, ecological investigations on qualitative and quantitative aspects of their foraging on economic crops need to be thoroughly understood. This will help in assessment of the resultant interrelationships for their effective management and utilisation as prospective pollinators. Though pollination effectiveness of various bee pollinators has extensively been studied in the past, the studies are mainly based on a limited set of environmental conditions. For instance, Cirudarescu (1971) found that the number of insect visitors on lucerne was directly related to temperature and inversely to relative humidity, but the latter authors found it unaffected by relative humidity and vapour pressure. The flower visiting speed of honey bees increased with temperature (Benedek 1972; Burill and Dietz 1981). Wrona (1973) stated that pollination efficiency of honeybees increased with temperature and decreased with wind speed. Szabo and Smith (1972) found that foraging activity was positively correlated with a suitable combination of light intensity and temperature combined but not with the light intensity independent of temperature. Nunez (1977) reported that the morning activity was related to nectar

flow and in the evening it was correlated with photoperiod These reports indicate no fair general pattern of effects of different environmental factors influencing the pollination activity of bees The probable reason seems in omission of such contributing factors actually influencing the pollination activity and in random selection of a few convenient ones having either no interaction or working in diverse ways, generating thus inconclusive results Since environment is a complex of interrelated factors which influence the bee activity, and also plant physiology, a study of a complex phenomenon like pollination shall remain incomplete until a sizeable matrix of factors are taken on ensanable These were the reasons for the present investigations which include air temperature, relative humidity, light intensity, solar radiation, nectar-sugar concentration, soil temperature and wind velocity as factors probably influencing bee-flower relationships

2 Materials and methods

This study was conducted during September 1984 in sub-tropical Hissar located in the North Western plains of the country between 28° 59′–29° 46′ N (latitude) and 75° 11′–76° 18 E (longitude) at 215·2 m (altitude) on the Plant Breeding Farm of Haryana Agricultural University, Hissar where *Crotalaria juncea* is grown regularly for seed production Hourly observations starting from 0800–1800 h on population/ m^2 of *Megachile lanata* were recorded on *C. juncea* following Sihag (1982) Concurrent with the forager counts hourly measurements of environmental factors were made in the experimental field Atmospheric temperature (T) and relative humidity (RH) were measured with a 'dry and wet' bulb thermometer Soil temperature (ST) was recorded with a soil thermometer at a depth of 25 cm Light intensity (LI) was recorded with a Luxmeter, model Luxomet–300 manufactured by M/s Research Instrumentation, Naraina Industrial Area, New Delhi Similarly solar radiation (SR) was recorded by solarimeter, model SM 201, manufactured by M/s Central Electronics Ltd, Sahibabad, UP Wind velocity (WV) was recorded with a hand Anemometer manufactured by M/s Research Instrumentation, Naraina Industrial Area, New Delhi held vertically at a height of about 1 meter above the crop surface Total dissolved solids in the nectars (NSC) were estimated with the pocket refractometers (model 1093, Range, 0–50%; model 312, Range, 40–85%) manufactured by M/s Toshniwal Brothers Pvt Ltd, New Delhi The recorded data were analysed on TDC-316 computer for simple correlation and path coefficient analysis following Dewey and Lu (1959)

3 Results

3.1 *Commencement and cessation of foraging activity*

The data in table 1 show the temperature, relative humidity, light intensity, solar radiation, soil temperature and wind velocity in relation to the commencement and cessation of field activity by *M. lanata* on *C. juncea* flowers during September 1984 The time at which the commencement of field activity occurred varied from one day to another, which was perhaps dependent upon the attainment of minimum threshold conditions required for the initiation of field activity

Table 1. Temperature, relative humidity, light intensity, solar radiation, soil temperature and wind velocity in relation to the commencement and cessation of field activity of *M. lanata* on *C. juncea*.

Date of observations (Sept. 1984)	Commencement							Cessation						
	Time (h)	T (°C)	RH (%)	LI (lx)	SR (mw/cm²)	ST (°C)	WV (kmph)	Time (h)	T (°C)	RH (%)	LI (lx)	SR (mw/cm²)	ST (°C)	WV (kmph)
11	0855	22·5	75·00	2700	41·00	22·00	3·70	1820	26·00	78·00	2000	35·00	35·00	3·0
14	0810	27·5	80·00	2100	30·00	25·00	3·00	1825	28·50	74·00	1600	20·00	20·00	3·5
19	0750	28·0	82·00	2600	25·00	29·00	3·50	1810	30·00	65·00	1800	22·00	30·5	3·5

Table 2. Estimates of correlation coefficients exhibiting interrelationships of different environmental factors influencing pollination activity of *M. lanata*.

Factors	Relative humidity	Light intensity	Solar radiation	Nectar-sugar concentration	Soil temperature	Wind velocity	Bee activity
Air temperature	−0·359*	0·690**	0·0670	0·547**	−0·176	−0·264	0·650**
Relative humidity		−0·0661	0·833**	−0·871**	0·977**	0·987**	−0·357*
Light intensity			0·462**	0·364*	0·0632	0·0040	0·826**
Solar radiation				−0·542**	0·880**	0·865**	0·1548
Nectar-sugar concentration					−0·819**	−0·810**	0·584**
Soil temperature						0·984**	−0·260
Wind velocity							−0·286

*$P \leq 0{\cdot}05$, $n-2=31$ **$P \leq 0{\cdot}01$, $n-2=31$.

Variation in commencement of the field activity, however, could not be explained by any one factor A complex combination of various factors was perhaps responsible for initiation of field activity The studies further revealed that, in general a temperature of 22 5°C, 75% relative humidity, 2100 lx light intensity, 25 mw/cm^2 solar radiation, 22°C soil temperature and 3 0 kmph wind velocity appeared to be the minimum threshold conditions for initiation of field activity. The cessation of activity was, however, governed mainly by the fast decline in values of light intensity and solar radiation, which were appreciably low than that required for commencement of field activities It was found that cessation of activities occurred even before the air temperature dropped to the values associated with the commencement of field activity (22 5°C)

The critical examination of the data further revealed the occurrence of factor compensatory mechanism for initiation of bee activity within the foraging ranges of the bees, where low values of one factor were compensated by the higher values of others For instance, on 11 September 1984, foraging flight occurred when air temperature was 22 5°C light intensity 2700 lx and solar radiation 41 mw/cm^2, while on 14 September 1984, it started at a higher temperature (27 5°C) when values of other factors like light intensity (2100 lx) and solar radiation (30 mw/cm^2) were comparatively lower than those required for the initiation of field activity on 11 September 1984 Similar situation was observed on 19 September 1984, when the foraging flight commenced at 28°C, but the values of light intensity (2600 lx) and solar radiation (25 mw/cm^2) were lower than those associated with initiation of field activity on 11 September 1984. Evidently, the observations on 11 September 1984 indicate that low values of air temperature were compensated by higher values of light intensity and solar radiation while on 14 and 19 September, the reverse was true Thus, existence of factor compensating mechanisms governing initiation of bee activity is a clear possibility

3.2 *Diurnal trends in bee activity in relation to various environmental factors*

Hourly observations on bee counts showed that their abundance followed air temperature, light intensity, solar radiation, soil temperature and nectar-sugar concentration fluctuations but was inversely related to relative humidity and wind velocity (figure 1). Maximum foraging population of *M. lanata* was observed between 1200–1400 h when the air temperature ranged between 29 5–38°C, relative humidity between 45 0–67%, light intensity between 4700–7400 lx, solar radiation between 58 00–94 00 mw/cm^2, nectar-sugar concentration fluctuated between 46 30–54 2%, soil temperature between 25 00–36 00°C and wind velocity between 3 2–5–5 kmph The conditions optimum for maximum bee activity lie between these values on all the days of observation

3.3 *Relationship of foraging population of M lanata with environmental factors*

Correlation coefficients between bee activity and 7 environmental factors were calculated The data in table 2 showed the extent to which these factors were associated with number of *M. lanata* foraging on *C. juncea*. The results highlighted that within the limits of environmental conditions prevailing during the experimental

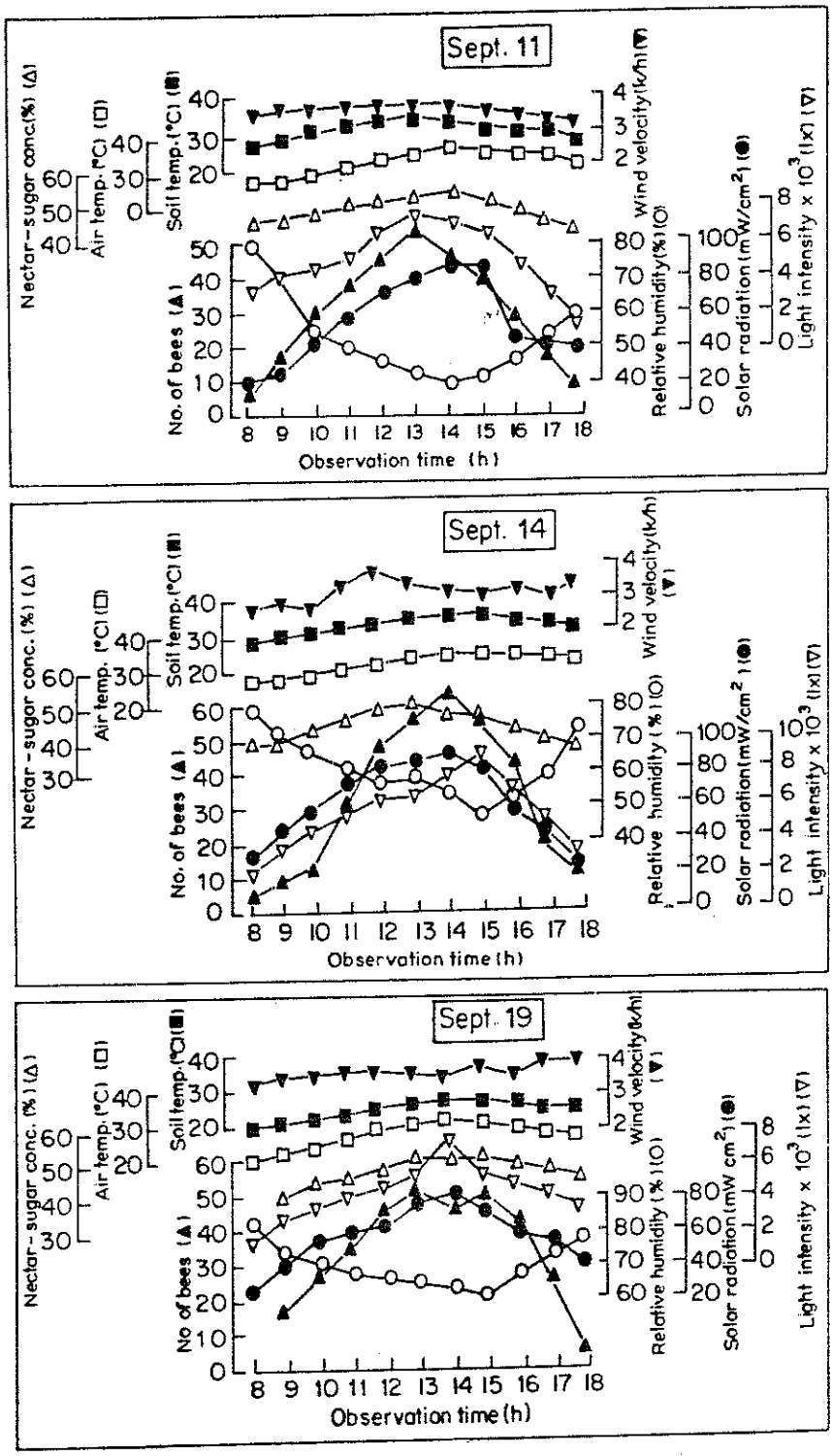

Figure 1. Diurnal trends in activity of *M lanata* on *C juncea* in relation to air temperature, relative humidity, light intensity, solar radiation soil temperature, nectar-sugar concentration and wind velocity.

period, foraging population of *M. lanata* was significantly affected by higher values of air temperature, light intensity and nectar-sugar concentration fluctuations occurring together with lower values of relative humidity. The diurnal variations in soil temperature, solar radiation and wind velocity had a negligible effect on bee activity, and were not found to be associated with changes in the field population of *M. lanata*

The environmental factors themselves are found to interact in several complex ways which is evident from their interrelationships. For instance, nectar-sugar concentration draw high positive correlation with temperature, solar radiation and nectar-sugar concentration while solar radiation make significantly positive correlation with relative humidity, soil temperature and wind velocity, but negative with nectar-sugar concentration. Soil temperature has a high positive correlation with relative humidity, solar radiation and wind velocity and significantly negative with nectar-sugar concentration. Likewise, wind velocity is highly and positively correlated with relative humidity, solar radiation and soil temperature but negative with nectar-sugar concentration.

Due to such complex web of interactions, the relationship between bee activity and environmental factors may not be direct as some of them are causal act directly whereas others may be influencing the activity indirectly, through the causal factors which further demanded investigation. For this purpose, correlations were further analysed by path coefficient technique. This technique involves the partitioning of the apparent association of different factors into direct effects (unidirectional pathways, P) and indirect effects (alternate pathways through factor interaction, pathways, $P \times$ correlation coefficient, r) and thus facilitates precise determination of relative importance of each factor. Bee activity was considered as the resultant variable and air temperature, relative humidity, soil temperature, wind velocity, light intensity, solar radiation and nectar-sugar concentration as the causal variables. Path coefficients were obtained by solution of a simultaneous equations through the method of least squares as given by Dewey and Lu (1959). The path coefficient analysis of interrelationships of temperature, relative humidity, light intensity, solar radiation, nectar-sugar concentration, soil temperature and wind velocity is shown by a schematic model (figure 2). The double-arrow lines indicate the mutual association as measured by correlation coefficients and the single-arrow lines represent direct effects in one direction as measured by path coefficients. The residual factors unaccounted for and considered independent of other variables are represented as px 8. The estimates of direct effect path coefficients and indirect effect path coefficients are presented in table 3.

3.4 *Bee activity versus air temperature*

The direct effect of air temperature on bee visits was positive (0·07946) but of very low magnitude and more or less negligible. It affected positively the bee activity, indirectly through relative humidity (0·4216), light intensity (0·3113), solar radiation (0·06004), and soil temperature (0·2164). But a strong negative influence of air temperature on bee visits was registered indirectly through nectar-sugar concentration (0·1463) and wind velocity (0·2921). Its negative interactions with nectar-sugar concentration and wind velocity tend to reduce its overall influence on bee activity,

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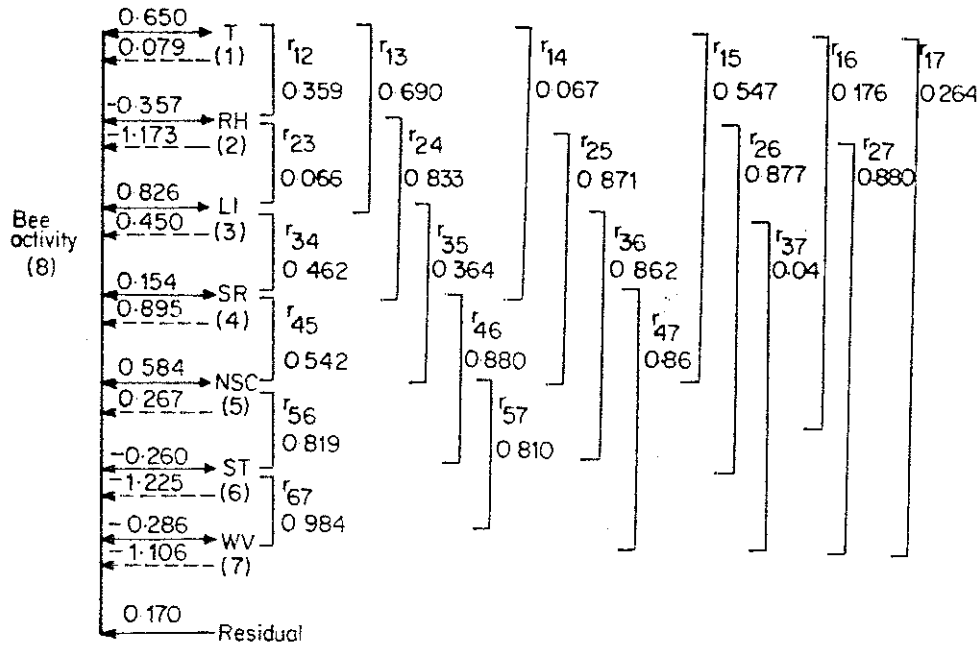

Figure 2 Schematic model exhibiting interrelationships of different environmental factors with bee activity

but its overall positive association with bees ($r = 0{\cdot}650$) was largely a reflection of its favourable interactions with other factors.

3.5 *Bee activity versus relative humidity*

The relative humidity had a strong negative direct effect (1·1737) on the bee activity. However, its positive effect on the bee activity was indirect via solar radiation (0·7458), nectar-sugar concentration (0·2329), and wind velocity (1·092). The positive interactions of relative humidity with these factors reduce its overall negative effect. However, it affected negatively the bee activity indirectly via soil temperature (−1·1972) and air temperature (−0·02854). Its overall negative association with bees ($r = -0{\cdot}357$) was strengthened through its negative interactions with air and soil temperatures.

3.6 *Bee activity versus light intensity*

Simple correlation between the bee activity and light intensity was very high and positive (0·826). It was made up largely of the positive direct effect of light intensity (0·4509) and positive indirect effect via solar radiation (0·4139) on bee activity. Light intensity positively affected the bee activity indirectly via air temperature (0·0548), relative humidity (0·0776) and wind velocity (0·00440) by a negligible magnitude. Its negative indirect effects via nectar-sugar concentration (−0·0975) and soil temperature (0·0773) on the bee activity were relatively unimportant being negligible.

300

Table 3. Path coefficient analysis of bee activity vs air temperature relative humidity, light intensity, solar radiation and nectar-sugar concentration soil temperature and wind velocity.

Path ways of association		Direct effect path coefficient (P)	Indirect effect path coefficient ($P \times r$)	Correlation coefficient (r)
1	Bee activity vs air temperature			0·650
	Direct effect	0·0794		
	Indirect effect via RH		0·4216	
	" " LI		0·3113	
	" " SR		0·0600	
	" " NSC		−0·1463	
	" " ST		0·2164	
	" " WV		−0·2921	
	Total			0·650
2	Bee activity vs relative humidity			−0·357
	Direct effect	−1·1737		
	Indirect effect via T		−0·0285	
	" " LI		−0·0298	
	" " SR		0·7458	
	" " NSC		0·2329	
	" " ST		−1·1972	
	" " WV		1·0925	
	Total			−0·357
3	Bee activity vs light intensity			0·826
	Direct effect	0·4509		
	Indirect effect via T		0·0548	
	" " RH		0·0776	
	" " SR		0·4137	
	" " NSC		−0·0975	
	" " ST		−0·0773	
	" " WV		0·0044	
	Total			0·826
4	Bee activity vs solar radiation			0·1548
	Direct effect	0·8953		
	Indirect effect via T		0·0053	
	" " RH		−0·9778	
	" " LI		0·2083	
	" " NSC		0·1450	
	" " ST		−0·0790	
	" " WV		0·9576	
	Total			0·1548
5	Bee activity vs nectar-sugar concentration			0·584
	Direct effect	−0·2674		
	Indirect effect via T		0·0434	
	" " RH		1·0223	
	" " LI		0·1644	
	" " SR		−0·4854	
	" " ST		1·004	
	" " WV		−0·8971	
	Total			0·584

Table 3 (*Contd*)

Path ways of association	Direct effect path coefficient (P)	Indirect effect path coefficient ($P \times r$)	Correlation coefficeient (r)
6. Bee activity vs soil temperature			−0·260
Direct effect	−1·2250		
Indirect effect via T		−0·0140	
" " RH		−1·1470	
" " LI		0·0284	
" " SR		0·7886	
" " NSC		0·2196	
" " WV		1·0890	
Total			−0·260
			−0·286
7 Bee activity vs wind velocity			
Direct effect	−1·1062		
Indirect effect via T		−0·2098	
" " RH		−1·1592	
" " LI		0·1017	
" " SR		1·2173	
" " NSC		1·8860	
" " ST		−1·2048	
Total			−0·286
			0·170
8 Residual			

3·7 *Bee activity versus solar radiation*

The direct effect of solar radiation on the bee activity was much pronounced and positive (0·8953). Solar radiation positively affected the bee activity indirectly through air temperature (0·00532), light intensity (0·2083), nectar-sugar concentration (0·1450) and wind velocity (−0·9576). It was however negative indirect effect on the bee activity through relative humidity (0·9778) and soil temperature (−1·079). The negative interaction of these factors tended to reduce the overall influence of solar radiation on the bee activity. The total correlation between bee activity and solar radiation ($r = 0·1548$) was largely due to its negative interaction with relative humidity and nectar-sugar concentration.

3·8 *Bee activity versus nectar-sugar concentration*

Surprisingly, the direct effect of nectar-sugar concentration on the bee activity was negative (−0·2674). Nectar-sugar concentration negatively affected the bee activity indirectly through solar radiation (−0·4854) and wind velocity (−0·8971). But these negative effects were diluted by its positive indirect effects on the bee activity through air temperature (0·04347), relative humidity (1·0223), light intensity (0·1644) and soil temperature (1·004). The overall significant yet positive contribution of nectar-sugar concentration to bees activity ($r = 0·584$) was supported by its favourable interactions with air temperature, relative humidity, light intensity and soil temperature

3.9 *Bee activity versus soil temperature*

The direct effect of soil temperature on the bee activity was strongly negative (−1·2250). Its indirect effects on the bee activity was positive via light intensity (0·02848), solar radiation (0·7886), nectar-sugar concentration (0·2192) and wind velocity (1·089). Its indirect negative influence on the bee activity was reckoned through air temperature (−0·0140) and relative humidity (−1·1470). The negative interaction of soil temperature with solar radiation was largely responsible for its overall negative association with the bees' activity ($r = 0·2607$).

3.10 *Bee activity versus wind velocity*

The correlation coefficient between wind velocity and the bee activity was moderately low and negative (−0·286). But its indirect effects on the bee activity was strongly negative (−1·1062), which it did through air temperature (−0·02098) relative humidity (−1·1592) and soil temperature (−1·2048) and positively via light intensity (0·1017), solar radiation (1·2173) and nectar-sugar concentration (1·8860). The net effect of these opposing influences was that 3 negative ones counter balance against the 3 positive ones, making overall correlation between wind velocity and bee activity negative ($r = -0·286$). An overall examination of the correlation components revealed that solar radiation exerted the greatest positive influence on bee activity followed by light intensity, while soil temperature, wind velocity, nectar-sugar concentration and relative humidity negatively affected the bee activity directly. The direct effect of air temperature was almost negligible; however, it strongly affected the bee activity indirectly.

4. Discussion

The reproductive success and perpetuation of cross-pollinated plant species depend heavily on the abundance of associated pollinators and their pollinating efficiency which is under short duration turn-key control of the physical environment. Each bee species is guided by the specific ecological threshold for normal foraging activity whose maintenance differ inter and intra specifically according to their adaptability (Abrol 1985). *M lanata* responds to increasing temperature in the morning until it touches 22·5°C which initiated the field activity. The ambient temperature was found to be the predominant factor governing morning flight of *M rotundata* (Osgood 1974; Lerer *et al* 1982). But the latter authors observed that once the flight is initiated and temperature is maintained, it is solar irradiance that controls the pollination activity. According to Szabo and Smith (1972) it occurs due to combined effect of temperature and light intensity but in no case they work independent of each other. Karmo (1961) could place premium on temperature for initiation of foraging activity of *Apis mellifera* but not for its cessation. Observations by Cirusdarescu (1972) indicate that number of insect visits on crop was directly related to temperature and inversely to relative humidity. Wrona (1973) found pollinating activity of honey bees increased with temperature and decreased with wind speed. An increase in wind velocity has been reported to cause almost directly proportional reductions in the number of *A mellifera* visiting apple bloom (Brittain 1935) and wind velocities above

17 kmph have been observed to greatly hamper their pollen gathering activities during Spring (Rashad 1957) The present investigations differ from these reports possibly because during the present studies wind invariably remained below 17 kmph When acting in combination, the joint influence of other factors may have been far more strong and favourable to the foraging bees, and they may have masked any negative effect of wind on diurnal basis However, changes in wind velocity when other factors are nearly constant can be expected to be indirectly proportional to population of foraging bees (Brittain 1935; Rashad 1957) Corbet (1978) attributed the changes in the spectrum of flowers visitors to fluctuations in nectar-sugar concentration

The cessation of activity by *M lanata* occurred when light intensity and solar radiation dropped for critical values although temperature was yet adequate to keep going the activity

Once the minimum threshold conditions for initiation of activity were exceeded foraging population followed air temperature, light intensity, solar radiation, soil temperature and nectar-sugar concentration fluctuations but was inversely related to relative humidity and wind velocity In general, maximum population was observed between 1200–1400 h, when the air temperature ranged between 29 5–38°C, light intensity between 4700–7400 lx, solar radiation between 58 0–94 0 mw/cm^2, relative humidity 45–67%, nectar-sugar concentration between 46 30–54 20, soil temperature between 25 0–36 and wind velocity between 3 2–5 5 kmph and the effects of other factor was negligible The solar radiation could hardly be of any value independently as the bee activity never occur at 16–17°C And it exerts influence only after 22 5°C as the minimum temperature threshold struck Obviously, major contribution to the extent of 83% in causation of foraging activity is explained by environmental factors studies, remaining 17% seems to be due to atmospheric pressure, caloric award and also unknown factors It is thus evident that air temperature provides a minimum threshold for initiation of flights, hence pollination activity of *M lanata* and once flight is initiated and temperature level is kept up, solar radiation and light intensity takes over The conditions optimum for maximum bee activity may however vary depending upon geographical regions, time of the year, crops or species of bees For example, Cherian *et al* (1947) found 20 5 as the range of temperature suitable for the activity of *Apis cerana indica* on cotton crop at Coimbatore (South India), Kapil and Brar (1971) recorded peak activity of *A florea* on *B compestris* var *toria* when the temperature ranged between 21–25°C and relative humidity 50–57 at Ludhiana (North India) during November Dhaliwal and Bhalla (1983) reckoned maximum population of *A c indica* on cauliflower when the air temperature ranged between 25 1–27 6°C, light intensity between 2000–3233 lx and relative humidity 26–29 4% during April at Solan (North India) Factor compensating mechanisms were also observed operating the commencement of pollination activity of *M lanata* in which lower values of temperature were compensated jointly by higher values of light intensity and solar radiation and vice versa A similar phenomenon has been reported by Szabo and Smith (1972) who found that *M rotundata* foraged at 1075 lx when the temperature was 25°C but needed 6450 lx at 17°C

In contrast, the cessation was killed by light intensity (Osgood 1974) or by evening radiations dropping to 0 3 langleys normally or even by intervening clouds (Gerber and Klostermeyer 1972)

The direct and indirect influences of various environmental factors as measured by

path coefficient analysis indicated that light intensity and solar radiation exerted the greatest positive influence directly. This may in part be due to their direct influence on the physiological and metabolic processes of the plants which are known to yield higher amounts of nectar and pollen at relatively higher values of these factors, while the other factors, viz soil temperature, wind velocity, relative humidity and nectar-sugar concentration negatively affected the bee activity. The direct effect of air temperature was nearly negligible, however, it strongly affected the bee activity indirectly through other factors.

It is thus evident that path coefficient analysis yielded an entirely different picture of the effects than by simple scatter diagrams or simple correlations used by earlier workers (Benedek and Prener 1972; Kapil and Brar 1971; Nunez 1977; Szabo and Smith 1972; Corbet 1978). For instance, simple correlation between bee activity and air temperature was highly significant and positive ($r = 0.650$) which means that with increase in temperature bee visits would increase provided other variables are maintained constant. But path coefficient analysis, however revealed little effect of air temperature on bee activity as its direct effect was of very low magnitude (0.0794). Its overall significant positive association with bees ($r = 0.650$) was strengthened through its favourable interactions with other factors. Similarly, simple correlation between the bee activity and solar radiation ($r = 0.1548$) is having little influence on the bee activity. The path coefficient enhanced its influence on foraging population as pronounced and positive (0.8953). The accentuation of its overall effect was caused by its negative interactions with other factors. Likewise, widely held contention that nectar-sugar concentration directly influences the bee activity (Corbet 1978) is also belied by this analysis.

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With best compliments to Gadagkar
19.8.88

Ecology and Behaviour of Three Bee Species Pollinating Loquat (*Eriobotrya japonica* Lindley)

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(Accepted on 25 March 1988)

Foraging behaviour of *Apis cerana indica* F. workers, *Bombus asiaticus* Morawitz and *B. albopleuralis* Friese was studied on flowers of loquat (*Eriobotrya japonica*) at four sites. Flight activity was initiated only when a minimum threshold of 6.5°C for *Bombus* species and 10.5°C for *A. c. indica* was available. Honeybees visited more middle branches than the upper or lower ones whereas bumble bees collected nectar and pollen mostly from the upper branches. The pollinating efficiency of the bees was: *B. asiaticus* > *B. albopleuralis* > *A. c. indica*. The cessation of flight activity was independent of the prevailing ambient temperature in all the bee species.

Key Words : *Apis cerana indica, Bombus asiaticus, B. albopleuralis,* **Loquat, Environmental factors, Pollination**

Introduction

Loquat (*Eriobotrya japonica*) — an important fruit crop (contains 81.4% water, 0.7% protein, 0.3% fats, 5% minerals, 0.9% fibers, 10.2% carbohydrates, 0.03% calcium, 0.02% phosphorus and 0.7% mg iron/100gm) is canned for preparing jams, jelly, etc. (Rajput & Singh 1964, Randhawa & Singh 1970). In subtropical areas, loquat fruit production depends greatly on insect pollination, especially the honeybees (Singh 1955, Rajput & Singh 1963, Singh & Rajput 1964). The present study examines the pollinators of loquat and their behavioural characteristics in relation to certain eco-physiological factors.

Materials and Methods

The studies were carried out on three species of bees, viz. *Apis cerana indica, Bombus asiaticus* and *B. albopleuralis* on Shalimar Campus of Sher-e-Kashmir University of Agricultural Sciences & Technology, Srinagar. The study site is located in North-Western India between 32° 17′ -37° 50′N and 73° 26′ -80° 36′E at 1670m altitude. Four trees of *E. japonica* at distances 10-15m (referred as sites 1-4) were selected for the study. The flowering shoots about 1.5 — 2m above the ground were characterized into lower, middle and upper branches (located at 1m from one another). Observations on bee counts for 5 min. in each of the five fixed plots (size 1 x 1 m) were made each hour and the number of bees of each species recorded. Temperature and relative humidity were recorded with a 'Dry and Wet' bulb thermometer. Data were recorded for 15 days between October 12 and November 10, 1986. The percentage of each bee species on upper, middle and lower branches was calculated as follow:

$$\text{Percentage of a species (say } X_1\text{) on a branch (say } Y_1\text{)} = \frac{\text{No. of bees of species } X_1 \text{ on } Y_1 \text{ branches}}{\text{Total No. of bees of species } X_1 \text{ on all the branches (i.e. } Y_1 + Y_2 + Y_3\text{)}} \times 100$$

Likewise, the percentage of species X_2 and X_3 was calculated.

The pollinating efficiency of bees was assessed by the time spent/flower(s), flowers visited/min and the stigmas touched/min, as per the method of Abrol (1986a). The time spent by a bee gathering nectar and pollen was recorded with a chronometer of 0.01s accuracy, by following its movements as long as possible. Five such observations were made in the beginning of each hour and the number of flowers visited/min was estimated accordingly. The recorded data were analysed following Snedecor and Cochran (1967).

Results and Discussion

Flight activity started at a minimum temperature threshold of 6.5°C (for *Bombus asiaticus* and *B. albopleuralis*) and 10.5°C (for *A. c. indica*), Abrol (1986b) reported

that each bee species has a specific ecological threshold for initiation of flight activity which differs inter and intra specifically, depending upon its level of adaptibility in a particular environment. Lerer et al. (1982) reported that in case of *Megachile rotundata* F. no flight activity was observed below the critical air temperature of 16-17°C. Likewise, 15-18°C temperature has been reported for *Apis florea* F. (Kapil & Brar 1971) and *A. dorsata* F. (Kapil & Kumar 1974, Abrol 1985, 1986b). Cessation of flight activity in all the three bee species, however, occurred even before the air temperature dropped to the values associated with the commencement of field activity. Evidently cessation of flight activity was independent of the air temperature and may possibly be governed by diminishing light intensity and solar radiation (see Lerer et al. 1982, Abrol & Kapil 1986).

In between initiation and cessation, interesting foraging differences between honeybees and bumble bees were observed (table 1). Maximum abundance of honeybees was observed 2-3m above ground and relatively low populations were reckoned on lower or upper branches at all the sites. Their percentage abundance was in the order: middle branches>upper branches>lower branches. Similar results were obtained by Chauhan (1985) who found that honeybees visiting apple flowers were more abundant on middle branches than the upper or lower ones. Whereas in case of bumblebess reverse was true (table 1). Maximum populations were recorded on upper or top branches. Their percentage abundance was in the order: upper branches>middle branches>lower branches.

The pollinating efficiency of bees in terms of flowers visited/min is presented in table 2. The number of flowers visited/min, on an average, was 5.67, 10.85, 13.17 for *Apis cerana indica*, *B. asiaticus* and *B. albopleuralis* respectively. Evidently, *B. asiaticus* had the highest pollinating efficiency than the *B. albopleuralis* and *A. c. indica*. In general, *B. asiaticus* was larger than *B. albopleuralis* and *A. c. indica*. They also differed in their body size and energy requirements in the order: *B. asiaticus*>*B. albopleuralis*>*A. c. indica* (Abrol unpublished data). The differences observed in flower visitation rates may possibly be explained by similar effects. More future research in this direction is promising for utilisation of these bees as prospective pollinators of various agricultural/horticultural crops.

Table 1 *Abundance of different bee species on upper, middle and lower branches of* Eriobotrya japonica *on different experimental sites during October-November 1986*

Bee species	Position of flowering branches	percentage proportion Site				Average
		1	2	3	4	
Apis cerana indica	Lower	52.00	50.00	45.80	44.50	48.07
	Middle	26.50	29.80	30.80	28.50	28.90
	Upper	21.50	20.20	23.50	23.00	22.05
Bombus asiaticus	Lower	25.00	15.20	17.30	39.00	24.12
	Middle	32.00	37.30	31.30	18.00	29.65
	Upper	43.00	47.50	51.40	43.00	54.00
B. albopleuralis	Lower	20.00	17.00	11.00	13.00	15.25
	Middle	25.00	30.00	34.00	36.00	31.25
	Upper	55.00	53.00	55.00	51.00	53.50

Each percentage value is calculated from 135 observations

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Table 2 *Rate of flower visitation by different bee species*

Bee species	Flower visited/min Site				Average
	1	2	3	4	
Apis cerana indica	5.34±0.88	5.90±1.21	6.70±1.60	5.10±0.92	5.76
Bombus asiaticus	10.30±1.80	12.20±1.97	11.50±2.10	9.40±1.37	10.85
B. albopleuralis	12.50±2.50	15.20±2.17	14.30±1.98	13.10±2.10	13.77

(Values are mean ± SD of 135 observations)

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STUDIES ON ECOLOGY AND BEHAVIOUR OF INSECT POLLINATORS FREQUENTING STRAWBERRY BLOSSOMS AND THEIR IMPACT ON YIELD AND FRUIT QUALITY

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Abstract: Insect pollinators of strawberry and their effect on yield and fruit quality was studied The percentage of fruit set and well formed fruits was much higher in open pollinated plants as compared to those where pollinating insects were not allowed access The bees, *Lasioglossum* sp and *Apis cerana indica* were the most numerous visitors Flies, *Syrphus* sp. *Musca* sp., mosquitoes, and butterflies were poorly represented and frequented at interrputed hours Bees species differed in their responses to abiotic conditions The honeybee, *A.c indica* appears to be the efficient pollinator on the basis of its field behaviour, nectar-pollen carrying capacity and ability to pollinate flowers per unit time

Résumé: Les insectes pollinisateurs des fraises et leurs effects sur la production et la qualité des fruits ont été étudiés Le pourcentage de fructification et de furits bien formés est bien plus élevpour les plantes librement pollinisées que pour celles pour lesquelles l'accès des insectes pollnisateurs était empêché Les abeilles *Lasioglossum* sp et *Apis cerana indica* sont les visiteurs les plus nombreux Les mouches *Syrphus* sp., *Musca* sp., les moustiques et les papillons sont faiblement représentés et fréquentent les fleurs de façon discontinue Les espéces d'abeilles diffèrent dans leurs réponses aux conditions abiotiques L abeille à miel *A C. indica* semble êtra un pollinisateur efficace, d'après son comportement sur le terrain, sa capacité à transporter le pollen et le nectar et à polliniser les fleurs par unité de temps

Resúmen: Se estudiaron los insectos polinizadores de las flores de fresa y sus effectos en el rendimiento y calidad de los frutos. El porcentaje de frutos producidos bien formados fué mucho más alto en plantas polinizadas libremente. comparadas con aquellas donde se restringió el acceso de insectos Las abejas *Lasiogglosum* sp y *Apis cerana indica* fueron los visitadores más numerosos Moscas, *Syrphus sp. y Musca* sp., mosquitos y mariposas estuvieron pobremente representadas y se presentaron interrumpidamente Las especies de abjas diferen en su rspuesta a las condiciones abioticas. La abeja de la miel, *A C. indica* aparece como el polinizador mas eficiente en base a su comportamiento de campo capacidad de acarreo de polen y néctar y habilidad de polinización por unidad de tiempo

Resumo: Os insectos polinizadores dos morangueiros e o seu efeito na produção e qualidade dos frutos foram estudados neste trabalho. A percentagem de vigamentos e de frutos bem formados foi muito mais elevada em plants dexiadas sob polinização livre do que naquelas defendidas dos insectos polinizadores As abelhas *Lasioglossum* sp. e *Apis cerana indica* foram os polinizadores mais frequentes As moscas. *Syrphus* sp. *Musca* sp., mosquitos e borbuletas estavam pouco representadas e frequentaram as flores em horas esporadicas As espécies de abelha diferiram nas suas repostas as condiçóes abióticas A abelha melifera *A C. indica* parece ser o polinizador mais eficiente na base do seu comportamento no campo, capacidade detransporte de nectar-pólen e aptidão poliniziadora em termos de flores visitadas por unidade de tempo.

Key Words: *Apis cerana indica*, *Lasioglossum* sp., Environmental factors, Strawberry, Pollination, Yield and Fruit quality.

INTRODUCTION

As in many cross-pollinated plants, varieties of commercial strawberries depend upon insect pollination for yield and fruit quality (Free 1968, Nye and Anderson 1974); Honeybess have

been recognised as chief pollinators of strawberry (Nye and Anderson 1974). Also Jaycox (1970) reported that bees and flies were the important agents of strawaberry pollination They not only carried pollen between flowers but al so agitated the blossoms, thereby aiding release of pollen. During inclement weather pollination is mostly carried out by insects other than honeybess, especially Diptera (Hooper 1912). the present investigation deals with the role of pollinating insects in strawberry production and their foraging behaviour in relation to some weather factors

MATERIALS AND METHODS

This study was conducted during April-May, 1987 at a strawberry farm in Harwan, Srinagar (32° 50′ – 37° 50′ N and 73° 26′ – 80° 30′ E). For assessing the role of pollinating insects, 100 randomlyselected unopened flower buds were islolated from insect visits by enclosing in muslin cloth, perforated with pin holes for free aeration to avoid any microclimatic effects (mesh size 70 pores per square inch) (self-pollination) and another 100 left for open pollination. After the maturity, the fruit under self-pollination and open pollination were harvested separately and compared foryieldand fruit quality. The relative abundance of pollinating insects was determined as per the method of Abrol and Kapil (1986). Ten plots of 1×1 m size were selected randomly in the crop. Bees were counted at hourly intervals from 09.00–16.00 h and the sum of these counts constituted the reading for each hour. Rate of flowers visited/min was recorded following Abrol (1986). For measuring nectar loads, the bees were caught from the wings and their abdomen slightly pressed. The drop of nectar that oozed out of the tongues was measured with the 5 λ micro-capillary pipette. Likewise, pollen loads were brushed from the collected bees and weighed using single pan analytical balance with an accuracy of 0.01 mg. Simultaneously, measurements of enviromental factors were also made in the experimental field. Atmospheric temperature and relative humidity were measured with a 'dry and wet' bulb thermometer General weather conditions were also recorded. The recorded data were analysed follwoing Snedecor and Cochran (1967).

RESULTS AND DISCUSSION

The data presented in Table 1 show that percentage of fruit set was much higher in insect pollinated plants than in those isolated from insect visits. The flower buds open for pollination and or caged for self-pollination set 75 and 47 fruits, respectively Likewise, percentage of malformed fruits was higher in self-pollinated plants (33%) as compared to those left for open pollination (11%). Evidently, insect pollination is essential for maximum yield and fruit quality. Earlier investigators have reported a similar role of pollinating insects in strawberry porduction For instance, Free (1968) found that pollination by honeybees increased fruit set, berry weight and percentage of well formed fruits. Moore (1969) found that exclusion of pollinating insects delayed fruit maturity and reduced yields. Nye and Anderson (1974) reported that plots of strawberry caged with honeybees produced fewer malformed fruits than plots screened to exclude pollinating insects.

The data presented in Fig. 1 show that *Lasioglossum* sp., and *Apis cerana indica* were the most numerous vistors. *Syrphus* sp., *Musca* sp , mosquitoes, butterflies, black ants and thrips were the other insects associated with strawberry blossoms. *Syrphus* sp., *Musca* sp., and butterflies were rare vistors and frequented at interrrupted hours (referred to as 'Others') The data presented

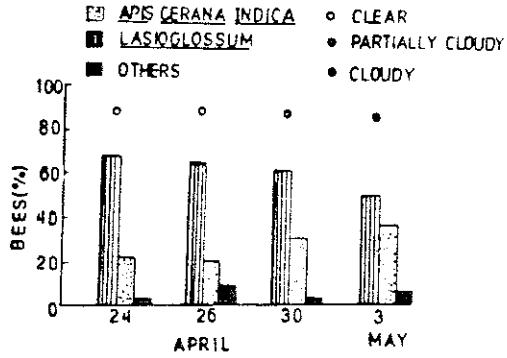

FIG 1 Histogram exihibiting percentage proportion of insect pollinators frequenting strawberry blossoms on four different days

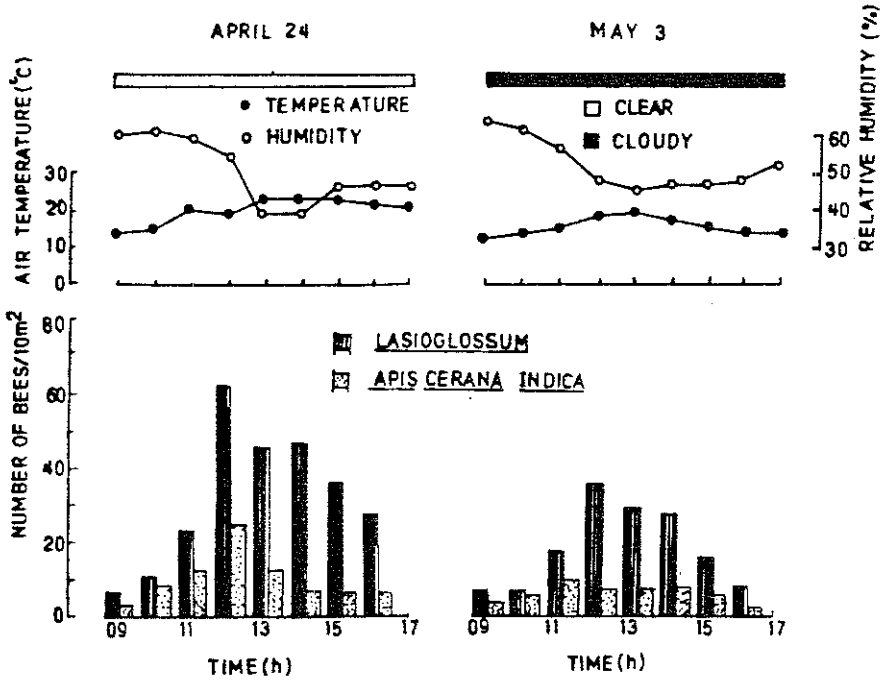

FIG 2 Diurnal acitivity or insect pollinators on strawberry blossoms on clear and cloudy days in relation to ambient temperature and humidity.

in Table 2 and Fig 2 show that activity of *A C. indica* and *Lasioglossum* sp. was positively related to temperature but was inversely related to relative humidity. Similar results have been reported by earlier investigators (Cirudarescu 1971, Benedek and Prener 1972) The data in Table 3 show that number of flowers visited/min varied considerably *A.c. indica* on an average visited the highest number (6 2) followed by *Lasioglossum* sp. (3.0). Likewise, nectar and pollen loads carried by *A c. indica* were much higher than those carried by *Lasioglossum* sp (Table 4). The honeybees, *A.c. indica* appears to be the most useful pollinator of strawberry, yet the role of

TABLE 1 Effect of pollination on strawberry yield and fruit quality.

Treatment	Flowers observed	Fruit set	Malformed fruits	Percentage
Open-pollination	100	75	8	1
Self-pollination	100	47	11	23

TABLE 2 Correlation coefficient (r) between be activity and environmental factors

Factors	*A c. indica*	*Lasioglossum* sp	Temperature	Relative humidity	N
Temperature	0.580**	0.610**	1.000	–0.810**	40
Relative humidity	–0.497**	–0.647**	–0.810**	1.000	40

** $P < 0.01$

TABLE 3 Number of flowers visited/min by *A.c. indica* and *Lasioglossum* sp

Insect pollinator	Flowers visited/min		N
	Mean	S.E	
A c. indica	6.2	0.27	32
Lasioglossum sp.	3.0	0.14	32

TABLE 4 Nectar and pollen loads of *A c. indica* and *Lasioglossum* sp

Insect pollinator	Reward/bee					
	Nectar (µl)			Pollen (mg)		
	Mean	S.E	N	Mean	S.E	N
A c. indica	3.8	0.09	20	4.8	0.12	20
Lasioglossum sp	0.6	0.02	20	3.0	0.07	20

abundant *Lasioglossum* sp is substantial. In general, both the species were most active between 12-14 h when the temperature ranged between 18–23°C and relative humidity between 40–56%. *Lasioglossum* sp, was most active on clear sunny days. Cloudiness was, found to reduce the numbers of both *A c. indica* and *Lasioglossum* sp , the latter being more affected Thus, the two beee species respond somewhat differently to variations in light intensity and temperature caused by intervening clouds This further substantiates the earlier observation that these two bee species differ considerably in their thermal requirements for initiation of flight activity (Abrol 1988). The preference for different abiotic conditions enable the two bee species to partition the flowers, thereby reducing competitive interaction and obtaining higher yields Strawberry pollination can be improved by providing sufficient numbers of bee colonies near the plantings and by managing soilnesting wild populations of *Lasioglossum* sp. Disturbance to their nesting areas should be avoided and pesticides (if necessary) should be applied only before or after the period of strawberry flowering

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QUANTITATIVE ETHOLOGY OF SOCIAL WASPS — A CASE STUDY

BY

RAGHAVENDRA GADAGKAR

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QUANTITATIVE ETHOLOGY OF SOCIAL WASPS: TIME–ACTIVITY BUDGETS AND CASTE DIFFERENTIATION IN *ROPALIDIA MARGINATA* (LEP.) (HYMENOPTERA: VESPIDAE)

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Abstract. Time–activity budgets of several individually identified members of *Ropalidia marginata* colonies have been constructed with the aim of studying caste differentiation in social wasps that show no morphological differences between individuals. Analysis of these data by multivariate statistical techniques including principal components analysis and hierarchical cluster analysis has demonstrated the presence of three different behavioural castes which we have named Sitters, Fighters and Foragers. The Sitters in a colony consist of the queen and also some non-egg-laying individuals. The Fighters are non-egg-layers that show alarm reactions in response to disturbances and also fight with other individuals on the nest to a very large extent. The Foragers are also non-egg-layers and they spend a large proportion of their time making trips to places away from the nest to collect food, building material etc.

The social insects comprising ants, bees, wasps and termites are remarkable in that they exhibit extreme degrees of social organization and division of labour within members of a social group or colony. The present day species of bees and wasps exemplify a series of stages in the spectrum of social organization and caste differentiation from solitary to eusocial. In insect societies, a caste is defined as a set of individuals that are both morphologically distinct and specialised in behaviour (Wilson 1971). By this definition, the caste systems of social wasps (Vespidae) are often not as highly developed as those of the other social insects (West-Eberhard 1969; Jeanne 1972; Litte 1977). Morphological differentiation is not common and when present has a simple nutritional basis (Wilson 1971).

However, even in the complete absence of morphological differentiation, there could be behavioural differences between the members of a colony. At a very primitive level of division of labour, it is probable that the behavioural repertoire of all the individuals would be similar and the differences quantitative rather than qualitative. Such differences could be best detected by studying how each individual allocates its time between the different possible behaviour patterns. Hence, we have constructed time-activity budgets for individually identified members of *R. marginata* colonies and looked for evidence of behavioural caste differentiation.

Ropalidia marginata is a common paper wasp in India that builds small open nests on the eaves of undisturbed buildings or on the twigs of cypress bushes (*Cupressus sempervirens*) (Gadagkar 1980). The nests contain up to 100 adults, although smaller nests (< 10 adults) are more common. Small nests have a single egg-layer whereas large nests tend to have several egg-layers. No morphological differences are noticeable between egg-layers and non-egg-layers or between any of the adults on a nest, though individuals with well-developed ovaries tend to be among the heavier individuals (Gadgil & Mahabal 1974; Gadagkar et al., unpublished observation).

In this paper we show that analysis of the time–activity budgets of the adults of *R. marginata* colonies yields three distinct behavioural castes which we have named Sitters, Fighters and Foragers after their distinguishing attributes.

Subjects and Methods

A. Study Animal

The study was conducted on two small post-emergence nests of *R. marginata* (the total number of adults per nest varied between four and 40 during the period of study) built on cypress bushes (*Cupressus sempervirens*) in Cubbon Park in the city of Bangalore (13°00′ N and 77°32′ E), India, between November 1979 and April 1980. All the adults in the colonies were individually labelled by marking them with one or more spots of aeroplane paint of different colours on different parts of the body. The marking was done immediately after the emergence of an adult. A census of all the wasps present at the nest was taken at about 0700 hours since none of them was ever

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seen to leave the colony before this time during preliminary ad libitum observations. Both the colonies had a single egg-layer (queen) each during the entire period of study. Males disappeared from the colony within a few days after emergence. Thus all the data in this paper pertain to the females.

B. Sampling Methods

Four kinds of sampling methods were used in the study (Altmann 1974).

(1) **Ad libitum sampling** was employed for constructing an ethogram, i.e. we compiled a descriptive catalogue of the behavioural repertoire of the species to get preliminary information on the basis of which subsequent sampling methods were chosen.

(2) **Instantaneous scanning** of the behavioural states of all animals in a colony was performed at 134 randomly chosen times during the period of study.

(3) **All occurrences of rare behaviours** were noted. Some behaviours that appeared to be relatively rare on the basis of ad libitum sampling were recorded in 100 separate 5-min sessions during which all occurrences of each such behaviour by every animal in the colony were recorded. Here every behaviour was treated as an event and no information on its duration was recorded.

All sampling sessions were begun and terminated by time-contingent rules using a stop watch accurate to 0.1 s. Observations were made for a total of 160 h. Ad libitum observations showed that the wasps were relatively inactive between 1800 and 0900 hours. Hence all sampling sessions were randomly chosen between 0900 and 1800 hours. All data were recorded on coding sheets in an 80-column format ready to be punched on computer cards. The data were analysed using a DEC 1090 computer at the Indian Institute of Science, Bangalore, India.

C. Analysis of Data

(1) **Behavioural repertoire.** The behavioural repertoire of *R. marginata* was classified into 37 distinct behavioural categories (Gadagkar, unpublished data; Gadagkar and West-Eberhard, in preparation). However, data on the following 11 categories alone were analysed in this study.

(i) **Sit and Groom.** By sitting is meant simply sitting quietly without doing anything in particular and without being alert to any external disturbance. In this position the wasps sit with their bodies held compactly in one plane and their legs and wings drawn close to the body with the antennae lowered. Grooming is always self-grooming and no allogrooming has been observed. The most frequent forms of grooming involve rubbing posterior legs against each other and against wings and abdomen, anterior legs against mouth parts, antennae and head, and antennae against mouth parts.

(ii) **Raise Antennae.** This involves sitting with wings drawn close to the body but the antennae raised above the body plane. There is a transition from Sitting to Raising Antennae when there is any disturbance.

(iii) **Raise Wings.** This involves sitting with both antennae and wings raised above the body plane. The legs are either folded or stretched so as to raise the body above the substratum. Raising Antennae is followed by Raising Wings if the disturbance continues.

(iv) **Walk.** The wasps walk from the face of the nest and back; when they walk they sometimes reach different cells in the nest and sometimes reach other adults sitting on different parts of the nest.

(v) **In Cells.** The wasps get inside the cells with only their head or the entire body either simply 'inspecting' the contents or receiving secretions from the larvae or transferring liquid to larvae.

(vi) **Absent from Nest.** Absence from the nest is considered here as one category although a wasp temporarily absent from the nest may return with food, building material, liquid or nothing.

(vii) **Bring Food.** As mentioned earlier the wasps sometimes bring back food, building material or liquid.

(viii) **Attack.** The wasps fight with each other. Attacking involves climbing over the opponent and sometimes chewing the dorsal part of its body, but more often bending itself over the head of the opponent and biting its mouth parts.

(ix) **Attacked.** The wasp that is being attacked is very subdued and keeps its body stiff with antennae, legs and wings all drawn close to the body.

(x) **Snatch Food.** This is the act of acquiring solid food from another individual. The other individual is said to **(xi) Lose Food.**

(2) **Time–activity Budgets.** With the data available it was possible to calculate the time–activity budgets of 20 wasps derived from the two

colonies for the six activities, Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest

(3) **Frequencies of rare behaviour.** For behaviour that tended to occupy a very small proportion of time as observed from the scans, and for behaviours that are better treated as events rather than states, frequencies were computed from the all-occurrences recording sessions. These behaviours included Bring Food, Attack, Attacked, Snatch Food and Lose Food.

(4) **Principal components analysis.** From the time-activity budgets, every individual can be characterized by the proportion of time it spends in each of the six different behaviours. The method of principal components analysis (Frey and Pimental 1978) yields a new set of uncorrelated variables. Moreover, the new variables are maximally powerful in bringing out the differences between individuals in the sense that, of all the possible linear combinations, the proportion of total variance accounted for by each of the new variables is maximal (Anderberg 1973). It is often possible that only a small number of these new variables account for almost all the variance between the individuals.

(5) **Hierarchical cluster analysis.** Using the proportion of time spent in the six activities by different individuals as input data, Pearson product moment correlation was obtained as an index of similarity between pairs of individuals. Using these indices of similarity, a hierarchical cluster analysis was performed with the single linkage algorithm (DeGhett 1978)

Results

Time-activity budgets calculated for 20 individuals reveal that adults of *R. marginata* spend 85–100% (mean ± SD = 95.9 ± 4.4) of their time in the six activities Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest. However, the manner in which a given wasp allocates its time among these six activities is highly variable. For example, the queens (individuals 1 and 14) spend no time at all in Absence from Nest and among the other individuals; the time allotted to this activity varies from 4–69%. Similarly, the time spent in Sit and Groom varies from 7–56%, with the queen representing the highest value.

The results of principal components analysis performed using data on the time-activity budgets of 20 wasps are presented in Table I. The first principal component accounts for 72.3% of the total variance with Absence from Nest as its dominant term (weightage = 0.8289). The second principal component, whose dominant term is Raise Antennae (weightage = 0.8219), accounts for 20.2% of the total variance. Since the first two components together account for 92.5% of the total variance, we have represented each individual as a point in the coordinate space of the associated amplitudes of these two principal components. As seen from Fig. 1, the points fall into three obvious clusters. This has been confirmed by the method of nearest centroid; the distance between any individual and the centroid of the cluster to which it belongs is less than its distance from the other two centroids. Individual 13 alone does not fall into any of the three clusters. This we believe is because most of the data on this animal was collected when the nest was in the process of being abandoned because of extensive predation by *Vespa tropica*, a common predator of *R. marginata* colonies.

It must be emphasized here that the three clusters have emerged as a result of an objective analysis of the data in as much as no prior

Table I. Eigenvectors of Principal Components, Eigenvalues, Percentage of Variance, and Cumulative Percentage of Variance

Behaviour	Principal components			
	1	2	3	4
Sit and Groom	−0.5305	−0.5025	0.0118	0.5835
Raise Antennae	−0.1056	0.8219	−0.1701	−0.4060
Raise Wings	0.0152	0.1012	0.9052	0.1252
Walk	−0.1343	−0.0690	−0.2960	0.6004
In Cells	−0.0457	−0.0524	−0.2357	0.1169
Absent from Nest	0.8289	−0.2328	−0.0917	−0.3238
Eigenvalue	1.27×10^4	3.54×10^3	7.33×10^2	4.34×10^2
Variance (%)	72.30	20.20	4.18	2.48
Cumulative variance (%)	72.30	92.50	96.68	99.16

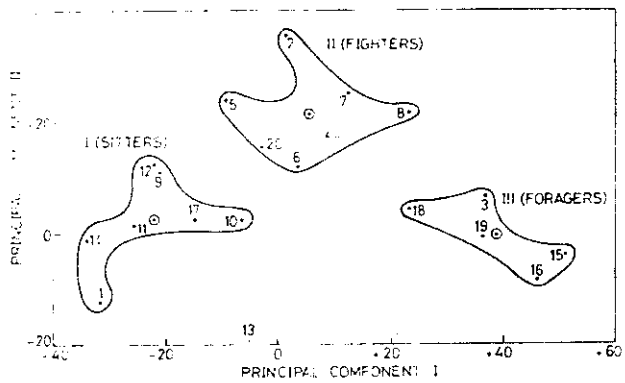

Fig. 1. Behavioural castes of *R. marginata*. Twenty wasps are shown as points in the coordinate space of the amplitudes associated with the first two principal components. The points fall into three clusters (or castes) by the criterion of nearest centroid. Circled dot = centroid.

assumptions were made regarding the criteria to be used for classification or the number of clusters required.

Absence from Nest is the dominant term in the first principal component, and clusters I and III thus represent two extremes for this activity, while cluster II is intermediate. Similarly, Raise Antennae is the dominant term in the second principal component and the members of cluster II are thus different from those of clusters I and III in the time spent with Raised Antennae. An independent method of classification, namely hierarchical cluster analysis using the Pearson product moment correlation as an index of similarity between individuals also gives identical clusters (Fig. 2). Individual 13 is again separated from all the others and one can recognize three clusters with the same composition as the clusters obtained from the principal components analysis. Although this method does not permit us to identify the distinguishng features of each cluster, we would like to interpret the complete concurrence of the two methods as an indication of the robustness of the clusters.

The mean profiles of the three clusters with reference to the six activities used in the classification are shown in Fig. 3A. Figure 3B shows the mean profiles of the same three clusters using the frequencies of the five other activities not used in the classification. Although it is not necessary for any one activity alone to show significant differences between the clusters (as the clusters have been obtained by the consideration of six activities simultaneously), it is obvious from Fig. 3A that the time spent in Sitting and Grooming, Raised Antennae, and Absence from the Nest are the most distinguishing attributes of clusters I, II and III respectively. The difference in the time spent in Raised Antennae between clusters I and II is rather small. On the other hand if we look at Fig. 3B, a high frequency of Attacking emerges as a very conspicuous attribute of cluster II. Moreover, there is a significant positive correlation between the time spent by an individual with Raised Antennae and its frequency of attacking

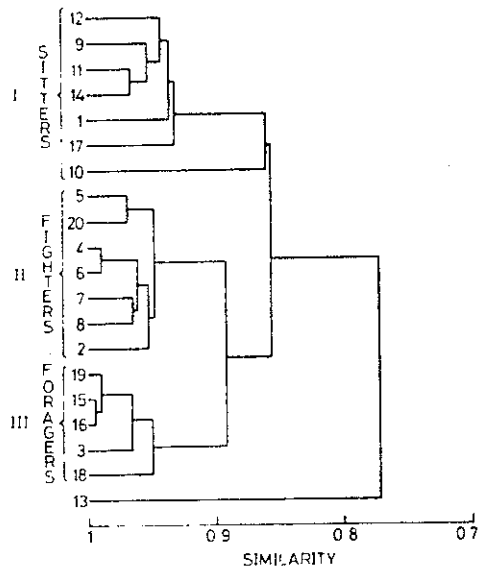

Fig. 2. Hierarchical cluster analysis of 20 adults of *R. marginata* numbered as in Fig. 1. The similarity between individuals shown in the Pearson product moment correlation calculated using the percentage of time spent in six activities as input data. The method of single linkage algorithm has been used in clustering.

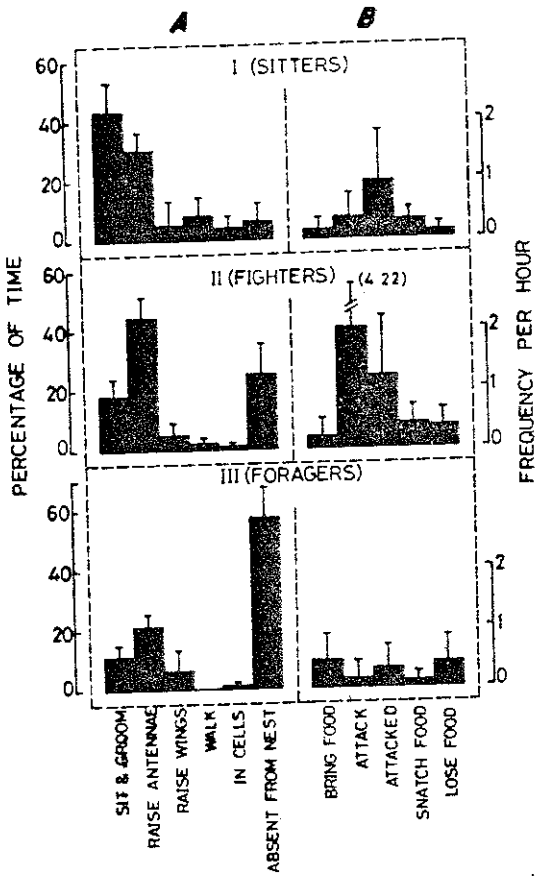

Fig. 3. Mean behavioural profiles of the clusters obtained in Figs 1 and 2. A, mean percentages of time spent in each of the six activities that were used in obtaining the clusters are shown for Sitters, Fighters and Foragers. B, mean frequencies per hour of the five activities that were not used to obtain the clusters are shown for Sitters, Fighters and Foragers

other individuals ($P < 0.01$). Hence we wish to consider Attacking or Fighting as the distinguishing attribute of cluster II. Wasps in cluster III spend a great deal of time being Absent from the Nest. Because these wasps often bring back food loads or building material (confirmed by casual observations on wasps away from their nests), we consider Foraging as the distinguishing attribute of cluster III. Thus we see that the adults of R. *marginata* colonies can be classified into three behavioural castes which can be called Sitters, Fighters and Foragers.

Discussion

Multivariate analysis of data on time-activity budgets of individually identified members of colonies of the social wasp *Ropalidia marginata* reveals the presence of three behavioural clusters despite the absence of any obvious morphological caste differentiation. These three behavioural clusters have been named Sitters, Fighters and Foragers on the basis of their most distinguishing features.

Sitters are those that spend much more time Sitting and Grooming than others. They do little or no foraging and seldom fight either with members of their own group or those of other groups (Fig. 4). It is important to note that the queens of both the colonies (individuals 1 and 14) belong to this group. However, there are other non-egg-laying members of this group. Whether these are 'hopeful queens' who may still have some chances or reproducing on their own (see West-Eberhard 1978), or naive workers yet to be recruited into the worker force, is not clear at present. These questions are being investigated by queen removal experiments.

Fighters are individuals that spend a large proportion of their time with Raised Antennae, and they also Attack other individuals frequently. They show the highest frequency of attacking other members of their own group and a lower frequency of attacking a Sitter or a Forager (Fig. 4). Sitting with Raised Antennae probably serves the function of guarding the nest and its brood against parasites and predators. This is supported by the fact that wasps remain in this position for extended periods of time if the nest is disturbed either by the investigator or by tachinid flies known to parasitize their brood (unpublished observations). It is conceivable that Attacking induces the other

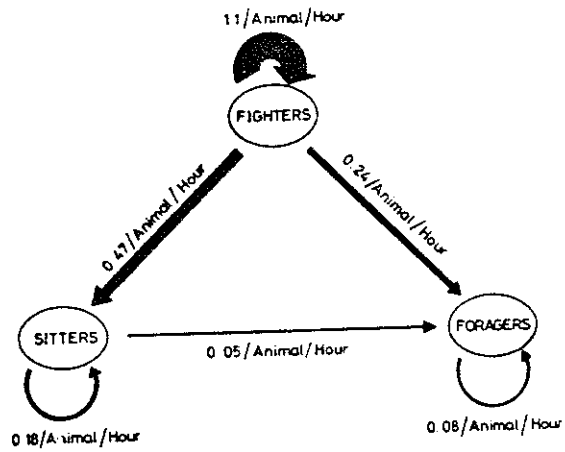

Fig. 4. Mean attacking frequencies within and between Sitters, Fighters and Foragers.

members of the colony to work. We have sometimes observed wasps leave the nest as a result of repeated attacks from nest mates and later return with food or building material. Further support for this idea comes from the observation that Fighters also snatch food from other individuals to a large extent; there is a significant positive correlation between the frequency of Attacking and that of Snatching Food ($P < 0.01$) (see also Gadagkar 1980). Fighters may also have some chance of becoming egg-layers if the colony becomes large and polygynous or if some accident were to befall the queen. In *Mischocyttarus mexicanus*, for example, the next most dominant individual becomes the egg-layer if the queen is removed (Litte 1977). This is one possible reason why Fighters show the highest frequency of attacking another Fighter (Fig. 4). By means of attacking, a linear dominance hierarchy can be recognized among the members of a colony (Gadagkar 1980). In one instance we observed that a queen had disappeared from a nest and the most dominant individual of the remaining wasps immediately began to lay eggs (unpublished observations).

Foragers constitute the principal worker force of a colony. They show the lowest frequencies of Sitting and Grooming, Attacking and being Attacked (see also Fig. 4). Thus, they do not seem to be involved in reproductive competition with their nest mates and we suggest that they have the least chance of becoming egg-layers.

It should be pointed out that egg-laying itself was not used as one of the activities in the present analysis. This is because egg-laying occupies an extremely small proportion of the time available to a wasp and we were more interested in classifying individuals according to the manner in which they allocated their time between different activities. Moreover, differentiation into reproductive and non-reproductive castes is very well established in all eusocial insects. On the other hand, the fact that both the queens fall in the same cluster in spite of egg-laying not being included in the analysis can be considered as evidence of the biological significance of the kind of behavioural classification we have attempted.

The results of this study are remarkably similar to those of the only other similar study concerning social insects. Brothers and Michener (1974) collected behavioural data on the primitively social bee *Lasioglossum zephyrum* and subjected them to principal components analysis. Their results show that the bees can also be clustered into three groups which they call queens, guards and workers. It is interesting to speculate that the queens, guards and workers of *L. zephyrum* correspond to the Sitters (with queens as some of their members), Fighters (that also spend the maximum time with Raised Antennae) and Foragers respectively of *R. marginata*.

Further work is in progress to elucidate the effects of age of the animals and stage of colony development on such a behavioural caste differentiation.

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Social Organisation in the Indian Wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae)

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With 7 figures

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Abstract and Summary

Multivariate analysis of time-activity budgets of several individually marked adults of the primitively eusocial Indian wasp *Ropalidia cyathiformis* shows the existence of three behavioural clusters (or castes) which are called Fighters, Sitters and Foragers, after their most distinguishing features. The principal egg layers who are also the most dominant individuals are the Fighters. The Sitters are idlers who are speculated to be 'hopeful queens' and the foragers are the principal worker force of the nests. Such a behavioural differentiation does not normally appear to change drastically with age of the animal. Nor does it change when an individual leaves a nest and founds or joins a different nest. It probably could however change in response to major perturbations such as death of the queen. Males as a class do not form a separate cluster distinct from the females but may either be Sitters or Foragers. Comparison of these results with those of *R. marginata*, a related social wasp, whose queens are Sitters, suggests that there is a higher level of reproductive competition in *R. cyathiformis*.

Introduction

Ropalidia is a large genus of exclusively Old World tropical paper wasps. About 28 species have been reported from India (GUPTA and DAS 1977) while a large number of species are known from Africa, South-east Asia and Australia (RICHARDS 1978; VAN DER VECHT 1962). However, biological studies on this genus have almost been non-existent although the genus itself has been recognised to be of special interest among the Vespidae (JEANNE 1980). In recent years two species *R. marginata* and *R. cyathiformis* have been the subject of a series of biological studies (GADAGKAR 1980; GADAGKAR and JOSHI

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1982a, b, 1983; GADAGKAR and WEST-EBERHARD in prep.; GADAGKAR et al. 1978, 1982; GADGIL and MAHABAL 1974). The nests of both these species consist of small open combs initiated by one or several females (foundresses) and their social systems may be classified as primitively eusocial.

Eusocial insects are characterised by three properties, cooperative brood care, reproductive division of labour and overlap of generations (MICHENER 1974; WILSON 1971). Among these, primitively eusocial forms are those that show no morphological differentiation between the adults and highly eusocial ones are those that exhibit well defined morphological castes. Termites, most ants and some bees are highly eusocial and have been well studied for many years (BREED et al. 1982; MICHENER 1974; WILSON 1971, 1975). Several species of wasps and bees are primitively eusocial and these are receiving increasing attention in recent years primarily because of the hope that, by virtue of their primitiveness, an understanding of their societies would throw light on questions concerning the origin and evolution of social behaviour (BROTHERS and MICHENER 1974; GREENBERG 1979; JEANNE 1972, 1980; LITTE 1977, 1979, 1981; MARINO PICCIOLI and PARDI 1970, 1978; PARDI and MARINO PICCIOLI 1970, 1981; PICKERING 1980; STRASSMANN 1981a, b; WEST-EBERHARD 1969).

The picture that has begun to emerge from these studies suggests that not only do these primitively eusocial forms lack any significant morphological caste differentiation but the role that an individual might play in a nest is rather flexible. In many instances a colony consists of several females each of which is physiologically capable of assuming the role of the queen but only one or a small number of them actually do so and this is decided largely by social interactions (PARDI 1948; WEST 1967). When only one or a small number become queens, the others sometimes stay on at the nest and assume subordinate worker roles (PARDI 1948; WEST 1967) and at other times they leave the colony to found their own nests. It is this flexibility in roles that makes the primitively eusocial species particularly attractive model systems for investigating the forces that might lead to the evolution of sterile castes — a prime question in sociobiology.

The first step in such an investigation is to understand in more detail and in quantitative terms the social organisation that characterises the social groups. It is essential to know in precise terms the behaviour of different individuals comprising a social group rather than merely identifying egg-layers from sterile ones. Here an attempt has been made to do this with *R. cyathiformis*. The main aim has been to study the behavioural differences between adults on a nest. Preliminary observations showed that all the adults are capable of and in fact do perform most of the behaviours that form the repertoire of the species. The differences between individuals are therefore more likely to be quantitative rather than qualitative. Hence, time-activity budgets have been constructed for several individually identified members of a few nests. Analysis of such data by multivariate statistical techniques reveals the presence of three behavioural clusters that we call Fighters, Sitters and Foragers after their distinguishing features.

Materials and Methods

A. Study Animal

This study was conducted on a group of 4 separate nests built on a metallic pole (one nest) and on the leaves of a croton bush (3 nests) on the grounds of the Indian Institute of Science, Bangalore (13°00 N and 77°32 E), India, between 24 April and 21 June 1980. All the adults of the colonies were individually identified by marking with spots of coloured paint without removing them from the nest. The marking was done immediately after emergence of an adult. A census of all the adults present at the nest was taken before 05.30 h since none of them left the colony before this time. A list of the animals, their sex, and the nests to which they belonged is given in Table 1.

B. Sampling Methods

Three kinds of sampling methods were used in the study (ALTMANN 1974)

1. *Ad libitum sampling* was employed for constructing an ethogram, i e, a descriptive catalogue of the behavioural repertoire of the species, and to get preliminary information on the basis of which subsequent sampling methods were chosen.

2. *Instantaneous scanning* of the behavioural states of all animals in a colony was performed at randomly chosen times

3. *All occurrences of rare behaviours* Some behaviours that appeared to be relatively rare on the basis of ad libitum sampling were recorded during separate 5-min sessions during which all occurrences of each such behaviour by any animal in the colony were recorded. Here every behaviour was treated as an event and no information on its duration was recorded.

All sampling sessions were begun and terminated by time-contingent rules using a stop watch accurate to 0.1 s. Observations were made for a total of 225 h which included ad libitum observations, 282 instantaneous scanning sessions and 51 all occurrences recording sessions. Ad libitum observations showed that the wasps were relatively inactive between 18.00 and 6 00 h. All sampling sessions were therefore chosen randomly between 06 00 and 18.00 h. All data were recorded in a pre-coded form on coding sheets in an 80 column format ready to be punched on computer cards. The data were analysed using a DEC 1090 computer at the Indian Institute of Science, Bangalore.

C. Analysis of Data

1. Time-Activity Budgets

Time-activity budgets, namely, the proportion of time spent in different behaviours by different animals, were estimated using data from instantaneous scans The following 6 behaviours, Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest, descriptions of which are given below under the section on behavioural repertoire, are the most prominent ones accounting for approximately 95 % of a wasp's time. Data on these 6 behaviours were hence chosen for analysis

Table 1. Animals used in the study

Animal number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Sex	M	F	M	F	F	F	F	M	M	F	F	F	F	F	F	F
Nest	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Animal number	17	18	19	20	21	22	23	24	25	26	27	7*	12*	17*	19*	22*
Sex	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
Nest	1	1	1	1	1	1	1	1	1	2	3	4	4	4	4	4

2. Frequencies of Rare Behaviours

Certain behavioural categories occurred rather infrequently making it difficult to accurately estimate the proportion of time spent in them using the instantaneous scans. The hourly frequencies with which these behaviours were performed were therefore estimated from the all occurrences recording sessions. Five of these behavioural categories, Dominant and Subordinate Behaviours, Dominance Display, Bringing Food, Pulp or Liquid and Egg Laying, all of which are defined below, are the most frequent ones and our analysis is thus restricted to these.

3. Behavioural Repertoire

The behavioural repertoire of *R. cyathiformis* was classified into 54 distinct behavioural categories (GADAGKAR, unpubl. obs.; GADAGKAR and WEST-EBERHARD in prep.). The definitions of the 11 most prominent ones are given below:

(i) *Sit and Groom*: By sitting is meant sitting without doing anything in particular and apparently without being alert to any external disturbance. In this position the wasps sit with their bodies held compactly in one plane with legs and wings drawn close to the body and the antennae lowered. Grooming is always self-grooming and no allogrooming has been observed. The most frequent forms of grooming involve rubbing posterior legs against each other and against wings and abdomen; anterior legs against mouth parts, antennae and head; and antennae against mouth parts.

(ii) *Raise Antennae*: This involves sitting with wings drawn close to the body but the antennae raised above the body plane. There is a transition from Sitting to Raising Antennae when there is any disturbance.

(iii) *Raise Wings*: This involves sitting with both antennae and wings raised above the body plane. The legs may still be folded or may be stretched so as to raise the body above the substratum. Raising Antennae is followed by Raising Wings if the disturbance continues.

(iv) *Walk*: The wasps walk on the face and back of the nest; when they walk, they sometimes reach different cells in the nest and sometimes other adults sitting on different parts of the nest.

(v) *In Cells*: The wasps get inside the cells with only their head or the entire body, either simply 'inspecting' the contents or receiving secretions from the larvae or transfering liquid to larvae.

(vi) *Absent from Nest*: Temporary Absence from nest is considered here as one category although a wasp temporarily absent from the nest may return with food, pulp, liquid or nothing.

(vii) and (viii) *Dominance and Subordinate Behaviour*: A variety of dominance and subordinate behaviours are shown by this species (GADAGKAR and JOSHI 1982b). Very briefly, dominance behaviour (by definition) consists of one of the following: climbing on top of another individual and attempting to bite its mouth parts; sitting on top of another individual, sometimes for several min on end; sitting close to another individual and holding one of the latter's legs or antennae in its mouth; chasing; nibbling or pecking at another individual. In all such interactions the individual towards which such dominance behaviour is directed remains passive or attempts to withdraw and this, by definition, is called subordinate behaviour.

(ix) *Dominance Display*: Dominant individuals often showed certain kinds of behaviour which are termed Dominance Displays. These behaviours involve a rapid up and down or side to side movement of the abdomen or a single rapid flap of the wings. One of these, namely rapid side-to-side movement of the abdomen, appears to correspond to 'Lateral Vibrations' as defined by GAMBOA and DEW (1981) who also suggested that it was involved in adult dominance communication.

(x) *Bringing Food, Pulp or Liquid*: On occasions wasps returned to the nest with food, pulp or liquid. Both because we observed these events very rarely and also because we could not always distinguish between food, pulp or liquid, this is treated here as a single behavioural category.

(xi) *Egg-laying*: This is self-explanatory and needs no description.

4. Principal Components Analysis

From the time-activity budgets, every individual can be characterised by the proportion of time it spends in each of the 6 different behaviours, i.e. in terms of 6 variables, which may be correlated. For the purpose of analysis, however, it is desirable to have variables which are uncorrelated and also to reduce the number of variables while retaining most of the information in the data. The method of principal components analysis (FREY and PIMENTEL 1978) yields such a new set of uncorrelated variables. These new variables are linear combinations of the old variables; each old variable being multiplied by a weightage term which reflects the extent of variance contained in it. The new variables are maximally powerful in bringing out the differences between individuals in the sense that, of all the possible linear combinations, the proportion of total variance accounted for by each of the new variables is maximal (ANDERBERG 1973). In addition, it is often possible that only a small number of these new variables account for almost all the variance between the individuals.

5. Hierarchical Cluster Analysis

Using the proportion of time spent in the six activities by different individuals as input data, Pearson product-moment correlation was obtained as an index of similarity between pairs of individuals (DE GHETT 1978). Using these indices of similarity, a hierarchical cluster analysis was performed with the single linkage algorithm (DE GHETT 1978).

Results

A. Time-Activity Budgets

The time-activity budgets of 32 individually identified animals belonging to 4 nests (Fig. 1) reveal that adults of *R. cyathiformis* spend 95 ± 6 (mean ±

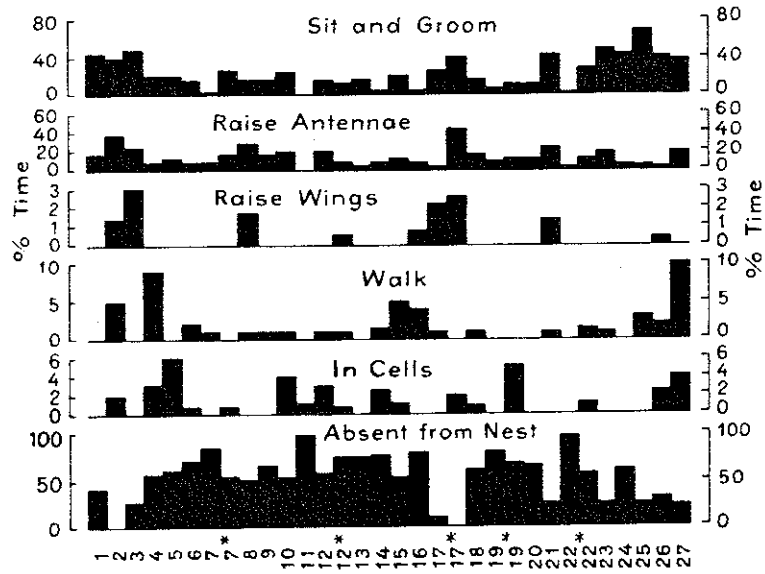

Fig. 1. Time activity budgets of 32 individually identified animals from 4 nests of *R. cyathiformis* for 6 behaviours. The animals are numbered serially and their sex and nest affiliations are listed in Table 1. When a wasp left a nest to found or join another nest it was treated as a separate individual.

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SD) % of their time in the 6 activities Sit and Groom, Raise Antennae, Raise Wings, Walk, In Cells and Absent from Nest Note that there is little variation in the total amount of time spent by different individuals in these 6 activities taken together. However, the manner in which they allocate their time among these 6 activities is highly variable suggesting that there is indeed a quantitative variation among individuals in their behaviour. This is strikingly brought out in Fig. 1. The time spent in Absence from Nest for example, varies between 0 and 98 % and similarly, the time spent in Sit and Groom between 0 and 68 %.

B. Principal Components Analysis

The results of the principal components analysis are shown in Table 2. The first principal component accounts for 89.91% of the total variance with Absent from Nest as its dominant term (weightage = 0.8442). The second principal component whose dominant term is Sit and Groom (weightage = 0.7507) accounts for 8.23 % of the total variance. Thus the first two principal components together account for 98.14 % of the total variance and can therefore be considered adequate for describing the individuals The behavioural description of the individuals has thus been reduced from a six-dimensional to a two-dimensional problem. Moreover, the original variables, namely, the proportions of time spent in different activities, are often correlated with each other. The new variables, namely the amplitudes associated with the principal components, are always uncorrelated. Representing each individual as a point in the coordinate space of the associated amplitudes of the first two principal components should thus be very effective in bringing out the differences among individuals. This is illustrated in Fig. 2. The points (each point corresponding to a wasp) fall into three clusters. This has been confirmed by the method of nearest centroid; the distance between any individual and the centroid of the cluster to which it belongs is less than its distance from the other two centroids. Individual 25 alone does not fall into any of the three clusters.

Table 2: Eigen vectors of principal components, Eigen values, percentage of variance, and cumulative percentage of variance

Behaviour	Principal components		
	1	2	3
Sit and Groom	-0.4773	0.7507	0.3926
Raise Antennae	-0.2425	-0.6100	0.6560
Raise Wings	-0.0162	-0.0380	0.0574
Walk	-0.0219	-0.0095	-0.4905
In Cells	-0.0036	-0.0357	-0.1141
Absent from Nest	0.8442	0.2481	0.3983
Eigen value	2.9×10^4	2.6×10^3	3.8×10^2
Percentage of variance	89.91	8.23	1.19
Cumulative percentage of variance	89.91	98.14	99.33

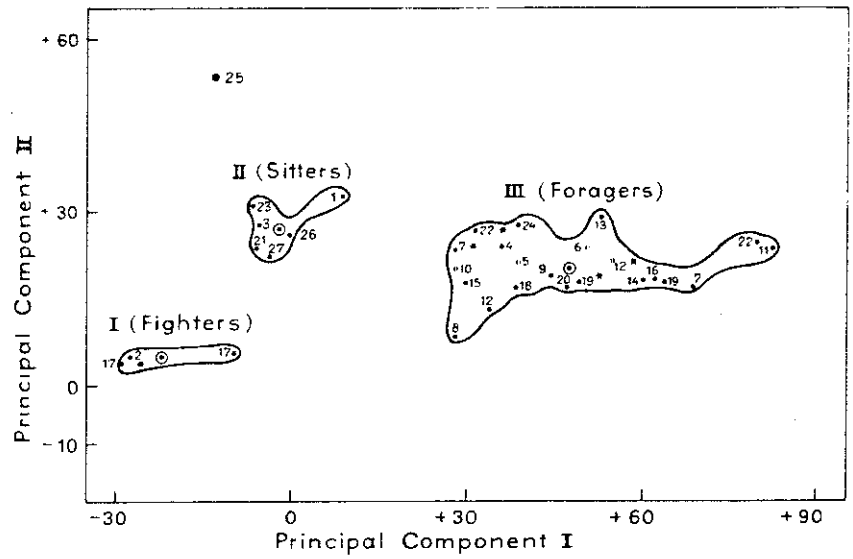

Fig 2. Behavioural clusters of *R. cyathiformis*. Time-activity budgets of 32 wasps are shown as points in the coordinate space of the first two principal components. The points fall into three clusters by the criterion of nearest centroid. Circled dot = centroid

It is possible that this is because of sampling error since individual 25 is the animal on which we have the least data.

It is important to emphasize that the three clusters emerged as a result of an objective analysis of the data and no a priori assumptions were made regarding the criteria to be used for classification or the number of clusters required. The behavioural categories used in the analysis were chosen neither subjectively nor blindly. We chose those 6 behaviours that had the highest ranks in the proportion of time the wasps devoted to them.

C. Hierarchical Cluster Analysis

An independent method of classification, namely, hierarchical cluster analysis using the Pearson product moment correlation as an index of similarity between individuals gives identical clusters (Fig. 3). Here again, individual 25 is separated from all the others and one can recognize three clusters with identical composition as those of the clusters obtained from principal components analysis. This complete concurrence is interpreted here as an indication of the robustness of the clusters we have obtained. Moreover the three clusters obtained here were found to be significantly different from each other ($p < 0.05$) by the randomization test described by SOKAL and ROHLF (1969).

D. Mean Profiles of the three Clusters

In order to understand the biological significance of the clusters we have obtained, let us go back to the time-activity budgets and look at the me

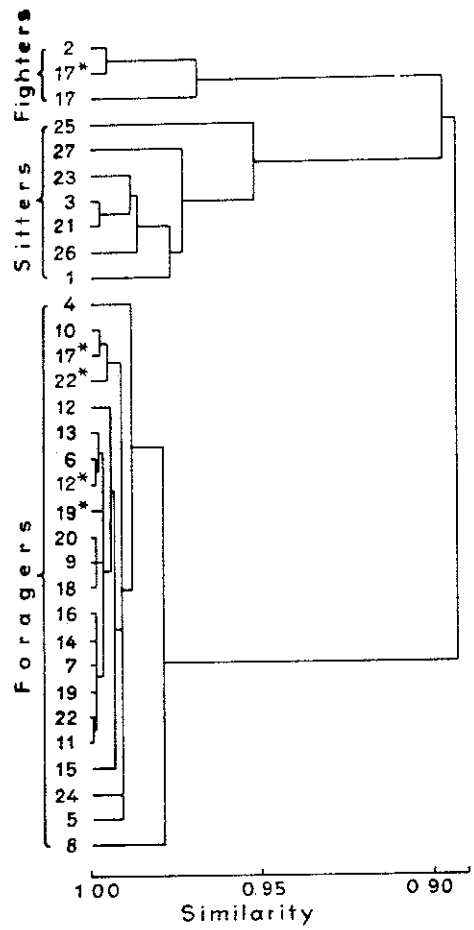

Fig 3: Hierarchical cluster analysis Time-activity budgets of the same 32 animals as in Fig. 2 are used. The similarity between individuals shown is Pearson product moment correlation calculated using the proportion of time spent in 6 behaviours. The method of single linkage algorithm is used for clustering

behavioural profiles of each cluster. These are plotted in Fig. 4. The clusters were obtained by a consideration of all the 6 activities simultaneously and any two clusters therefore need not necessarily be significantly different from each other in any single activity alone. However, Fig. 4 reveals that Absent from the Nest is obviously the most significant attribute of cluster III. Because wasps in this cluster returned to the nest with food, pulp or liquid more often than other wasps (Fig. 5) this cluster will be called "Foragers". Cluster II has the highest rank for Sit and Groom (Fig. 4); this will hence be known as "Sitters". Cluster I ranks slightly lower than cluster II in Sit and Groom and slightly higher than cluster II in Raise Antennae (Fig. 4). At this point let us look at some of the additional data that were obtained from sampling sessions in which all occurrences of certain rare behaviours such as Dominance Behaviour, Subordinate Behaviour, Dominance Display, Bringing food, pulp or

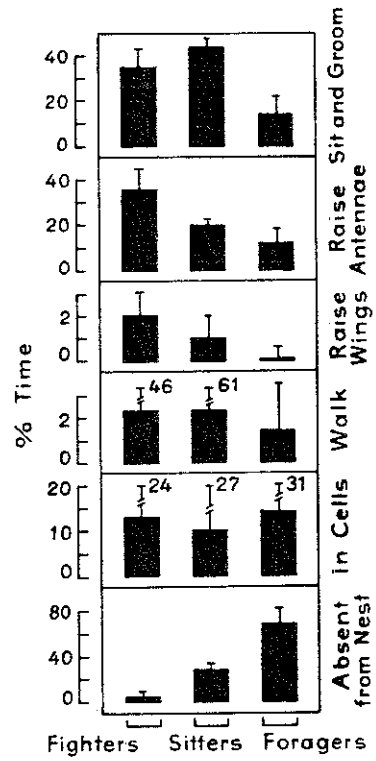

Fig. 4: Mean time-budgets for the clusters obtained in Figs. 2 and 3. The mean proportion of time spent, per animal, in each of the 6 behaviours used in the analysis is shown for each cluster

liquid and Egg Laying were recorded (see Materials and Methods). These data are not in the form of time-activity budgets but as frequencies of each behaviour for each animal per hour (except in the case of egg laying). Since several animals did not perform some of these behaviours at all, it seemed inappropriate to simply consider the mean rate per animal in a given cluster. We have therefore considered both the proportion of animals performing a given behaviour and the mean rate among the animals that performed the behaviour in question (Fig. 5). Notice that these quantities are correlated. It now becomes obvious that cluster I is strikingly different from the other two clusters in showing a high level of Dominance Behaviour and Dominance Display and a complete absence of Subordinate Behaviour. This cluster will therefore be called "Fighters". To summarise, multivariate analysis of time-activity budgets of individually identified adults of *Ropalidia cyathiformis* nests shows the presence of three clusters or behavioural castes namely, Fighters, Sitters and Foragers. The names Fighters, Sitters and Foragers are derived from the most important correlate of each cluster and are used only for convenience. It should by no means be assumed that Sitters only sit or that Fighters do not sit. The clusters were derived by a simultaneous consideration of all 6 behaviours; most wasps perform most behaviours and the differences are only quantitative.

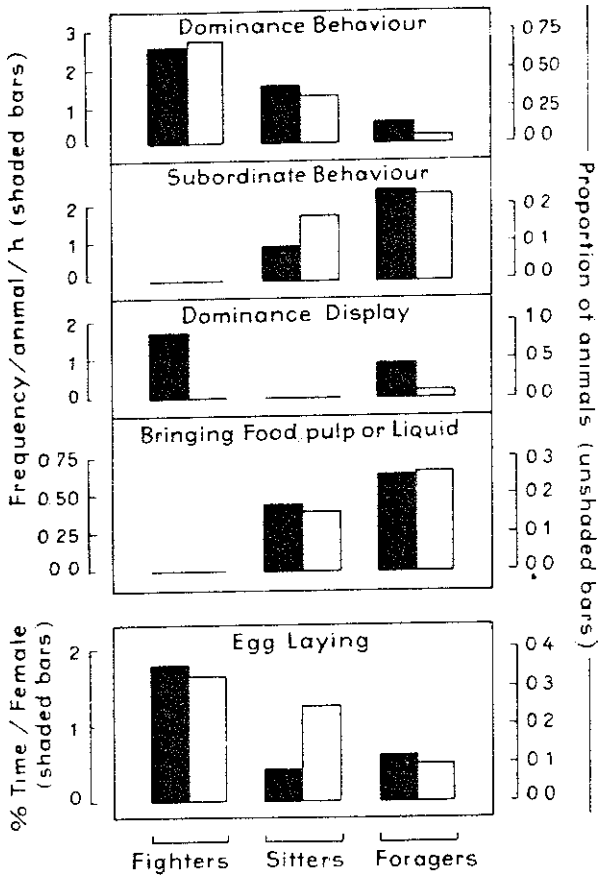

Fig 5 Mean frequencies of, or percentage time spent in rare behaviours. In each cluster the proportion of animals showing a given behaviour (unshaded bars) and the mean frequency per h per animal amongst those showing the behaviour (shaded bars) are shown. In the case of egg laying the proportion of females that laid eggs (unshaded bars) in each cluster and the mean percentage of time spent by the females that laid eggs (shaded bars) are shown

E. Duration of Residence of Adults on a Nest

A question of obvious interest is whether these behavioural characteristics of individuals keep changing drastically with time or remain rather fixed. It is essential to have an estimate of the life span of adults before attempting to understand any changes in behaviour with age. The fact that all wasps were individually identified by paint marks and that a census of all those present on the nest was made every two days provides a record of the duration of residence on a nest for 94 wasps. When a wasp disappears from one nest, it may either have died (mortality) or, founded or joined another nest (emigration). In most cases these two components cannot be distinguished and what is presented here is simply the duration of residence on a given nest. Even when a wasp was known to leave one nest and found another, its duration of residence on each nest was calculated separately. The duration of residence of wasps on a nest varied from 1 to 134 days. The 96 records constitute 78 female and 16 male wasps. The mean duration of residence for females was 24 ± 26

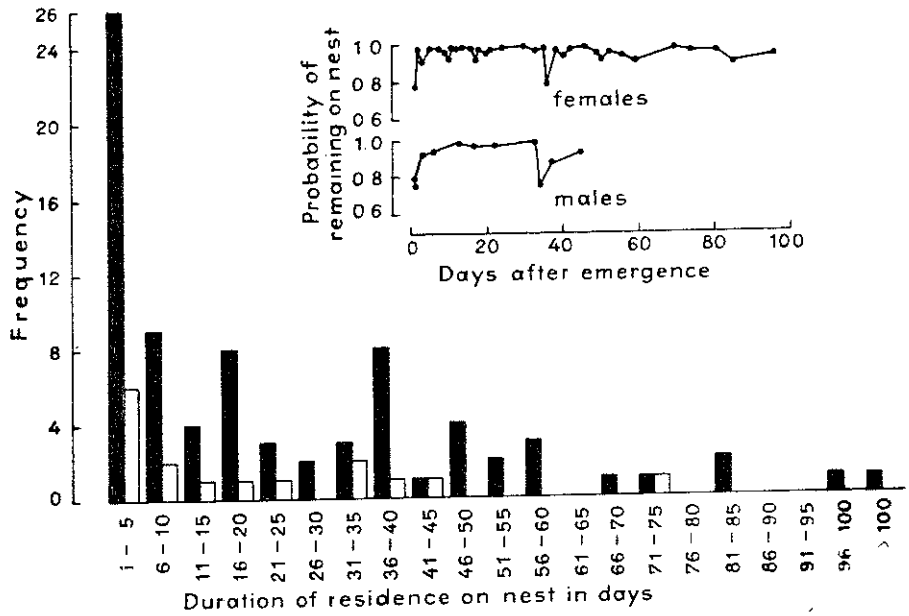

Fig. 6: Frequency distribution of residence times on a given nest of 78 female (shaded bars) and 16 male (unshaded bars) paint-marked wasps of *R. cyathiformis*. The age-specific day-to-day probability of remaining at the same nest (inset) of 0.90 ± 0.09 for males and 0.95 ± 0.05 for females is nearly constant with age. Notice that most points lie between 0.90 and 1.0

(mean ± SD) days and 19 ± 21 (mean ± SD) days for males. The frequency distribution of residence times is shown in Fig. 6. It may be mentioned parenthetically that the day-to-day probability of survival having values of 0.90 ± 0.09 for males and 0.95 ± 0.05 for females does not seem to vary with age (see inset in Fig. 6). This seems to suggest that mortality forms a very large component of the present estimates and emigration only a small component. The reasoning is as follows. Mortality seems to occur largely during the foraging trips, for the wasps simply do not return to their nests. They are probably lost or preyed upon. We do not expect the probability of these events to depend upon the age of the wasp while it is reasonable to expect the probability of emigration to found or join new nests to show some age dependence.

F. Developmental Changes in Behaviour

Thus far, all the behavioural data available on each wasp throughout the period of observation were pooled to give an average time-budget for each wasp. To understand the effect, if any, of the age of the animal on its behaviour it would be necessary to construct separate time-activity budgets for each wasp at different times in its life span. Unfortunately, data are insufficient to permit such a break up for all the animals. However, for 9 animals (numbers 1, 2, 4, 6, 7, 9, 17, 18, 21 in Table 1 and Figs. 1, 2 and 3) time activity

budgets have been prepared for each fortnight of their lives. With these time budgets their corresponding positions in the coordinate space of the principal components in Fig. 3 are computed. The results, illustrated in Fig. 7, show that the fortnightly behavioural profiles are rather close to each other and to their corresponding mean profiles. This suggests first, that most animals did not drastically change their behavioural profiles with age and second, that using the life-time mean behavioural profiles as we have done, does not therefore distort the picture to any significant extent. It must be pointed out that in the first week of their lives, however, all wasps do little other than Sit and Groom (GADAGKAR unpubl. obs.). After this they seem to adopt a certain time-budget for the rest of their lives. This does not of course mean that the time-budgets cannot change in response to such drastic perturbations as death of the queen or of a significant fraction of the foragers. In fact our preliminary results indicate that some individuals change their time-budgets to become replacement queens upon removal of the original queen (GADAGKAR unpubl. obs.). We therefore make the assumption that the time-budgets are in fact flexible in interpretating the biological significance of the clusters (see Discussion). The results in this section merely show that, in the absence of any major perturbations, most wasps do not change their time-budgets during their life span.

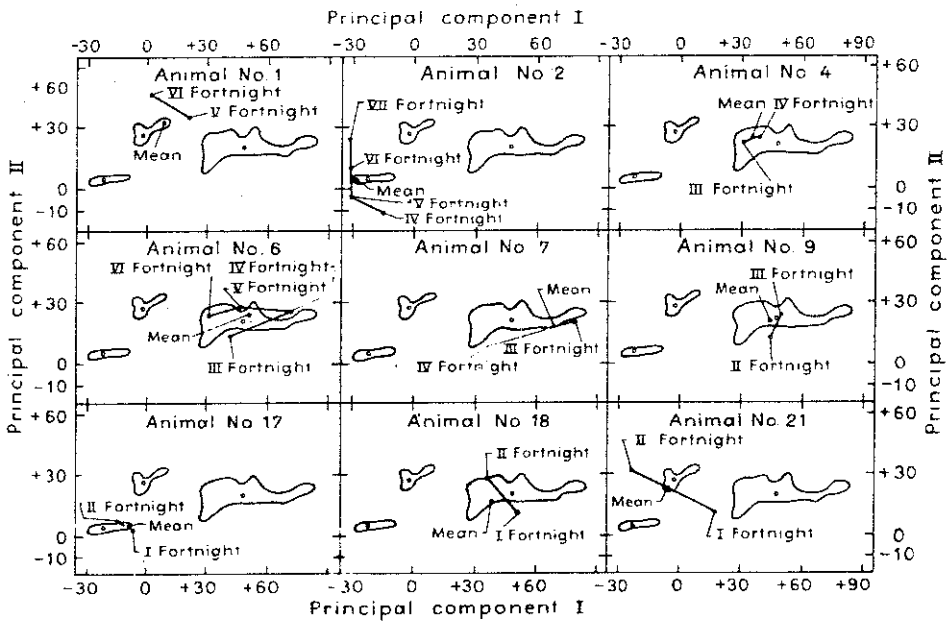

Fig. 7: Age dependent changes in behaviour. For 9 animals with large amounts of data, the time-activity budgets are calculated separately for each fortnight of their life (for those fortnights that data were available). These fortnightly time-budgets are used to compute their corresponding positions in the coordinate space of the first two principal components in Fig. 2. There are 9 panels, one for each animal. The outline and centroid of each cluster and the position of the mean and all available fortnightly time budgets for the animal under consideration are shown in each panel.

G. Behaviour of Males

Males as a class do not differ from females on the basis of the 6 behaviours used in this analysis. Notice from Table 1 that four of the animals used in this analysis (animal numbers 1, 3, 8 and 9) were males. In *R. cyathiformis* the males remain at the nest and do not disappear immediately after emergence as in the case of *Ropalidia marginata* (GADAGKAR and JOSHI 1982b, 1983) (Fig. 6). It has therefore been possible to construct time-activity budgets for the males as well. Of the four males, two (animals 1 and 3) fall in cluster II (Sitters) and the other two (animals 8 and 9) fall into cluster III (Foragers). It may seem surprising that two males are in a cluster that we call Foragers. We have never observed a male to bring anything back to the nest. But we have occasionally observed males to feed larvae with food taken from other individuals. The males did spend a considerable portion of their time away from the nest. It is possible that they foraged for their own food and consumed it before returning to the nest. On the other hand, it cannot be ruled out that the males in this species sometimes bring food and feed the larvae. For a number of examples of male social wasps feeding larvae, see HUNT and NOONAN (1979). Alternatively the situation could be similar to that recorded in *Mischocyttarus labiatus* by LITTE (1981). In this species too, males are produced rather early in the colony cycle and remain at the nest throughout their lives, soliciting nectar and food from returning foragers, but spend about 4 h each day patrolling distant sites where mating presumably occurs.

H. Behaviour of Individuals after Switching Nests

When wasps left an existing nest and went on to found new nests nearby (Table 1), the data on each wasp on each nest were treated separately. As seen from Table 1, animals 7, 12, 17, 19 and 22 left their old nests and on their new nests they are labelled 7*, 12*, 17*, 19* and 22* respectively. It is interesting that in each case the animal falls into the same cluster before and after it switched nests. This, we believe, gives further support to the idea that an individual adopts a certain behavioural profile and retains that profile for most of its life time. Notice the very significant fact that this is also true of an individual that was not an egg layer in the old nest but was the sole egg layer on the new nest (17 and 17*).

Discussion

Multivariate analysis of time-activity budgets of the social wasp *R. cyathiformis* shows the presence of three behavioural clusters which we have called Fighters, Sitters and Foragers on the basis of their distinguishing features. Recall that such a behavioural differentiation has been detected despite the absence of any obvious morphological differentiation.

It should be emphasized that Egg-Laying itself has not been used as one of the activities in this analysis. The reasons for this were two-fold. Firstly, Egg-Laying itself takes only a very small proportion of time, whereas we were

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primarily interested in classifying the wasps on the basis of how they distributed the bulk of their time between different activities without any pre-conceived notions of which activities were important. Secondly, eusocial insects have long been known to be differentiated into reproductives and non-reproductives. What is not known in many species is how this differentiation is correlated with the overall behaviour of the individuals. This is indeed what we can begin to understand for *R. cyathiformis* from the present study. Having obtained the classification without using egg-laying as one of the input parameters, we can now look at the data on Egg Laying and other rare behaviours shown in Fig. 5.

The cluster that we call Fighters has three representatives: 2, 17 and 17*. Animal no. 2 was the most dominant wasp on nest 1 and laid most of the eggs on this nest. Animal no. 17 belonged to the same nest but was not observed to lay any eggs. However, it subsequently left this nest to found a new one of its own where it was the principal egg layer. Its time-budget on the new nest is analysed separately and represented as 17*. Two principal egg layers (animals 2 and 17*) and one potential egg layer (animal 17) thus constitute this cluster. This we believe is evidence of the biological significance of the behavioural classification we have obtained. Wasps in this cluster have two distinctive features. One is that they show a very high frequency of Dominance Behaviour and Dominance Display. Second, they show the highest frequency of sitting with Raised Antennae. Sitting with Raised Antennae, we suspect, serves the function of guarding the nest and its brood against parasites and predators. This is supported by the fact that the wasps immediately raise their antennae at the slightest disturbance. Since the principal and potential egg layers are the Fighters, it appears that being dominant over their nest mates is important for these individuals to maintain their status as principal or potential egg layers.

The second cluster consists of Sitters, individuals that spend more time sitting and grooming than others. Two of these, individuals 26 and 27, were the foundresses of nests 2 and 3, respectively, and were attending their nests without the aid of any co-foundresses or workers during the period of data collection. An obvious question that comes to mind is the role of the rest of the individuals of this cluster in the social organisation of the species. Every wasp spends the first few days of its life doing little other than sitting and grooming but the Sitters in this cluster obviously represent something quite different. Data in Fig. 7 have demonstrated that there are no significant developmental changes in behaviour and that a Sitter continues to be a Sitter even in the 5th and 6th fortnight of its life (see animal 1 in Fig. 7 for example). It is interesting to speculate that these individuals are "hopeful queens" (see WEST-EBERHARD 1978) who may have some chance of becoming dominant egg-layers such as the Fighters. They may thus be avoiding performing risky and energy consuming tasks such as Foraging.

A large number of individuals belonged to the cluster Foragers. These individuals spend a great deal of their time away from the nest often returning with food or building material, but they are seldom involved in Dominance

Behaviour, Dominance Display or Egg Laying. Notice however, that they show a very high frequency of subordinate behaviour. These individuals thus constitute the principal worker force on the nest and are unlikely to be involved in reproductive competition with their nest mates.

We have recently completed a very similar study with a related species of social wasp, *R. marginata* (GADAGKAR and JOSHI 1983) and it is of obvious interest to compare the results of the present study with those of *R. marginata*. Using multivariate analysis of time-activity budget data, individuals of *R. marginata* were also classified into three behavioural clusters: Sitters, Fighters and Foragers. However, there was one important difference. The queens of *R. marginata* were amongst the Sitters while the principal egg layers of *R. cyathiformis* are the Fighters except when they had no one to compete with (animals 26 and 27). The nests of *R. marginata* studied were monogynous, the queens did little other than Sit and Groom and Lay Eggs. Although they appeared to be at the top of the dominance hierarchy, they seldom engaged in actual physical interaction with their nest mates. On the other hand at least one of the nests of *R. cyathiformis* (nest 1, the nest from which most of the animals in this study are derived) was polygynous; the principal egg layers (which we interpret as corresponding to the queens of *R. marginata*) showed the highest frequency of Dominance Behaviour and Display. For these and similar reasons, we have recently argued that *R. cyathiformis* is at a somewhat more primitive level of social organization than *R. marginata* (GADAGKAR and JOSHI 1982b). The fact that the queens of *R. marginata* are Sitters and the principal egg layers of *R. cyathiformis* are Fighters suggests a much greater degree of reproductive competition by overt dominance behaviour in *R. cyathiformis* than in *R. marginata*, at least in so far as the nests we have studied are concerned. Furthermore, the two queens of *R. cyathiformis*, 26 and 27, on single foundress nests who did not have any other wasps to compete with were Sitters.

One other difference between the two species that needs to be mentioned is the fact that in *R. marginata*, males are produced only very late in the colony cycle and disappear from the nest within two or three days after emergence (GADAGKAR and JOSHI 1983). On the contrary in *R. cyathiformis* males are sometimes produced relatively early in the colony cycle (GADAGKAR unpubl. obs.) and stay on at the nest for long periods of time (Fig. 6). This is perhaps further evidence of the primitiveness of the *R. cyathiformis* social system. Recall that some of the Sitters and even some of the Foragers in *R. cyathiformis* laid some eggs. In a situation such as this it is possible that some unmated females lay a few haploid male-producing eggs. Queen-worker conflict and the success of workers in sneaking in a few of their own male eggs or replacing the queen's male eggs with their own are all well known in Hymenoptera (WILSON 1971).

Apart from *R. marginata* and *R. cyathiformis* there is another instance of a similar study in social insects. This is the study of BROTHERS and MICHENER (1974) who subjected rather similar data on the primitively eusocial bee

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Lasioglossum zephyrum to principal components analysis. Their bees also clustered into three groups which they call Queens, Guards and Workers.

We have speculated before (GADAGKAR and JOSHI 1983) that the Queens, Guards and Workers of *L. zephyrum* correspond to the Sitters, Fighters and Foragers of *R. marginata*. It is possible that such a behavioural caste differentiation into three groups with Sitting, Fighting and Foraging as their main attributes is a common feature of primitively eusocial insects. Our analysis of time-activity budgets of another primitively eusocial wasp, *Polistes versicolor*, also shows the presence of behavioural caste differentiation into Sitters, Fighters and Foragers (GADAGKAR and JOSHI in prep.). LITTE (1981) who studied another primitively eusocial wasp *Mischocyttarus labiatus* in Colombia showed that the colonies are composed of three kinds of females: egg-layers; non-foraging, aggressive females; and non-aggressive foragers.

Zusammenfassung

Imagines der primitiv eusozialen indischen Wespe *Ropalidia cyathiformis* wurden individuell markiert. Ihre Zeit- und Aktivitätsaufteilung belegt die Existenz dreier Ethotypen (oder Kasten), die nach ihrem typischen Verhalten als Kämpfer, Sitzer und Futtersucher bezeichnet werden. Eierleger und zugleich die dominantesten Tiere sind hauptsächlich die Kämpfer. Die Sitzer sind „Faulenzer", vermutlich künftige Königinnen. Die Futtersucher sind die hauptsächlichen Arbeitskräfte. Diese Verhaltensdifferenzierung scheint sich normalerweise nicht mit dem Alter der Tiere zu ändern. Das Verhalten ändert sich auch nicht, wenn das Individuum sein Nest verläßt und ein anderes gründet oder sich einem anderen anschließt. Es ist jedoch möglich, daß es sich als Reaktion auf einschneidende Zwischenfälle, wie z. B. Tod der Königin, ändert. Männliche Wespen bilden keine von den Weibchen unterschiedene Gruppe, sondern sind entweder Sitzer oder Futtersucher. Ein Vergleich dieser Ergebnisse mit denen bei *R. marginata*, einer verwandten sozialen Wespe, deren Königinnen Sitzer sind, weist darauf hin, daß bei *R. cyathiformis* ein stärkerer Fortpflanzungswettbewerb besteht.

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Behavioural Castes, Dominance and Division of Labour in a Primitively Eusocial Wasp

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Abstract

Female wasps of the primitively eusocial species *Ropalidia marginata* may be classified, by a statistical analysis of their time-activity budgets, into three behavioural castes namely Sitters, Fighters and Foragers. We show that Foragers are primarily responsible for the risky task of foraging for food and have very poorly developed ovaries. Sitters and Fighters forage rarely if at all but share the bulk of the intra-nidal tasks such as feeding larvae and building the nest. Both Sitters and Fighters have better developed ovaries than Foragers. Queens of most colonies belong to the Sitter caste. There are no obvious morphological differences between queens and workers or between the behavioural castes. Queens are not necessarily the most dominant individuals in their colonies. Instead, most dominance behaviour is performed by a group of workers (the Fighters). Division of labour and social organization are achieved through behavioural caste differentiation and not, as in many other species studied, through a dominance hierarchy led by a despotic queen suppressing all her nestmates into worker roles. This suggests that behaviour patterns in such primitively eusocial insects are likely to be moulded by a complex interaction between selection at the individual and colony levels.

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Introduction

Eusocial insects, namely those that live in colonies comprising individuals of more than one generation, cooperate in brood care and relegate reproduction to one or a small number of their colony members (MICHENER 1969; WILSON 1971), may be classified into two broad groups. Highly eusocial insects such as all termites, most ants and some bees and wasps are characterized by a morphological distinction between reproductive and worker castes and often between different subcastes among the workers as well. This leaves little or no reproductive opportunity for workers who are destined to remain sterile but leads to

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efficient division of labour and a near harmonious social organization (WILSON 1971; SPRADBERY 1973; MICHENER 1974; HÖLLDOBLER & WILSON 1990). Primitively eusocial insects such as many species of bees and wasps on the other hand lack morphological caste differentiation. This provides considerable flexibility in the social roles that the adult insects may adopt but raises questions such as: why do some individuals accept sterile worker roles and how division of labour and social organization are achieved?

These questions have motivated many investigations of primitively eusocial polistine wasps (e.g. WEST-EBERHARD 1969; JEANNE 1972; LITTE 1977, 1979, 1981; STRASSMANN 1981 a, b; for reviews and additional references see ROSS & MATTHEWS 1991). Most of these studies have used one of the two large polistine genera, *Polistes* and *Mischocyttarus*. *Ropalidia* is a polistine genus that is often thought to be crucial for an understanding of social organization and evolution of social life in wasps (e.g. WILSON 1971; JEANNE 1980). Although several studies on *Ropalidia* have been published in recent years (e.g. GADGIL & MAHABAL 1974; DARCHEN 1976; SUZUKI & MURAI 1980; GADAGKAR 1980; GADAGKAR et al. 1982; GADAGKAR & JOSHI 1983, 1984; KOJIMA 1984, 1989; ITÔ 1985, 1986; YAMANE 1986; for a review and additional references see GADAGKAR 1991), our understanding of the biology and social organization of *Ropalidia* lags considerably behind that of other polistine genera. Many investigators have therefore called for more intensive studies of this genus (e.g. KOJIMA 1984; ITÔ 1985).

Here we describe a study of post-emergence colonies of *Ropalidia marginata* (Lep.), a primitively eusocial wasp lacking morphological castes, which attempts to understand the roles of behavioural dominance and behavioural caste differentiation in division of labour and social organization.

Materials and Methods

Study Sites

The study was conducted between Jan. 1986 and May 1987 on 12 naturally occurring post-emergence colonies of *R. marginata*. 7 of the 12 colonies studied were located in Bangalore (13° 00′ N and 77° 32′ E) and 5 were in Mysore (12° 25′ N and 76° 50′ E), India. All colonies were built on eaves of buildings or other man-made structures.

Data Collection

Behavioural data presented in this paper are based on 230 h of observation of 12 natural colonies by methods described earlier (GADAGKAR & JOSHI 1983, 1984). In all colonies only one individual was ever seen laying eggs. This individual was designated the queen. At the end of the observations, nests were collected along with all the adults present on them. All female wasps present on a nest (nest 10 was an exception) at the time of collection were examined under a binocular dissection microscope to measure their body size, dissected to assess their ovarian condition and dried at 80 °C to record their dry weight. The non-structural fat content of each wasp was estimated following the method of FOLCH et al. (1957).

Variables Used in the Study

In all, 20 variables were used in this study. They are the proportions of time spent in five common behaviours, (1) Sit and Groom, (2) Raise Antennae, (3) Walk, (4) In cells, (5) Absent from nest, and the frequencies per h of 11 rare behaviours, (6) Dominance behaviour, (7) Subordinate

behaviour, (8) Bring food, (9) Snatch food, (10) Lose food, (11) Feed larva, (12) Bring building material, (13) Snatch building material, (14) Lose building material, (15) Extend walls of cells, (16) Build new cells; (17) an Index of ovarian condition (computed as the amplitude along the first principal component of six input measures of ovarian condition namely, length of the largest oocyte, width of the largest oocyte, mean length of the proximal oocytes, mean width of the proximal oocytes, number of mature eggs (proximal oocytes that, on microscopical examination, appeared to have a fully formed chorion which gave them a characteristic pearly white appearance) and the total number of oocytes), (18) an Index of body size (computed as the amplitude along the first principal component of seven input measures of body size namely, inter-ocellar distance, right ocello-ocular distance, head width, head length, mesoscutum width, mesoscutum length and right wing length), (19) Dry weight (mg) and (20) Non-structural fat content (mg)

Data Analysis

Principal components analysis Time-activity budgets constructed from data on proportions of time spent in five common behaviours were subjected to principal components analysis (FREY & PIMENTEL 1978) Principal components analysis and identification of the resulting clusters were performed separately for each colony as described by GADAGKAR & JOSHI (1983, 1984) For all subsequent analysis data from all the colonies were combined

Logistic regression analysis Each of the 20 variables used in the study was modelled to test its influence on the probability of an animal being a Sitter, a Fighter or a Forager such that,

$$\ln (p_1/p_3) = a_1 + \beta_1 X$$
$$\ln (p_2/p_3) = a_2 + \beta_2 X$$

where p_1, p_2 and p_3 are the probabilities of being a Sitter, a Fighter or a Forager respectively ($p_1 + p_2 + p_3 = 1$), a_1 and a_2 are intercepts, β_1 and β_2 are regression coefficients and X is the independent variable. The unknown parameters in the above regression equations were estimated by maximizing the likelihood:

$$L = \left(\prod_{i=1}^{k} p_1\right) \left(\prod_{i=k+1}^{m} p_2\right) \left(\prod_{i=m+1}^{n} p_3\right)$$

and the estimates were used to calculate p_1, p_2, and p_3 1 to k are Sitters, k+1 to m are Fighters and m+1 to n are Foragers (for further details see, SHANUBHOGUE & GORE 1987; GADAGKAR et al 1988, 1990 b; COX & SNELL 1989)

Correlates of Dominance Each of the 20 variables used in the study were examined as potential correlates of dominance. Pooling all dominance interactions seen in the 12 colonies, the number of interactions 'h' where the dominant animal had a larger value for a variable and those 's' where the dominant animal had a smaller value for the variable were computed The departures of these numbers from those predicted on the basis of a null hypothesis postulating no effect of the variable (h = s) were tested by a normal approximation of the binomial distribution where the test statistic was computed as

$$z = (h - np)/\sqrt{(npq)}$$

where n is the total number of interactions, and $p = q = 0.5$ (FELLER 1968) This was repeated for each of the 20 variables

Results

Identification of Behavioural Castes

Time-activity budgets constructed for individually identified animals from 12 colonies of *R marginata* revealed that female wasps spend 69 %—100 % ($\bar{x} \pm SD = 94.61 \pm 5.23$) of their time in the five common behaviours, Sit and Groom, Raise Antennae, Walk, In cells and Absent from nest The manner in

which each wasp allocated her time between these five behaviours was however highly variable. In an attempt to discern a pattern in the allocation of their time, these time-activity budgets were subjected to principal components analysis. Our results show that the first two principal components together account for 97.9 %—99.7 % of the variance in the input data. The position of each wasp is therefore plotted as a point in the space of the first two principal components (Fig. 1). This results in a distribution of the points into three distinct clusters. The boundaries of the three clusters were not equally obvious in all 12 colonies but the distinctness of the clusters was always confirmed by the nearest centroid criterion (GADAGKAR & JOSHI 1983). Following GADAGKAR & JOSHI (1983, 1984) the cluster showing the highest mean proportion of time in Sit and Groom was labelled Sitters, the cluster showing the highest mean proportion of time in Raise antennae or the highest frequency of Dominance behaviour was labelled Fighters and that showing the highest mean proportion of time spent in Absent from nest was labelled Foragers. In 11 out of 12 colonies the queen belonged to the Sitter caste while in colony 3 alone the queen was a Fighter.

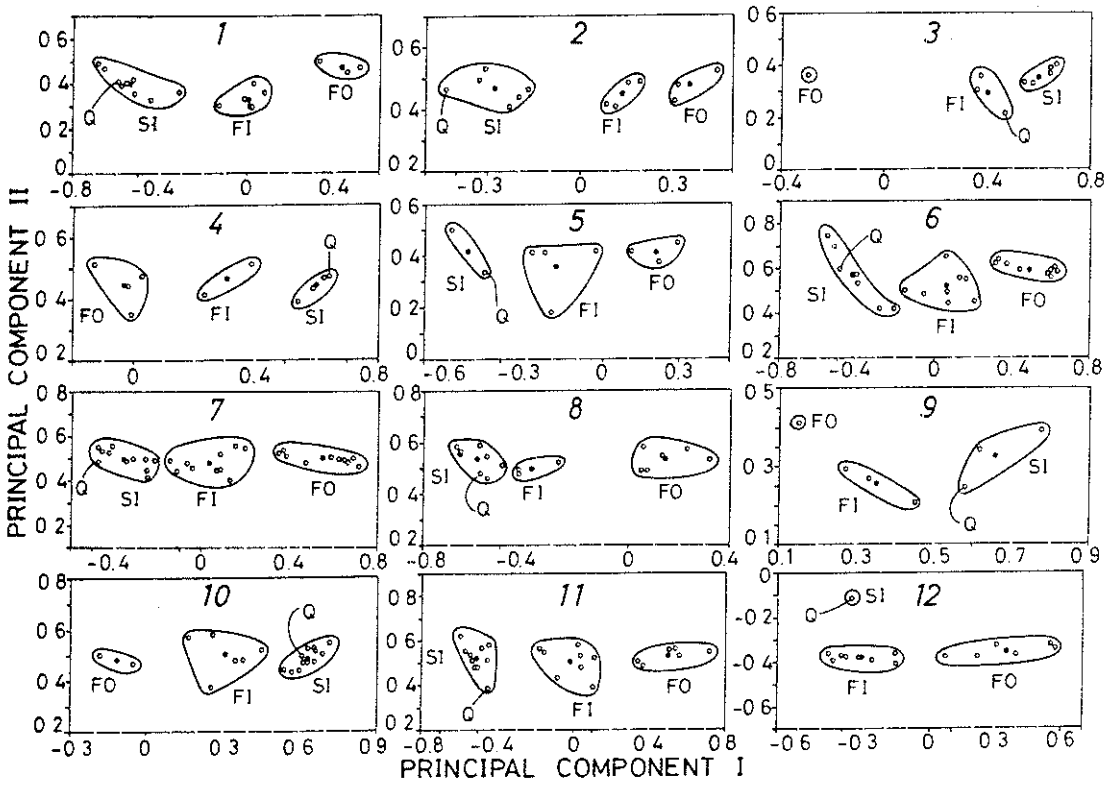

Fig. 1. Behavioural castes in 12 colonies of *Ropalidia marginata* identified by principal components analysis of time-activity budgets. Each point (open circles) plotted in the coordinate space of the first two principal components represents a wasp. Solid circles are the centroids of their respective clusters. SI = Sitters, FI = Fighters, FO = Foragers, Q = queen

Table 1: Correlates of the behavioural castes assessed by logistic regression analysis

	Sitters vs. Fighters			Sitters vs. Foragers			Fighters vs. Foragers		
	estimated coeff.	SE	test statistic Z	estimated coeff.	SE	test statistic Z	estimated coeff.	SE	test statistic Z
Sit and groom	14.7247	2.2954	6.4148***	38.3711	5.4040	7.1004***	23.1266	4.7865	4.8316***
Raise antennae	−20.2737	5.0746	−3.9951***	11.6375	6.3765	1.8251	31.9113	6.6997	4.7631***
Absent from nest	−20.0904	3.3298	−6.0336***	−39.6311	5.3988	−7.3407***	−19.5407	4.2070	−4.6448***
Dominance behaviour	− 1.6502	0.8424	−1.9589*	5.4913	2.0838	2.6353**	7.1415	2.0966	3.4062***
Bring food	− 8.8942	2.9594	−3.0054**	−11.1089	2.9671	−3.7440***	− 2.2147	1.1199	−1.9776*
Snatch food	1.2926	0.7559	1.7099	9.5742	1.8177	5.2673***	8.2816	1.8173	4.5569***
Feed larva	− 0.3546	0.2980	−1.1896	0.9110	0.4446	2.0490*	1.2656	0.4490	2.8187**
Extend walls of cells	− 0.0022	0.4641	−0.0048	1.9292	0.7622	2.5311*	1.9068	0.7790	2.4477*
Index of ovarian condition	0.2195	0.0099	2.1961*	0.8109	0.2319	3.4959***	0.5914	0.2332	2.5362*
Index of ovarian condition#	0.1125	0.1714	0.6565	0.7469	0.2449	3.0498**	0.6344	0.2479	2.5586*
Index of body size	− 0.1295	0.1054	−1.2288	0.0061	0.1187	0.5166	0.1909	0.1248	1.5288
Dry weight (mg)	0.0025	0.0067	−0.3727	0.1707	0.0097	1.7466	0.1955	0.1004	1.9473
Fat (mg)	0.1326	0.2668	0.4968	0.5816	0.3453	1.6814	0.4490	0.3642	1.2330

*: $0.05 > p > 0.01$; **: $0.01 > p > 0.001$; ***: $p < 0.001$.

#: index of ovarian condition was retested after the queens (egg layers) were deleted from the data set.

Correlates of the Behavioural Castes

In what ways are Sitters, Fighters and Foragers different from each other? In other words which, if any, of the 20 variables studied here permit us to distinguish different behavioural castes? We have attempted to answer this question by using the method of logistic regression analysis (Table 1).

The coefficient of regression associated with Sit and Groom is significantly greater than zero ($p < 0.001$) in a comparison of Sitters either with Fighters or Foragers. This is interpreted to mean that Sitters spend significantly more time in Sit and Groom than either Fighters or Foragers. Interpreting other coefficients similarly, we find that Fighters spend significantly more time in Raise antennae than either Sitters or Foragers ($p < 0.001$) and Foragers spend significantly more time in Absent from nest than either Sitters or Fighters ($p < 0.001$). These results were expected on the basis of the mean behavioural profiles of the castes which were used to name the clusters. However, we have included these variables as internal controls to establish the correct interpretation of the results of logistic regression analysis and to justify the use of this method to identify the correlates of the behavioural castes.

By examining other variables which were not used in deriving the clusters, we have attempted to establish the patterns of task allocation between the castes. Foragers brought food significantly more often than either Sitters or Fighters ($p < 0.05$) and Fighters did so significantly more often than Sitters ($p < 0.01$). Fighters showed Dominance behaviour significantly more often than either Sitters or Foragers ($p < 0.05$) and Sitters did so significantly more often than Foragers ($p < 0.01$). Sitters and Fighters showed Snatch food, Feed larva and Extend walls of cells significantly more often than Foragers ($p < 0.05$). However Sitters and Fighters were indistinguishable from each other by any of these three variables.

Sitters had significantly better developed ovaries than either Fighters or Foragers ($p < 0.05$) and Fighters had significantly better developed ovaries than Foragers ($p < 0.05$). This result was obviously due to the inclusion of queens among the Sitter caste in 11 out of 12 colonies. When queens of all 12 colonies were excluded from the data set, we found that Sitters and Fighters still had significantly better developed ovaries than Foragers ($p < 0.05$) but Sitters and Fighters were now indistinguishable on the basis of their ovaries. The Index of body size, Dry weight and Fat content however did not differ significantly between castes.

Dominant-Subordinate Relationships

A variety of dominance behaviours were shown towards each other by the wasps in a colony. One animal, dominant by definition, Attacked, Pecked, Chased or Nibbled another, subordinate by definition (see GADAGKAR & JOSHI 1983, 1984 for a description of these behaviours). The frequencies of all these behaviours were pooled to obtain the frequency of Dominance behaviour. One member of a pair of animals was nearly always (in 159 out of 163 pairs of interacting animals observed) dominant over the other in all dominance interac-

tions between them and thus their dominant-subordinate status was unambiguous. We attempted to construct dominance hierarchies for animals in each colony by connecting dominant members of a pair to their subordinate partners by means of arrows. A simple linear dominance hierarchy could not be obtained because all animals did not interact with all the other animals in a colony. Instead a complex network of dominant-subordinate relationships was obtained for most colonies. One such network of intermediate complexity is illustrated in Fig. 2

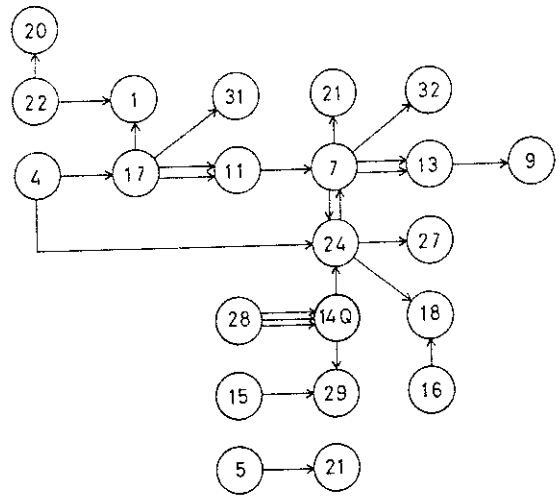

Fig. 2. The dominance-subordinate network of colony 7 as an example of intermediate complexity. Arrows connect dominant animals to their subordinate partners. Each arrow represents one instance of Dominance behaviour. Since all animals were observed for the same duration, these numbers are directly comparable. Each circle represents a wasp and the number inside, its code. Of 32 animals, only 22 figure in the dominance-subordinate network shown here; the remaining 10 animals did not show any Dominance or Subordinate behaviour

In 3 out of 12 colonies the queen did not participate in dominance-subordinance interactions at all, although several instances of such interactions were recorded among her nestmates. This could not have been merely because our sampling effort may have been insufficient. In one of these 3 colonies, we recorded 75 instances of dominance behaviours and 14 of them by a single animal. Nevertheless, none were shown by the queen. In another 3 of the 12 colonies, the queen participated in dominance-subordinance interactions in her colony but was dominated by one or more of her nestmates. Even in the remaining 6 colonies where none dominated the queen and where she participated in dominance-subordinance interactions, the queen was never the one to show the highest number of dominance behaviours in her colony. Out of the total number of dominance behaviours shown in a colony, the proportion shown by the queen was indistinguishable from that shown by one or more of her nestmates in 3 of these 6 colonies (test of proportions, $p < 0.05$) and significantly less than that shown by at least one of her nestmates in the remaining three colonies (test of proportions, $p < 0.05$). In no colony and by no criteria can we therefore conclude that the queen is at the top of the behavioural dominance hierarchy of her colony.

We also find that there was a strong and statistically significant positive linear dependence of the frequency per h of Dominance behaviour shown by an animal and the number of animals that it dominates (Fig. 3, $r^2 = 0.75$; $p < 0.01$;

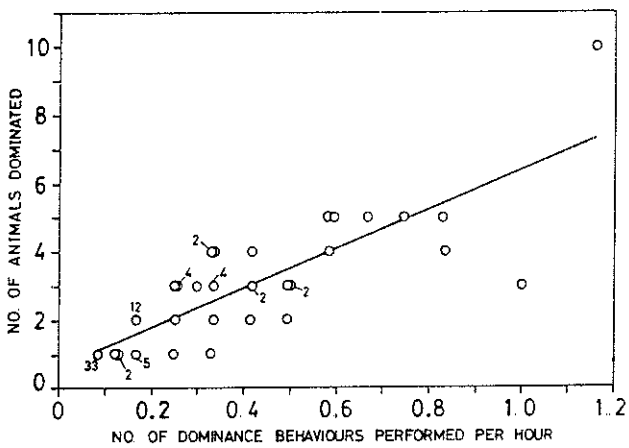

Fig. 3 Scatter plot showing number of animals dominated by a wasp as a function of the frequency per h of Dominance behaviour shown by her. The numbers adjacent to some points indicate the number of overlapping points represented by them. The fitted line is given by $Y = 0.6505 + 5.7602\ X$ ($r^2 = 0.75$; $p < 0.01$; slope significantly greater than zero, $p < 0.01$). The correlation between frequency per h of dominance and number of animals dominated is also evident by a non-parametric test, Kendall's coefficient of rank correlation = 0.8112, $p < 0.0001$)

slope significantly greater than zero, $p < 0.01$). Such a correlation between the rate of dominance behaviour shown by an animal and the number of animals that she dominates is also evident by a non-parametric test (Kendall's coefficient of rank correlation = 0.8112, $p < 0.0001$). This correlation persisted for most colonies when data were analyzed separately for each colony.

The Correlates of Dominance

What kinds of animals are predisposed to be dominant? This question can be asked in two ways. First, what kinds of animals show high frequencies of Dominance behaviour? We have attempted to answer this question by computing Kendall's rank correlation coefficients between frequency per h of Dominance behaviour on the one hand and other behaviours and the anatomical and morphological variables on the other. Two important results emerge from this analysis (Table 2), (1) the frequency of Dominance behaviour is significantly positively correlated with the frequency of Subordinate behaviour (2) the frequency of Dominance behaviour is positively correlated with the Index of ovarian condition, Index of body size, Dry weight and Fat content, but it is also positively correlated with frequency of Feed larva, Extend walls of cells and Build new cells.

Considering only those animals that participated in dominance-subordinance interactions and counting the number of such interactions that each animal was involved in, one can ask what kind of animals are dominant more often than they are subordinate? This is our second approach to understand the correlates of Dominance. We have attempted to answer this question by performing a binomial test where our null hypothesis is that any animal has an equal chance of being either dominant or subordinate. Two important results emerge from this analysis (Table 3). (1) Of 108 pairs of interacting animals where the two had different values of the Index of ovarian condition, in 63 cases the animal with a higher value

Table 2 Kendall's coefficient of rank correlation between Dominance behaviour and other variables

	tau	SE	z
Subordinate behaviour	0 1874	0 0476	3 9415***
Bring food	0 0041	0.0476	0 0856
Snatch food	0.2186	0.0476	4 5968***
Lose food	−0.0053	0 0476	−0 1123
Feed larva	0 1879	0.0476	3 9520***
Bring building material	0 0741	0 0476	1 5573
Snatch building material	0 1760	0 0476	3.7019***
Lose building material	0 1113	0.0476	2 3403*
Extend walls of cells	0 3560	0 0476	7.4864***
Build new cells	0 1478	0.0476	3 1075**
Index of ovarian condition	0 1856	0 0564	3 2886**
Index of body size	0 2823	0 0564	5.0017***
Dry weight (mg)	0 2326	0.0564	4 1216***
Fat (mg)	0 1972	0 0573	3 4437**

*: 0.05 > p > 0.01; **: 0.01 > p > 0 001; ***: p < 0.001

Table 3 Probability of winning or losing in aggressive interactions as a function of behaviour performed, ovarian condition and body size

Variable	No. of cases where dominant and subordinate animals have the same value	No of cases where animal with higher value of the variable is dominant	No of cases where animal with lower value of the variable is dominant	Test statistic Z
Raise antennae	30	113	68	3 3448**
Absent from nest	7	71	133	− 4 3409***
Dominance behaviour	11	172	28	10 1823***
Subordinate behaviour	16	38	157	− 8 5218***
Snatch food	37	113	61	3 9421***
Feed larva	31	113	67	3.4286***
Snatch building material	131	55	25	3.3541***
Extend walls of cells	42	114	55	4 5385***
Build new cells	166	33	12	3 1305**
Index of ovarian condition	24	63	45	1 7321
Index of body size	0	84	48	3 1334**
Dry weight (mg)	0	80	52	2 4371*
Fat (mg)	1	73	51	1 9757*

*: 0.05 > p > 0.01; **: 0.01 > p > 0 001; ***: p < 0 001

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of the Index was dominant and in 45 cases the animal with a lower value of the Index was dominant suggesting no significant influence of Ovarian condition on the outcome of a dominance interaction ($p > 0.05$) (2) Animals with higher values of Index of body size, Dry weight and Fat content were more likely to be dominant rather than subordinate ($p < 0.05$) but, animals that showed higher frequencies of Feed larva, Extend walls of cells and Build new cells were also more likely to be dominant rather than subordinate.

Discussion

Several investigators have found it useful to employ multivariate statistical techniques to discern clusters of functionally similar individuals in social insect colonies that contain morphologically identical or similar individuals. This approach has proved useful in the investigation of inter-individual variability, division of labour and social organization of insect societies (e.g. BROTHERS & MICHENER 1974; PARDI & MARINO PICCIOLI 1981; FRESNEAU et al. 1982; GADAGKAR & JOSHI 1982, 1983, 1984; FRESNEAU & DUPUY 1988; TSUJI 1988; CORBARA et al. 1989; PRATTE 1989). In one such study, GADAGKAR & JOSHI (1983) identified three behavioural castes namely Sitters, Fighters and Foragers in the primitively eusocial wasp *R. marginata*. The queens of both colonies in the study were Sitters. Speculating that some of the remaining Sitters and Fighters were potential queens they argued that Foragers had little or no chance of reproduction. The present study with a larger data base from 12 colonies confirms these basic findings. Three behavioural castes which may be labelled Sitters, Fighters and Foragers, by criteria similar to those used in the previous study, could be identified in each of the 12 colonies. In 11 out of these 12 colonies, the queens were Sitters. The lone exception was colony 3 where the queen was a Fighter. Any speculation to account for this exception would perhaps be premature. It is not clear at this stage whether the behavioural caste of a wasp changes with her age but GADAGKAR & JOSHI (1984) found that in *R. cyathiformis*, most individuals did little work in the first week after eclosion but thereafter followed a relatively constant time-activity budget for the rest of their lives.

Our results suggest that division of labour and social organization are closely linked to behavioural caste differentiation. The extra-nidal task of foraging is performed primarily by the Foragers while the intra-nidal tasks of feeding larvae and nest building are shared between Sitters and Fighters. Because both Sitters and Fighters have better developed ovaries compared to Foragers, but are indistinguishable from each other by their ovaries, potential queens to replace old queens are most likely to be drawn from amongst either Sitters or Fighters. Primitively eusocial species are characterized by the lack of morphological differentiation between queens and workers and the consequent flexibility in the social roles that the adult insects may adopt. The lack of morphological differences between the behavioural castes also adds to this flexibility.

Following the pioneering work of PARDI (1948), dominance hierarchies have been shown to or perceived as having a fundamental role in achieving division of

labour and social organization in many primitively eusocial wasp societies. In most species studied there is usually a despotic queen that is at the top of the dominance hierarchy who actively suppresses aggressive behaviour by nestmates through physical attack. Also, there is a strong correlation between dominance relationships and division of labour such that the most dominant animal monopolizes egg laying while the subordinates are forced to work for the colony both on the nest and outside (PARDI 1948; WEST-EBERHARD 1969, 1986; JEANNE 1972; GADAGKAR 1980; LITTE 1977, 1981; STRASSMANN 1981 a; KOJIMA 1984; ITÔ 1985; RÖSELER 1985; YAMANE 1986; PRATTE 1989). In *Polistes metricus* (DEW 1983) and in *P. fuscatus* (REEVE & GAMBOA 1983, 1987) the queen is the most dominant and active animal in the colony and has been regarded as the central pace-maker and coordinator of colony activity. There are some situations however, where the dominant-subordinate relationships are rather mild or may be nearly absent. But when this happens, the monopoly in egg laying also disappears and several females in a colony are known to have well developed ovaries with mature eggs and/or do actually lay eggs (YAMANE 1973; HOSHIKAWA 1979; KASUYA 1981; ITÔ 1985, 1986; YAMANE 1986).

R. marginata colonies appear to be different in that the queens do not necessarily participate in dominance-subordinance interactions and even when they do, the queens are not the most dominant animals in their colonies. And yet during the 230 h of observation reported here as well as during several 100 h of observations of other colonies of *R. marginata* (GADAGKAR 1980; GADAGKAR & JOSHI 1983, unpubl. obs.) we have never observed egg laying by more than one animal in a colony. The queens in *R. marginata* must have some other, more subtle, "non-confrontational" (WEST-EBERHARD 1986), perhaps pheromonal way of suppressing egg laying by their nestmates and thus maintain their unique egg-laying status. Similarly, there must be some other way by which colony activity is stimulated and integrated because the queen does not appear to act as central pace-maker and coordinator of colony activity.

We find a significant correlation between rates of Dominance behaviour and the number of animals dominated. This suggests that Dominance behaviour is not necessarily directed towards one or a small number of animals (perceived as a potential threat), but is distributed over a large number of animals with more or less the same rate of dominance shown towards each opponent. Rates of Dominance behaviour and probabilities of being dominant (rather than subordinate) are correlated with rates of Feeding larva, Extending walls of cells and Building new cells. That dominance behaviour is performed by a group of animals that specialize in several intra-nidal tasks is also consistent with the idea that division of labour and social organization are achieved by behavioural caste differentiation rather than simply by an animal's position in the behavioural dominance hierarchy.

Why is there a behavioural caste differentiation into Sitters, Fighters and Foragers and why do some animals show Dominance behaviour? In primitively eusocial species, many individuals have some chance of direct reproduction in

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their lifetime. This should select for behaviours that enhance the possibility of such direct reproduction. Many animals however die without reproducing. This should select for behaviours that enhance the colony's fitness and thereby the indirect component of the individual's inclusive fitness. Thus behaviour patterns in these species should evolve in response to individual as well as colony level selection.

Because Foragers appear to have little or no chance of direct reproduction, we suggest that their behaviour of taking up the risky task of foraging is the direct result of attempts to enhance the colony's fitness and thereby the indirect component of their inclusive fitness. Fighters show high frequencies of Dominance behaviour and we suggest that this serves to enhance both direct as well as indirect component of their inclusive fitness. Exhibiting high frequencies of Dominance behaviour may help individuals to enhance their chances of future reproduction by succeeding old and weak queens. On the other hand Dominance behaviour may also serve to keep the colony members active and working. We have often observed that periods of inactivity on nests are broken by one animal directing dominance behaviour towards one or more of its nestmates (GADAGKAR & CHANDRASHEKARA unpubl. obs., see also GADAGKAR & JOSHI 1983). For this reason and because Fighters perform many intra-nidal tasks, they must also enhance colony fitness. Sitters too appear to enhance colony fitness by performing intra-nidal tasks. But by participating little in foraging and dominance acts and thus avoiding risks and conserving energy, they are probably pursuing an alternate pathway of enhancing their chances of future reproduction. Most individuals therefore work for the colony but without entirely closing their option for direct reproduction and thus seem to attempt to maximize individual fitness without hurting the colony's interests too much. Such a compromise between individual fitness and colony fitness may be essential both due to the uncertainty of direct reproduction and because a female who inherits (as a queen) a large and healthy nest will be able to reproduce more efficiently than one who inherits a small and unhealthy nest.

Fighters are not significantly larger in body size than Sitters or Foragers. But there is a more subtle effect of body size on Dominance behaviour. The frequency of Dominance behaviour per hour is significantly positively correlated with body size (Table 2, $p < 0.05$). However, GADAGKAR et al. (1988, 1990 b) found no effect of body size on the egg laying ability of a large sample of *R. marginata* females under laboratory conditions. In 7 out of 11 colonies in this study (data on body size were not available for colony 10) one or more nestmates were larger than the queen and indeed in one of these colonies the queen was the smallest of all animals in her colony. Larger animals thus may not necessarily have better chances of becoming queens. On the other hand we have argued that dominance behaviour may also increase colony fitness by keeping its members active and working. We speculate therefore that the correlation of body size with frequency of Dominance behaviour is related to its possible colony level function of keeping nestmates active and working — a task perhaps best performed by larger individuals if it is achieved by overt physical aggression rather than by pheromones.

Queens of *R marginata* are known to mate multiply, use sperm from different males simultaneously and produce mixtures of full and half-sisters (MURALIDHARAN et al. 1986). This, coupled with frequent queen replacements (GADAGKAR et al 1990 a), should considerably lower worker-brood genetic relatedness It appears unlikely that full and half-sisters can be discriminated within a colony to restore genetic asymmetries created by haplodiploidy (VENKATARAMAN et al. 1988) Kin-selection facilitated by haplodiploidy (HAMILTON 1964 a, b, 1972) has therefore been considered unlikely to be entirely responsible for maintaining sociality in this species (VENKATARAMAN et al. 1988; GADAGKAR 1991). There is evidence for pre-imaginal caste biasing that programmes some animals to develop into poor eaters and poor egg layers but the extent of this is by itself insufficient to explain the presence of sterile castes in *R marginata* (GADAGKAR et al 1988, 1990 b) For these reasons and because of the great deal of behavioural flexibility shown by these wasps GADAGKAR (1991) has argued that opportunities for egg laying in future may be an important factor in maintaining eusociality in such species and indeed that mutualism (LIN & MICHENER 1972) may be the reason why individuals come together and establish groups in the first place. Division of labour and social organization achieved through behavioural caste differentiation, which in turn is moulded through an interaction between individual and colony level selection, rather than by a despotic dominant queen suppressing her nestmates and bullying them into worker roles by constant physical attack, constitutes an appropriate milieu for early social evolution through mutualism.

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ROPALIDIA RUFOPLAGIATA: A POLISTINE WASP SOCIETY PROBABLY LACKING PERMANENT REPRODUCTIVE DIVISION OF LABOUR

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Running title: A polistine wasp without reproductive division of labour?

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Summary

Ropalidia rufoplagiata Cameron (Hymenoptera: Vespidae), a polistine species from peninsular India, appears to be unique amongst all known primitively eusocial wasps. About 33 out of 46 identified females on an observed colony were found to oviposit on one to seventeen occasions. No single predominant egg-layer could be identified over a period of 45 days. The egg-layers, of which twelve out of seventeen individuals dissected were mated, showed several oviposition-related behaviours including systematic, but indiscriminate, cannibalism of eggs and larvae, cleaning of empty cells and guarding of freshly-laid eggs. There was no correlation between the egg-laying activity of the females (whether mated or not), oophagy, and their position in the dominance hierarchy. All nest-maintenance activities were performed exclusively by the egg-layers, while the non-egg-layers were mainly involved in the extra-nidal task of foraging. No significant morphometric differences between the egg-layers and the foragers could be discerned. Almost all the older individuals in the colony were egg-layers while foragers were mainly younger animals. Such a temporal differentiation in reproductive labour suggests the absence of a permanent reproductive caste in this species.

Introduction

Ropalidia is a large genus with about 136 known species confined to tropical and subtropical regions of the Old World, including Africa, southern Asia, Australia and Okinawa (for a review, see Gadagkar 1991a). This is the only genus which includes both independent-founding and swarm-founding species and consequently shows remarkable variation in adult social behaviour and colony organisation (Jeanne, 1980, 1991; Gadagkar, 1991a; Wenzel, 1987, 1992). The independent-founding species of *Ropalidia* are interesting in being characterised by a relatively primitive level of eusociality: they lack morphological caste differentiation and possess an essentially behavioural mechanism of queen control. A linear dominance hierarchy among founding females or among colony members results in the most dominant female being the principal or sole egg-layer ("queen"), rarely or never leaving the nest to forage while the subordinate "workers" rarely or never lay eggs.

Dominance interactions and dominance displays shown by colony members usually reflect the extent of reproductive competition that these individuals might face at different phases of colony development. Several behaviours involved in establishing reproductive dominance in multiple-foundress associations or in post-emergence colonies are common among polistine wasps. These include egg guarding, differential oophagy and egg substitution, or even physical prevention of subordinates from laying eggs. Such behaviours, however, appear to be rare in

Ropalidia. Cell guarding, for example, had never been recorded for any species so far while oophagy has only been demonstrated in *R. cyathiformis* (Gadagkar and Joshi, 1982) and *R. fasciata* (Itô, 1987b).

The nature and extent of reproductive competition, in turn, determines the number of functional egg-layers in a colony. Thus, even in species of *Ropalidia* where nests may be founded pleometrotically, monogyny is usually established at the early stages of colony development through a definite dominance hierarchy, *e.g.* in *R. revolutionalis* (Itô, 1986). Although typical of small colonies, monogyny may often give way to serial polygyny as a result of usurpation or queen succession, especially in species with indeterminate nesting cycles like *R. fasciata* (Turillazzi and Marucelli Turillazzi, 1985), *R. variegata jacobsoni* (Yamane, 1986), or *R. marginata* (Gadagkar *et al.*, 1991). It must be stressed, however, that at least in the case of *R. marginata*, there is only a single egg-layer at any given time. A different situation, on the other hand, occurs in species like *R. cyathiformis* (Gadagkar and Joshi, 1982) or *R. fasciata* from Okinawa (Itô, 1987b). Here, the dominance hierarchy established within the nest is weak, especially in large post-emergence colonies, and simultaneous polygyny may prevail, with the majority of eggs being laid by the most dominant α-female and the remaining small fraction by the higher-ranked subordinates.

This paper reports the social behaviour and colony organisation of an independent-founding, polygynous wasp, *Ropalidia rufoplagiata* Cameron (Hymenoptera: Vespidae) (see Das

and Gupta, 1989). This species appears to be unique amongst all polistines described so far in that the majority of adults in the colony regularly lay eggs. There does not appear to be any one predominant egg-layer of higher dominance rank than the others, and there is, in fact, no correlation between egg-laying activity and ranks in the dominance hierarchy. All the egg-laying individuals systematically guard cells and practise oophagy. Finally, there is some evidence of a temporal reproductive division of labour so that all colony members may ultimately lay eggs, an indication that this species may not have evolved permanent reproductive castes.

Materials and methods

Study colony

This study was conducted on a single post-emergence colony, in the Indian Institute of Science, Bangalore (13°00'N and 77°32'E), between 27 February and 15 April, 1991. A single multi-pedicellate nest, measuring approximately 12 cm x 6 cm, was found suspended in an inverted fashion from the portico of a house in the Malleswaram locality of the city and transferred to the vespiary at the Institute on 26 February. Here, the nest was maintained in an open cage such that the adults could forage freely not only from natural sources but also from a supply of honey, *Corcyra cephalonica* larvae and water provided within the vespiary.

At the time of collection, 47 adults were present on the nest consisting of 295 cells with 125 eggs, 118 larvae, 42 pupae and only 10 empty cells. All the adults were marked for individual identification with spots of coloured paint; newly-eclosed wasps were marked each day. A total of 153 animals was marked during the entire observation period, of which 96 individuals had eclosed in the vespiary. A census of all animals was made several times randomly during each day and a map of the nest and its contents maintained regularly. Unfortunately, it was not possible to distinguish between the sexes initially, this could be accomplished only after the individuals had been later collected and examined under a binocular microscope.

Sampling methods

Behavioural observations on the colony included *ad libitum* sampling, instantaneous scanning and recording all occurrences of selected behaviours, as described by Gadagkar and Joshi (1983).

A total of 25.5 h of observation was performed during a period of 7 days, between 9 April and 15 April, 1992. Initial *ad libitum* observations showed that the wasps were active mainly between 0800 and 1800 h. Observations were thus conducted during these hours with a random intermingling of instantaneous scans and sessions recording all occurrences of selected behaviours.

All adult females, considered in the final behavioural analysis, were at least 4 days of age on the first day of observation (9 April, 1991) and were also those present for at least 20 h within the entire observation period of 30 h.

Data on egg-laying and cannibalistic behaviour were collected during 46.5 h of observation distributed in two periods: from 21 March to 29 March, and again from 9 April to 15 April, 1991. The 15 sessions, dedicated to recording every occurrence of oviposition and oophagy, ranged in duration from 1 to 6.75 h with a median of 3.5 h, and spanned 10 h of the day, *i.e.* from 0800 to 1800 hours.

At the end of the observations, on 15 April, 1991, all adult wasps (with a minimum age of 9 days) were collected. The females were assessed in terms of their body size, ovarian condition (as measured by oocyte number) and mating status, and finally dried at 60°C for 15 days to record their dry weight.

Data analysis

1. Behavioural repertoire, time-activity budgets and rates of select behaviours

The behavioural repertoire of this species was classified into distinct categories which were similar to those of *R. marginata* and *R. cyathiformis* (Gadagkar and Joshi, 1983, 1984).

Time-activity budgets, or the proportion of time spent in different behaviours by different animals, were estimated using data from instantaneous scans. The hourly frequencies with which certain selected behaviours were performed were calculated from the sessions recording all occurrences of such behavioural events, as described earlier (Gadagkar and Joshi, 1984).

2. Principal component analysis

Time-activity budgets, constructed from the proportions of time spent in six common behaviours, were subjected to principal component analysis (Frey and Pimentel, 1978). The resulting clusters were identified as described earlier by Gadagkar and Joshi (1983).

3. Index of body size

An index of body size was computed as the amplitude along the first principal component of 27 input morphometric measures, namely, length and width of the head, inter-ocular distance, oculo-ocellar distance (left and right), inter-antennal socket distance, length and width of the frontal segment of the antennae (left and right), length and width of the clypeus, length and width of the mesoscutellum, alitrunk length, length of left and right wings, length of the first median wing cell (left and right), number of hamuli (left and right), and the length, width and height of the first and second gastral segments. Due to the wide variation in the absolute values of the different variables, a correlation matrix, rather than a covariance matrix, was used in performing the principal component analysis.

4. Dominance hierarchy

A dominance hierarchy was constructed for all the colony members using an index of dominance described by Premnath *et al.* (1990). The index was computed for each animal as:

$$\frac{\sum_{i=1}^{n} B_i + \sum_{j=1}^{m} \sum_{i=1}^{n} b_{ji} + 1}{\sum_{i=1}^{n} L_i + \sum_{j=1}^{p} \sum_{i=1}^{n} l_{ji} + 1}$$

where ΣB_i is the rate at which the subject shows dominance behaviour towards other colony members and Σb_{ji} is the sum of the rates at which all animals dominated by the subject, in turn show dominance behaviour towards other individuals. Similarly, ΣL_i is the rate at which the subject shows subordinate behaviour towards colony members and Σl_{ji} is the sum of the rates at which the latter, in turn, show subordinate behaviour towards other individuals.

5. All statistical tests were two-tailed, and performed according to Sokal and Rohlf (1981).

Results

Identification of behavioural groups

The most striking feature of the wasps in the study colony was their egg-laying behaviour. Approximately 70% (33 out of the 46 females observed for a minimum period of 14 days and 19 out of the 27 females for whom quantitative behavioural data were available) of the colony members were seen to lay an egg at least once. Furthermore, many of these individuals oviposited quite regularly and frequently.

There were two distinct behavioural groups in the colony. Of the 27 females whose behaviour has been analysed in detail, 17

laid eggs at least once but were never seen to forage while 6 brought food or liquid to the nest at least once but were never observed to lay an egg. There were, however, two Egg-layers who brought food and liquid on one occasion each, but also two females who neither laid eggs nor foraged (Table 1). Ignoring the latter and considering the former as Egg-layers, two behavioural groups have been considered in subsequent analysis, namely Egg-layers and Foragers. Three additional arguments justifying such a behavioural classification are given below.

Clusters identified by principal component analysis

First, in an independent approach to examine other behavioural criteria on the basis of which the wasps could be clustered, time-activity budgets were constructed for 27 individually identified members of the colony. It was found that the wasps spent 81% to 100% (mean ± s.d., 90.94 ± 0.04) of their time in six common behaviours, namely sit and groom, sit with raised antennae, absent from nest, walk, in cells, and guard cell (in which the wasp sits with her head inside a cell for a variable period of time). Individuals allocated their time differently to each of these behaviours. Accordingly, in order to discern behavioural patterns within the colony, these time-activity budgets were subjected to principal component analysis. The results show that the first two principal components together account for 98.24% of the total variance and may thus be considered adequate to describe the behaviour of these individuals (Table 2). The representation of each wasp as a point

in the coordinate space of the first two principal components results in two distinct clusters, further confirmed by the nearest centroid criterion (Gadagkar and Joshi, 1983) (Figure 1).

An examination of the behavioural profile of the individuals in the two clusters revealed that there was a significantly greater proportion of Egg-layers in Cluster I than in Cluster II (Table 3, G-test of independence, $p < 0.01$). The proportion of Foragers, in contrast, is significantly greater in Cluster II than in Cluster I (Table 3, G-test of independence, $p < 0.05$). One Forager (Wasp 24) who collected food from within the vespiary and therefore did not spend much time away from the nest, belongs to Cluster I. Three Egg-layers (Wasps 8, 9 and 14), on the other hand, have become members of Cluster II by virtue of the significant periods of time they spent away from the nest, although never returning with food or liquid. Two individuals (Wasps 21 and 27), one in each cluster, were neither seen to oviposit nor forage. It may be emphasised here that the two clusters emerged as a result of choosing, for analysis, those six behaviours that had the highest ranks in the proportion of time the wasps devoted to them, and not taking into consideration egg-laying behaviour. These behavioural clusters, nevertheless, appear to be principally represented by Egg-layers and Foragers, respectively.

Correlates of the behavioural groups

Second, in order to examine more closely the differences between Egg-layers and Foragers, the mean behavioural profiles of the two

groups for select behaviours were examined. As compared to the Foragers, Egg-layers invested a significantly greater proportion of their time in sitting and grooming on the nest (Mann-Whitney U-test, $p = 0.05$), while the former spent comparatively more time in being absent from the nest ($p < 0.01$) (Figure 2). It may be recalled that these are also the behaviours that had the maximum weightage on the first two principal components which permitted the earlier clustering of the two behavioural groups.

A remarkably distinct pattern of task-allocation between the Egg-layers and Foragers becomes evident on examining other behavioural variables not used in deriving the clusters (Figure 3). Thus, Egg-layers were significantly more responsible for nest-maintenance activities, such as breaking walls of unused cells (Mann-Whitney U-test, $p < 0.002$), extending old cell-walls ($p < 0.05$), or cleaning empty cells ($p < 0.002$). In contrast, Foragers brought food more often to the nest ($p < 0.002$) and fed larvae more frequently ($p < 0.05$) than did the Egg-layers. Dominance interactions on the nest were mainly restricted to the Egg-layers and they thus showed significantly higher levels of both dominance and subordinate behaviours than did the Foragers.

Clustering of behaviours by correlation analysis

In a third approach to discerning individual behaviour patterns, especially with reference to task-allocation, Kendall's rank correlation coefficients were computed for the proportion of time spent by the wasps in certain behavioural states, the frequency of occurrence of select behavioural events, and oocyte number.

Egg-laying was found to be strongly correlated with guarding cells, cleaning empty cells, breaking walls of cells, extending old walls of cells (for all behaviours, $p < 0.05$, $n = 27$), and oocyte number ($p < 0.05$). Bringing food and liquid was positively correlated with being absent from the nest and feeding larvae, but negatively correlated with egg-laying and many of its associated behaviours as well as oocyte number (for all correlations, $p < 0.05$). In order to visualise the association of different behaviours as an indication of possible task-allocation, the Kendall's rank correlation coefficients were used as indices of similarity between behaviours and a hierarchical cluster analysis performed with the single linkage algorithm (De Ghett, 1978) (Figure 4). The clustering of behaviours, obtained from this analysis, parallels closely the patterns of task distribution already evident from the behavioural profiles of the Egg-layers and the Foragers.

Absence of morphological differences between Egg-layers and Foragers

The index of body size and dry weight did not differ significantly between Egg-layers and Foragers (data not shown). A comparison of all the evaluated morphometric parameters also failed to discern any significant difference between the two behavioural groups. As might be expected, however, the oocyte number of Egg-layers (mean ± s.d., 17.4 ± 6.9) was significantly higher than that of Foragers (0.8 ± 1.6) (Mann-Whitney U-test, $p < 0.001$, $n = 17$ Egg-layers, 5 Foragers).

Age structure of Egg-layers and Foragers

Of the 27 individuals included in the final behavioural analysis, 17 were females originally present on the nest when it had been collected. The exact ages of these "old" wasps were thus not known although they were at least 25 days old at the beginning of the observation sessions. The ages of the other 10 "young" wasps, which had eclosed in the vespiary after transplantation of the nest, ranged from 6 to 21 days, with a mean of 14 ± 4.6 days.

The old wasps were overwhelmingly represented by Egg-layers, while the young wasps had a greater proportion of Foragers (Table 4, G-test of independence, $p < 0.002$). Two of the three Egg-layers in the young group were also Foragers and were observed bringing food and liquid to the nest, although, as mentioned earlier, only on a single occasion each. None of the 16 Egg-layers in the old group, in contrast, were ever seen to forage for either food or liquid. Assuming the older wasps to be only 25 days old, the mean age of the Egg-layers in the study colony was 23.6 ± 3.5 days and that of the Foragers significantly different at 15.3 ± 5.6 days (Mann-Whitney U-test, $p < 0.01$, $n = 19$ Egg-layers, 6 Foragers).

Analysis of egg-laying behaviour

Data from 46.5 h of observation, exclusively devoted to oviposition, yielded an average rate of 4 eggs laid per hour by a total of 28 individuals, with about 3 wasps laying eggs every hour. The frequency of oviposition per hour for each of the 28 egg-layers ranged from 0.06 to 0.55, with a mean of 0.19 ± 0.12.

This is probably the most prolific rate of egg-laying by the highest proportion of colony members (70%) ever to be reported for a polistine wasp, including the swarm-founding species (see Jeanne, 1991; Spradbery, 1991). There did not appear to be any significant difference in the rate of oviposition at different times of the day (data not shown). Notwithstanding the variation in the individual rates of egg-laying shown by the wasps, no single principal egg-layer was evident during this period.

Of the 28 individuals analysed for their egg-laying behaviour, 17 were dissected and found to have mature developed ovarioles with oocytes. No correlation could be established between the frequency of oviposition and the number of oocytes present in an individual. The most remarkable finding, however, was that 12 out of the 17 dissected egg-layers were mated (the spermatheca being lost during dissection for one wasp). Two individuals that had eclosed in the vespiary after the nest had been collected were also mated. This species is very rare; indeed this is the only colony we have ever seen. This suggests that, at least in this instance, mating had possibly been accomplished with males from the natal nest.

Dominance, cannibalism and egg-laying behaviour

A nearly universal feature of primitively eusocial wasp colonies is the presence of a dominance hierarchy amongst the adult females and the positive correlation of egg-laying ability of the individuals with their dominance rank. This species, however, proved to be an exception. Although dominance interactions

appeared to be restricted to the Egg-layers alone, with very little interaction between the Egg-layers and the Foragers, and none whatsoever amongst the Foragers (Figure 5), no apparent relationship was evident between egg-laying by an individual and its dominance profile, as measured by its index of dominance. Effective oviposition by an individual seemed also to be unrelated to its mating status (Table 5). A negative correlation, in fact, existed between the frequency of oviposition by an individual and its index of dominance when only Egg-layers were considered in the analysis (Figure 6; Kendall's rank correlation coefficient, $\tau = -0.4201$, $p < 0.01$, $n = 19$). When the two outlying individuals with the highest values for dominance index were removed, the negative correlation was still significant (Kendall's rank correlation coefficient, $\tau = -0.3866$, $p < 0.05$, $n = 17$).

From the very earliest observations *ad libitum*, it was noticed that oophagy was a regular feature of the colony. A stereotyped sequence of events, shown only by the Egg-layers, consisted of cannibalism of an egg, cleaning of the now-empty cell, oviposition, and finally, guarding of the cell for variable periods of time. The number of empty cells in the nest at any time probably constrained oviposition by the majority of the colony members constituting the Egg-layers. Oophagy, and less commonly, the destruction of larvae and pupae, could thus be a reflection of reproductive competition on the nest.

The observation sessions dedicated to oviposition and oophagy showed that of the 186 eggs laid during this period, 54 (29%) were eaten. Nest-map records indicated that of the 355 larvae already present on the nest when it was collected as well as those which had developed since, 186 (52%) were cannibalised. Similarly, 27 (22%) of a total of 123 pupae were destroyed or cannibalised.

The observation sessions on oviposition also provided an estimate of how long a freshly-laid egg survived prior to being eaten. A total of 17 eggs were observed to be cannibalised during periods of continuous observation. The time of survival of these eggs ranged from 6 to 223 min with a median value of 40 min. A detailed analysis of successive instantaneous scans and 'all occurrence' sessions also made it possible to examine the length of time an average egg was guarded by the egg-layer immediately following oviposition. Data from 85 instances of guarding cells showed that its duration ranged from 3 to 72 min with a median value of 18 min. Although an estimate of the effectiveness of guarding cannot be obtained from this data, it may be informative to note that of the 17 eggs seen to be eaten, only 3 (17%) were cannibalised within 18 min of being laid.

Was oophagy differential among the colony members? The 54 eggs observed to be eaten during the sessions belonged to 22 egg-layers out of the 28 seen to oviposit during this period. In 4 instances, an egg-layer even ate her own egg! During these observations, the number of eggs contributed by the 28 egg-layers (to a total of 186 eggs), before cannibalism, ranged from 1 to

15, with a mean of 6.6 ± 4.3. After oophagy, the contributions (to the remaining 132 eggs) varied from 0 to 12, with a mean of 4.7 ± 3.4. Two matrilines, consisting of only a single egg each, were entirely lost. The pattern of contribution to the brood by the colony egg-layers under the two conditions (before and after oophagy) are very similar (Kolmogorov Smirnov two-sample test, $p > 0.95$); an indication of the absence of selective oophagy. This is further reinforced by the strong positive correlation between the number of eggs contributed by each egg-layer before and after cannibalism (Figure 7; Kendall's rank correlation coefficient, $\tau = 0.8986$, $p < 0.001$, $n = 28$). A positive correlation was also evident between the number of eggs eaten by an individual and the total eggs laid by her (Kendall's rank correlation coefficient, $\tau = 0.5174$, $p < 0.001$, $n = 22$). This is not surprising since as already mentioned earlier, the number of empty cells was a possible constraint on the frequency of oviposition by an individual and wasps invariably had to cannibalise eggs in order to lay their own.

Discussion

The most distinguishing feature of *Ropalidia rufoplagiata* is that a large number of individuals in the study colony were mated egg-layers. Although several studies have reported polygyny in the independent-founding polistines, most are based on indirect evidence obtained from the ovarian condition of the individuals (*Ropalidia*: Itô, 1985, 1987a, submitted; Itô and Higashi, 1987; Spradbery and Kojima, 1989; Yamane, 1986; Yoshikawa *et al.*, 1969;

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Mischocyttarus: Itô, 1984; Litte, 1977, 1979, 1981; *Polistes*: Miyano, 1980; Reed *et al.*, 1988). Even in the few cases where egg-laying was observed, it is not clear whether more than one laying female was inseminated (*Ropalidia*: Gadagkar and Joshi, 1982; Yamane, 1986; Itô, 1987b; *Polistes*: Hoshikawa, 1979; Kasuya, 1981). A notable exception, however, is *Belonogaster grisea* where several inseminated females were observed to oviposit (Pardi and Marino Piccioli, 1970).

Several lines of evidence suggest the presence of two distinct behavioural groups of females in *R. rufoplagiata*: Egg-layers and Foragers. The two groups could be clearly distinguished on the basis of behaviours other than oviposition and foraging. Principal component analysis of time-activity budgets produced two clusters significantly represented by Egg-layers and Foragers, respectively. The two classes of individuals were, however, morphometrically indistinguishable. Pardi and Marino Piccioli (1981) observed a similar behavioural differentiation in *Belonogaster grisea*. Females of one class were more frequently dominant, oophagous, nest-builders and egg-layers. The other class rarely laid eggs, were never oophagous, and were usually subordinates and foragers. There was, however, a statistically significant difference in the size of the thorax in the two classes of females, that of the egg-layers being larger.

A most interesting finding in *R. rufoplagiata* is the correlation between behavioural differentiation and the age structure of the colony. Younger individuals were usually

Foragers while oviposition was confined to most of the older individuals. The only two Egg-layers observed to forage as well belonged to the younger group of wasps. Do these individuals represent the transition stage between the two behavioural clusters? This evidence for a temporal division of labour in this species is remarkably reminiscent of the classic observations of Roubaud (1916) who proposed a similar temporal differentiation of castes in *Belonogaster juncea*, although this has never been subsequently substantiated. In the queenless ant *Pristomyrmex pungens* young adults oviposit while the older ones forage (Tsuji, 1990). Similarly, younger workers (10 days from eclosion) of the wasp *Polistes jadwigae* perform intranidal work while middle-aged workers (11 - 25 days old) are foragers (Tsuchida, 1991). Counter-intuitive as it may seem, the involvement of younger animals in the risky task of foraging is not entirely without precedent. Miyano (1980) reported several long-lived workers in a colony of *Polistes chinensis antennalis* which emerged earlier, performed extranidal tasks for about 30 days, then stopped foraging and took charge of intranidal tasks. Although it was not known whether these workers were mated or not, they laid eggs at a rate not too different from that of the queen.

In almost all primitively eusocial species described so far, dominance hierarchies have been considered, and often shown, to have a fundamental rôle in reproductive success and division of labour within the colony. In most species, there is a dominant queen at the top of the hierarchy who usually monopolises oviposition and actively prevents all the subordinate females

from laying eggs through aggressive interactions (for a review, see Spradbery, 1991). Although there may be situations when the dominant female loses her position in the hierarchy as a result of the eclosion of a large number of individuals during the late post-emergence phase and several females begin to lay eggs, this is often temporary (Yamane, 1986; Itô, 1987b). Orphaned colonies of some species too may have several egg-laying "workers" (Miyano, 1986; Suzuki, 1987), but a dominance hierarchy again develops with the most dominant workers monopolising oviposition. Even in species where the dominant-subordinate relationships are mild or absent and several females lay eggs (Hoshikawa, 1979; Kasuya, 1981; Itô, 1986), a single female usually has a higher frequency of oviposition than all the other colony members. This is also true for the Stenogastrinae where even in those species with multiple egg-layers, there is a clear correlation between dominance status and reproductive capability (Turillazzi, 1991).

Ropalidia rufoplagiata presents a completely contrasting picture to this generalised scenario. There is no correlation between the rate at which individuals lay eggs and their position in the dominance hierarchy. Dominance-subordinate interactions were nearly restricted to the Egg-layers, the Foragers being attacked only rarely. This is in contrast to *Belonogaster grisea* where all the oophagous egg-laying females had higher dominance ranks than all the foragers (Pardi and Marino Piccioli, 1970). Several authors have also speculated on the rôle of mating in determining the dominant status of an individual (Pardi and Marino Piccioli, 1981; Kasuya, 1983). Although most of the egg-

layers in *R. rufoplagiata* were mated, this did not influence their rank in the dominance hierarchy.

Differential oophagy has long been recognised to be a common manifestation of dominance in primitively eusocial wasps with the dominant female(s) eating the eggs of their subordinates (Pardi, 1942; West-Eberhard, 1969; Gamboa *et al.*, 1978; Miyano, 1980; Pardi and Marino Piccioli, 1981; Suzuki, 1987). *R. rufoplagiata* again proves to be an exception in that there was no correlation between oophagy by an individual and her position in the dominance hierarchy. Wasps with higher rates of oviposition, however, ate more eggs, and as far as could be discerned, indiscriminately so. Egg guarding in this species, never reported earlier for any *Ropalidia*, appears to be a counter-measure against widespread oophagy (see West-Eberhard, 1981). Although its effectiveness in decreasing the probability of an egg being eaten cannot be readily estimated, its importance is evident in that it invariably forms part of the egg-layer's repertoire of oviposition-associated behaviours.

Individuals with higher rates of oviposition appeared to be successful in attaining greater reproductive success since they tended to leave behind more eggs. They, however, had lower ranks in the dominance hierarchy as compared to other egg-layers. The ability of an individual with low rates of oviposition to dominate another with a much higher potential to lay eggs could provide an alternative reproductive strategy for the former in their attempts to prevent the latter from laying eggs. The more active egg-layers, in contrast, possibly maximise their fitness

by spending a greater proportion of time in cannibalising eggs and larvae, oviposition, and the guarding of freshly laid eggs.

What are the implications of this unique social organisation of *Ropalidia rufoplagiata* for the evolution of sociality in wasps? West-Eberhard (1978), in her "polygynous family" hypothesis, envisaged a "rudimentary-caste-containing stage", an evolutionary intermediate between casteless group-living and a stage with a regularly-occurring worker caste. Although a temporal division of labour was considered one of the possible forms of a rudimentary caste, no example of this had ever been found amongst the polistine taxa (Carpenter, 1991). *R. rufoplagiata* could well-represent such a polygynous, rudimentary-caste-containing species. With such extensive polygyny, however, intra-colonial genetic relatedness could be rather low. But this should not really pose a serious problem for the origin of eusociality. One of us (Gadagkar, 1990, 1991a) has postulated that a "gambling stage", without high relatedness, kin recognition or manipulation but where an average member of the group has greater fitness than a solitary individual, may serve as the starting point for the evolution of eusociality. *R. rufoplagiata* appears to be an excellent example of a species at such an initial "gambling stage" of social evolution. This species also illustrates quite clearly the advantage of mixed reproductive strategies, namely working and reproducing within an individual's lifetime, in the early stages in the evolution of eusociality (Gadagkar, 1991b).

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Table 1. Task-allocation between the colony members with respect to egg-laying and foraging. The distibution was examined with the G-test of independence

Behavioural groups	Foragers	Non-foragers	G	p
Egg-layers	2	17	11.032	< 0.002
Non-egg-layers	6	2		

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Table 2. Principal component analysis of time-activity budgets of colony members

Behaviour	Principal components	
	I	II
Sit and groom	-0.5577	0.7409
Absent from nest	0.8204	0.4285
Raise antennae	0.0149	-0.0181
Guard cells	-0.0551	-0.3403
Walk	-0.0676	-0.1830
In cells	-0.0901	-0.3433
Eigen value	0.0624	0.0080
Percentage of variance	87.12	11.12
Cumulative percentage of variance		98.24

Table 3. Proportion of egg-layers and foragers in the two behavioural clusters obtained by principal component analysis of time-activity budgets. The distributions were examined with the G-test of independence

Behavioural group	Clusters		G	p
	I	II		
Egg-layers	16	3	8.8004	< 0.01
Non-egg-layers	2	6		
Foragers	2	5	5.9800	< 0.05
Non-foragers	16	4		

Table 4. Proportion of egg-layers and foragers in the two age classes of colony members. The distribution was examined with the G-test of independence

Behavioural group	Age class		G	p
	Old	Young		
Egg-layers	16	3	12.992	< 0.002
Non-egg-layers	1	7		
Foragers	1	7	12.992	< 0.002
Non-foragers	16	3		

Table 5. Hierarchical dominance relationships between colony members

Rank	Mating status	Oviposition	Oophagy	Foraging
1	+	+	+	-
2	+	+	+	+
3	?	-	-	-
4	+	+	+	-
5	-	+	+	-
6	+	+	+	-
7	-	+	+	-
8	-	+	+	-
9	?	+	-	+
10	-	-	-	+
11	-	-	-	+
12	+	+	+	-
13	?	+	+	-
14	+	+	-	-
15	?	-	-	-
16	-	-	-	+
17	+	+	+	-
18	+	+	+	-
19	+	+	+	-
20	+	+	+	-
21	+	+	-	-
22	?	-	-	+
23	-	-	-	+
24	?	+	+	-
25	+	+	+	-
26	-	+	+	-

+: Mated individuals; oviposition, oophagy and/or foraging observed
?: Mating status unknown

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Legends to figures

Figure 1. Behavioural clusters of *R. rufoplagiata*. Time-activity budgets of 27 wasps are shown as points in the coordinate space of the first two principal components. The points fall into two clusters by the criterion of nearest centroid. The centroids have been represented by circled points, the Egg-layers by filled squares, the Foragers by filled circles, the individuals showing both egg-laying and foraging by circled squares and those showing neither by open squares.

Figure 2. Mean time-activity budgets (mean + s.d.) for the Egg-layers (open bars) and Foragers (solid bars) in the study colony. The mean proportion of time spent by a wasp in six common behaviours has been compared for the two groups using the Mann-Whitney U-test (n_1 = 19 Egg-layers, n_2 = 6 Foragers). Significant differences between the groups are indicated as AB ($0.05 > p > 0.01$) and AC ($p < 0.01$). SG: Sit and groom; FG: Absent from nest; SA: Sit with raised antennae; WA: Walk; IC: In cells; GC: Guard cell.

Figure 3. Mean frequency of select behaviours (mean + s.d.) performed by the Egg-layers (open bars) and the Foragers (closed bars) in the study colony. The mean frequency of occurrence of each behaviour per hour per animal has been compared for the two groups using the Mann-Whitney U-test (n_1 = 19 Egg-layers, n_2 = 6 Foragers). The differences between the two groups are shown as AA (not significant at $p > 0.05$), AB ($0.05 > p > 0.01$) and AC ($p < 0.01$). CE: Clean empty cell; EL: Lay egg; BW: Break wall of cell;

EO: Extend old wall of cell; BF: Bring food; SF: Snatch food; FL: Feed larva; DB: Dominance behaviour; S-: Subordinate behaviour; CN: Cannibalism.

Figure 4. Hierarchical cluster analysis of the behaviours shown by *R. rufoplagiata*. Time-activity budgets and the frequency of occurrence of select behavioural events for 27 colony members have been used in the analysis. The similarity between individuals has been shown in terms of Kendall's coefficients of rank correlation between these variables. The method of single linkage algorithm was used for the clustering.

Figure 5. Mean frequency of dominance behaviour within and between the Egg-layers and the Foragers in the study colony.

Figure 6. Scatter plot showing the dominance index of an Egg-layer as a function of her frequency of oviposition per hour. Mated individuals are represented by filled squares, unmated individuals by open squares and those of unknown mating status by filled circles. Asterisks indicate individuals which eclosed in the vespiary. Data plotted on the two axes are negatively correlated (Kendall's coefficient of rank correlation, τ = -0.4201, z = -2.5135, n = 19).

Figure 7. Scatter plot showing the the proportion of eggs contributed to the final brood (after oophagy) by an Egg-layer as a function of the proportion of eggs originally contributed by her (before oophagy). Mated individuals are represented by filled squares, unmated individuals by open squares and those of unknown

389 mating status by filled circles. Animals which had eclosed in the vespiary are indicated by asterisks. Two overlapping points, both represented by mated individuals, are indicated as "2". Data plotted on the two axes are positively correlated (Kendall's coefficient of rank correlation, $\tau = 0.8090$, $z = 6.0419$, $n = 28$).

Sinha et al Fig. 1

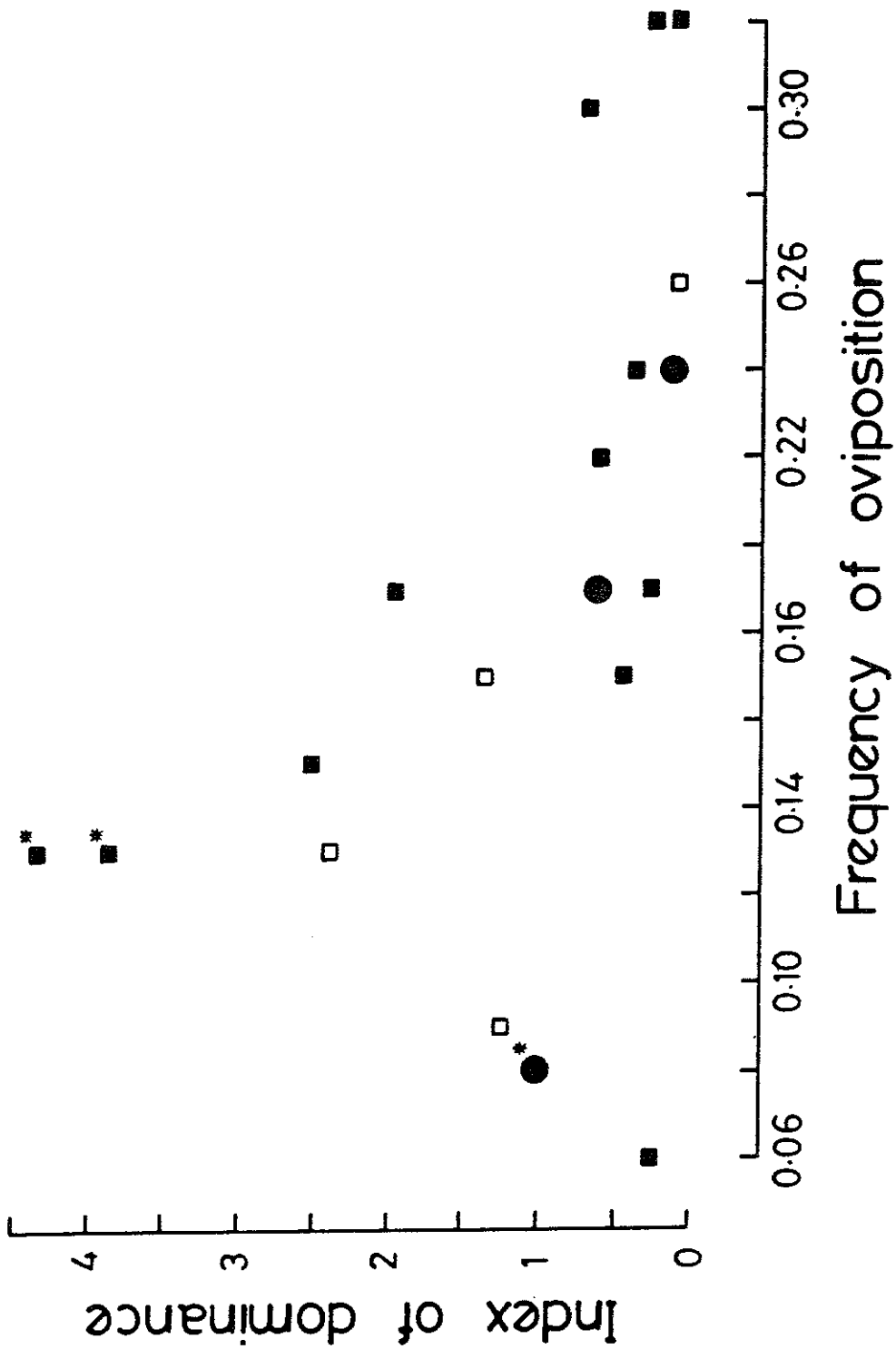
Sinha et al Fig 2

Sinha et al Fig. 3.392

Behaviours Characteristic of Foragers
Behaviours Characteristic of Egg-layers
Absent from nest
Bring food and liquid
Feed larva
Cannibalism
Dominance behaviour
Extend wall of cell
Break wall of cell
Subordinate behaviour
Guard cell
Clean empty cell
Lay egg
0·7
0·6
0·5
0·4
0·3
0·2
Kendall's coefficient of rank correlation

Snake eggs fig. 5

Sinha et al Fig. 6



Sinha et al Fig 7

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