LECTURE NOTES FOR

TRAINING PROGRAMME ON

" *CONSERVATION BIOLOGY* "

FOR OFFICERS OF THE INDIAN FOREST SERVICE

DATES: 25-29 JANUARY 1993

COURSE DIRECTOR: Dr. R. SUKUMAR

ORGANISED BY :

CENTRE FOR ECOLOGICAL SCIENCES
INDIAN INSTITUTE OF SCIENCE
BANGALORE 560 012

CES TECHNICAL REPORT NO. 67

COURSE ON "CONSERVATION BIOLOGY" FOR INDIAN FOREST SERVICE OFFICERS

CONDUCTED BY : CENTRE FOR ECOLOGICAL SCIENCES
INDIAN INSTITUTE OF SCIENCE
BANGALORE 560 012

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VENUE : RUSTOM CHOKSI HALL, IISc.
DATE : 25TH JANUARY - 29TH JANUARY 1993

25th January 1993 (Monday)

9.30 AM : Welcome and Introductions

10.00 AM : Inaugural talk : "Forest Policy and Conservation"
Mr. S. Parameswarappa (Principal Chief Conservator of Forests, Karnataka)

10.30 AM to
10.45 AM : Tea/Coffee Break

10.45 AM : "Processes influencing genetic diversity"
Dr. N.V. Joshi (CES, IISc.)

11.45 AM : "Genetic Diversity in Natural Populations"
Prof. Raghavendra Gadagkar (CES, IISc.)

12.45 PM to
2.00 PM : Lunch

2.00 PM : Case Study : "Conserving the Bird Fauna of Uttara Kannada"
Dr. R.J. Ranjit Daniels (Madras Crocodile Bank)

3.00 PM to
3.15 PM : Tea/Coffee Break

3.15 PM : "Global Patterns of Species Diversity"
Dr. R. Sukumar (CES, IISc.)

26th January 1993 (Tuesday)

9.30 AM	:	"How is Biodiversity Maintained ?" Dr. R. Sukumar
10.30 AM to 10.45 AM	:	Tea/Coffee Break
10.45 AM	:	Case Study : "Amphibian Diversity and Conservation in the Western Ghats" Dr. R.J. Ranjit Daniels
11.45 AM	:	Case Study : "Reptilian Diversity and Conservation" Mr. M.K. Srinath (World Wide Fund for Nature - India)
12.45 PM to 2.00 PM	:	Lunch
2.00 PM	:	"Extinction, Insular Biogeography and Design of Nature Reserves" Dr. R. Sukumar
3.00 PM to 3.15 PM	:	Tea/Coffee Break
3.15 PM	:	"Insect Diversity and Conservation" Dr. K. Chandrasekhara (CES, IISc.)

27th January 1993 (Wednesday)

9.30 AM : "Minimum Viable Populations for Conservation"
Dr. R. Sukumar

10.30 AM to
10.45 AM : Tea/Coffee Break

10.45 AM : Case Study : "Conservation Biology of Elephants"
Dr. R. Sukumar

11.45 AM : Computer Demonstration :
"Population Viability Analysis"

12.45 PM to
2.00 PM : Lunch

2.00 PM : Case Study : "Polyculture Gap Regeneration in the Moist Deciduous Forests of Uttara Kannada
Dr. S.N. Rai (Karnataka Forest Department)

3.00 PM to
3.15 PM : Tea/Coffee Break

3.15 PM : "Reproductive Biology of Tropical Forest Ecosystems"
Dr. K.N. Ganeshaiah (Univ. of Agricultural Sciences, Bangalore)

28th January 1993 (Thursday)

9.30 AM : "The Social Context of Conservation - I"
Prof. Madhav Gadgil (CES, IISc.)

10.30 AM to
10.45 AM : Tea/Coffee Break

10.45 AM : "The Social Context of Conservation - II"
Prof. Madhav Gadgil

11.45 AM : Panel Discussion :
"Forest and Wildlife Management : The need for professional scientific training"
Panelists : Dr. S.N. Rai (Conservator of Forests [Research], Karnataka Forest Department)
Dr. K. Ullas Karanth

12.45 PM to
2.00 PM : Lunch

2.00 PM : "Translocation of Problem Elephants"
Mr. M.K. Appayya (Chief Conservator of Forests [Wildlife], Karnataka)

3.00 PM : Trip to Bannerghatta National Park

29th January 1993 (Friday)

9.30 AM : "Climate Change and Conservation"
Prof. J. Srinivasan (Centre for Atmospheric Sciences, IISc.)

10.30 AM to
10.45 AM : Tea/Coffee Break

10.45 AM : Case Study : "Conservation Biology of Tigers"
Mr. K. Ullas Karanth (Centre for Wildlife Studies, Mysore)

11.45 AM : "Biotechnology and Conservation"
Prof. Raghavendra Gadagkar

12.45 PM to
2.00 PM : Lunch

2.00 PM : Panel Discussion :
"Need for improvement in working of forest departments"
Chaired by : Mr. A.N. Yellappa Reddy (Conservator of Forests, Western Ghats)

3.00 PM to
3.15 PM : Tea/Coffee Break

3.15 PM : Panel Discussion :
"Career development through improvement and training of skills
Participants

In Mani, G S (ed) 1984
Evolutionary Dynamics of Genetic Diversity
Springer-Verlag, Berlin.

THE PROBLEM

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The maintenance of genetic diversity is probably the most fundamental issue in population genetics. Only one generally accepted way exists for generating diversity - mutation - and there is only one force shaping the overall course of evolution - natural selection. There is no doubt, however, that the picture revealed by study of natural populations is quite incompatible with the suggestion that if most genetic loci are selected the diversity is simply the result of the balance of mutational input and selective elimination. There is far too much polymorphism for this to be true. There is also a great ability to respond in an adaptive manner to new environmental conditions, almost as if a high level of polymorphism is maintained for the purpose of making such responses possible. The central problem is to determine the purposeless combination of factors that brings this situation about. The literature of population genetics has circled round this issue for at least fifty years, and it is perhaps not too frivolous to compare the situation with one which arises in a science fiction novel called the Hitch Hiker's Guide to the Galaxy (Adams 1979). An immensely powerful computer called Deep Thought is set the task of finding the answer to the Ultimate Question of Life, the Universe and Everything. After an enormously long time it comes up with the answer, which turns out to be 42. "I checked it very thoroughly" said the computer, "and that quite definitely is the answer. I think the problem, to be quite honest with you, is that you've never actually known what the question is."

In relation to genetic diversity we now have a fair picture of how much polymorphism there is (the answer is 24 per cent, or thereabouts, for diverse sets of data such as random samples of enzyme loci (Nevo, Chapter 2) or visual shell characters in mollusc species (Clarke et al. 1978)). We also know the levels of heterozygosity and with less certainty, the average number of alleles per polymorphic locus. One of the main ways of trying to determine what this implies has been to ask the question: are the alleles concerned largely under the influence of natural selection or are they neutral?

Anyone who holds that most polymorphisms are maintained by balancing selection would be prepared to refer back to the Darwinian argument that evolution proceeds as a result of natural selection based on a struggle for existence and survival of the fittest. Most selectionist arguments in population genetics, however, are based on formal representations such as

$$\Delta q = \frac{q(1-q)}{k.\bar{w}} . \frac{d\bar{w}}{dq}$$

This approach has yielded a very rich scenario of possibilities to be investigated. It has, nevertheless, an undefined relation, and possibly no relation at all, to the verbal statement of Darwinian natural selection, because it by-passes the fact that the struggle for existence is a struggle, and therefore density-regulated. This issue was discussed in the 1950's (Cain and Sheppard 1956 give references), but with few exceptions such as the work of Roughgarden (1979), it seems to have died of exhaustion rather than to have been properly explored.

The classical selectionist position is that polymorphisms are maintained by balancing selection with constant fitnesses resulting in heterozygote advantage. One might reasonably ask how it came about that so many allele combinations, including multiple alleles, resulted in heterozygote advantage. An answer is available (the Sheppard, Caspari theory, Sheppard, 1975) which suggests that heterozygote advantage arises by modification of phenotypic expression as a result of selection of modifiers. Experimental evidence shows that modification of expression can be achieved over a very few generations (Ford, 1971), and the argument is an extension of Fisher's theory of the evolution of dominance. Yet it is almost impossible to see how either could come about as a result of change in frequency of alleles with modifying effect situated at unlinked loci unless the genome contains a ready supply of selectively neutral genic variability (Ewens, 1979).

To illustrate the bones of the problem, consider the argument in the following terms. A mutant showing incomplete dominance appears in a population where its net effect is advantageous. In order to become established as a polymorphism the advantageous effects of the gene have to become more dominant and the disadvantageous ones more recessive. A second, unlinked locus has a modifying effect on it. The relation between the two may be represented as follows.

				Locus Studied		
	Modifying locus		++	+a	aa	Genotypes
Geno-types	Frequency	Fitness	u^2	$2u(1-u)$	$(1-u)^2$	Frequency
++	q^2	1-t	1-s	1-½s	1	Fitness
+m & mm	$1-q^2$	1	1-s	1	1	

The problem is for the locus studied to move from the fitnesses shown in the top row to those in the second row. This can only occur if the modifier frequency q decreases. Change in q may be described approximately as,

$$\Delta q = -\frac{tq^2(1-q)}{1-tq^2} - \frac{su(1-u)q^2(1-q)}{1-suq^2-su^2(1-q^2)}$$

If s and t are small, this means that the term su(1-u) must overcome any selection on the modifier locus, measured by the selective coefficient t, tending to move the frequency in the other direction. The number of generations during which u(1-u) is reasonably large is inversely related to s, so that the total pressure applied to the modifying locus by an advantageous gene can never be large, and if this terminology is realistic, an effect is only conceivable if t is near zero. If heterozygote advantage is to arise an equivalent type of modification has to act on the disadvantageous properties of the gene, too.

One alternative is to consider the situation in which the modifier is closely linked to the locus it modifies (O'Donald and Barrett, 1973, Charlesworth and Charlesworth, 1976), but we then have to ask how commonly close linkage would be expected. Another possibility is that a genetic mechanism exists for modifying dominance, perhaps through the gene regulation system, but that it is not adequately represented by the type of formulation outlined above, being much more efficient. O'Donald (1968) obtained modification of dominance in a computer simulation by representing the modifying agency as genetic variance in the expression of fitness i.e. by using the methods of quantitative genetics. We know too little about gene regulation in higher organisms to chose between these types of representation. They illustrate the general problem of dealing with fitness conferred by interacting loci, using the existing analytical methods and the assumptions on which they are based.

Quantitative genetics is certainly seen by selectionists as part of their own programme. Genetic variability is maintained by stabilizing selection acting on the phenotype, and since selection is stabilizing for much of the time, variability is available to allow appreciable and rapid response to directional selection when it occurs. The formulation of the models of genetic systems giving rise to the phenotypes, however, suggests that to a large extent there is interchangeability between alleles, so that different sets may produce the same phenotype. In other words, they are selectively neutral.

If evolution of heterozygote advantage raises difficulties it is worth investigating the possibility that heterozygote advantage would arise by chance if fitnesses were assigned to genotypes at random. Depending on the model the probability of chance occurrence may be quite high (e.g. Avery, 1977). One simple formulation of the problem could run as follows. Starting as in Fisher's demonstration of the importance of mutants of small effect, we may ask what the probable consequences are of a rare mutation when it arises in a new environment. The mutant has an effect which is random with respect to the environment. If we compare the mutant homozygote with the "wild type" homozygote the probability distribution of its relative fitness is likely to be normally distributed. The chance that a given mutant is advantageous is calculable if we know the mean for such mutants and the standard deviation of the distribution. Now, the heterozygote is functionally related to the homozygotes, so that it must have a fitness which is on average related in some way to that of the homozygote. Suppose that x_1 and x_2 are the selective coefficients of the homozygote and the heterozygote, and that m_1 and m_2 are the means for all such homozygotes and heterozygotes. Because the heterozygote has an allele performing each of the alternative functions controlled by the locus, it is reasonable to suggest that $m_2 = \frac{1}{2}m_1$ and that $s_2 = \frac{1}{2}s_1$, where s_i are the respective standard deviations. For stable polymorphism to arise by chance it is necessary that $x_2 < x_1$ and $x_2 < 0$. A more restricting but simpler condition is that $x_2 < 0 < x_1$. We therefore need to know the probability that this will occur, which is given by the product $\int_0^{+\infty} y_{x_1}\,dx \int_{-\infty}^{0} y_{x_2}\,dx$, the y's being the respective probability distributions. If mutants are on average neutral, although individual fitnesses may be widely distributed about neutrality, then so long as the probability distributions are symmetrical the chance of heterozygote advantage at any locus is ¼.

If the average fitness is not zero then the answer depends on the values given to the s_i. It would be reasonable to suggest that, from the

Poisson distribution, $s_1 = \sqrt{m_1}$, so that

$$y_1 = \frac{1}{\sqrt{2\pi m_1}} \exp[\frac{-(x_1-m_1)}{2m_1}]$$

$$y_2 = \frac{1}{\sqrt{\frac{1}{2}\pi m_1}} \exp[\frac{-(2x_2-m_1)}{m_1}]$$

On these assumptions we may guess at the probability that a particular mutant will arrive by chance at a state of heterozygote advantage. This probability is quite high even when mutants are on average disadvanta- geous; with a disadvantage of 20 per cent there is still a chance of about 22 per cent that the mutant will form a polymorphism (Figure 1).

These assumptions are unrealistic, however, in several respects. In the first place they assume no correlation between the fitnesses of the heterozygote and the homozygote. With complete correlation heterozygote advantage would be impossible. Curves indicating the probability when there is partial correlation are shown in Figure 1, obtained by compar- ing the circular distribution of y_1 and y_2 when $r = 0$ with elliptical distributions in which the axes are $1+r$ and $1-r$. With a correlation in fitness between genotypes of about 0 3 and with an average disadvantage of new mutants of as much as 20 per cent there is still a 12 per cent probability that heterozygote advantage will arise by chance This type of argument would not, however, account for the fact that the majority of rare recurrent mutations affecting the phenotype are re- cessive.

A different selectionist position holds that fitnesses are not constant but are frequency-dependent, and that stable equilibria arise from the frequency dependence. There is an increasing amount of evidence for frequency dependence (Clarke, 1979) whereas there is an embarrassing shortage of examples of heterozygote advantage. Frequency dependent selection is capable of maintaining diversity when applied to phenotypes controlled by dominant alleles and in haploid and inbreeding species. With respect to genetic load there is a noteworthy difference between frequency-dependent and frequency-independent selection. Genetic load is a concomitant of polymorphism in frequency-independent systems as they are usually represented, and it becomes the more weighty the more poly- morphisms are present. As frequency-dependent systems are represented,

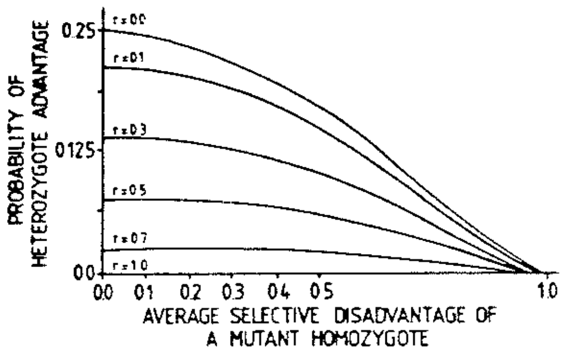

Figure 1. The probability that heterozygote advantage will arise by chance in a large population, given the parameters discussed in the text. It is intended to show that the probability is not necessarily negligible even when new mutations are assumed on average to be disadvantageous.

Table 1. Methods by which Polymorphism may be Maintained

Average level of selection	Environment	
	Spatially homogeneous	Spatially heterogeneous
$S < 1/2N$	(a) mutation balance	(h) mutation/migration balanced with selection
"neutralist"	(b) mutation, selection balance	
$S >> 1/2N$	(c) selective balance (d) genotype frequency dependent selection (e) cyclic selection (f) sex, self incompatibility meiotic drive and other systems	(i) selection, migration balance of various kinds
"selectionist"	(g) advantage to heteromeric molecules	

On the left are systems which do not require spatial heterogencity in the environment, on the right those which do. If the average level of selective difference is low then categories (a), (b) or (h) are the most important. For selective differences which are large category (i) is favoured by many modern workers. There is no evidence favouring (g) as a general mechanism maintaining polymorphism. Selective balance (c) may arise through adjustment of gene expression. If this is achieved by selection of alleles at other polymorphic loci then categories (a), (b) or (h) are implicated to maintain the variation at the modifying loci. (modified from Bishop and Cook, 1981.)

the load disappears at equilibrium. Nevertheless, concentration on the distinction between the two types of selection does not have as much heuristic value as these considerations seem to suggest.

Within the selectionist domain one of the important questions is whether or not the polymorphisms usually require environmental heterogeneity for their maintenance (Table 1). Heterozygote advantage can arise within a single habitat as a result of a balance of different types of selection acting on the homozygotes at some stage in the life cycle. Frequency-dependent selection (e.g. on a prey species as a result of predator behaviour) may do the same, and there are useful distinctions to be made between the two processes. A third class of models to be investigated involves selection acting in different directions on genotypes in different habitats, with movement between them. These models always require a limitation of the numbers of individuals of one morph which a segment of the environment may contain. This may be formulated as frequency-dependence. Often, but not necessarily, they result in net heterozygote advantage as well. Whether selection is frequency-dependent or independent is not as important as whether or not polymorphism depends on a varied environment.

With regard to the question of load, models of frequency-dependent selection predict only the load generated as a result of drift from the equilibrium frequency, whereas for frequency-independent selection there is also an appreciable load imposed at equilibrium. On average, this is half the average selective coefficient per locus. Ecological reality suggests, however, that most frequency-dependent selection is likely to be accompanied by some sort of load factor at equilibrium. Polymorphism resulting from frequency-dependent predation depends on the occurrence of predation, and that is not likely to disappear because the equilibrium frequency has been reached. If the selection is based on favoured niches then the load will arise as a consequence of imperfect ability to locate the favoured niche. The difference between the two types of selection in this respect is likely to be less great than it appears at first sight.

Does the load matter? The neutralist school would claim that it does, so that a scenario in which most polymorphic loci are subject to substantial selection is untenable. A variety of arguments have been put forward, however, to suggest that this is not so (discussed by Wallace, 1970, Wills, 1981). These involve truncation selection models, in which loci are selected in groups rather than individually, or "soft" selection models involving density-dependent modulation of the selection applied. The favoured phenotypes may be characterized by possession of particular genes, or gene combinations, or by a high average heterozygosity, and they may be subject to intraspecific competition. The supposed connectedness of phenotype to genotype is relaxed, as it is in quantitative models.

According to the neutralist position evolution takes place via selection on the phenotype. Because of the loose connectedness between phenotype and genotype this leaves a large number of mutations out of the selective net and functionally equivalent to each other. Mutations are effectively neutral to the product if the selective coefficient and the population size is less than 0.5. The selected part of the genome will be largely monomorphic; by picking on the polymorphic sector we are electing to study neutral mutations in a process of random drift.

A number of predictions follow, made possible because the mathematics of neutral systems is simple compared with that involving selection. The average rate of allele substitution should be constant in time. Comparing mutant with mutant, the rate of substitution should be inversely related to the functional constraints on the molecule. Thus, synonymous codons should be substituted at a higher rate than non-synonymous ones, mutations in introns at a higher rate than those in coding parts of the gene. The expected distributions of heterozygosity, allele frequency etc. are predictable as functions of mutation rate and population size.

Proponents of the neutralist position have emphasised its predictive power. It is claimed to be testable, and susceptible to refutation, where selectionist theories fail to make quantitative predictions (Kimura, 1979).

The fit to data has been tested. A number of predictions have been supported. Base substitution does appear to be higher in the third position (Brown et al. 1982). The expected relation between average heterozygosity and the variance in heterozygosity is obtained (Fuerst et al. 1977). Others fail the test. For example, the increase in heterozygosity with increase in population size does not follow the expected trend. Some enzyme loci which might have been expected to have neutral alleles have been shown experimentally to be subject to selection, most notable the alcohol dehydrogenase systems (e.g. Clarke, 1979, Kreitman, 1983). A large category produce results open to a variety of interpretations. The difference in frequency of silent-base and coding-base substitutions may be taken to show how important selective constraints on bases 1 and 2 actually are, or the silent bases may be subject to variable selection. The supposed constancy of amino-acid substitution rate may be disputed (e.g. Fitch 1976). Differences in frequency distributions between groups of organisms may indicate the effect of ecological factors on the loci concerned (Nevo, 1978 and Chapter 2). The neutralist model has not emerged unscathed from the testing process. It is necessary to postulate weakly deleterious mutations in quantities which, because of the definition of effective neutrality, are functions of population size. Worse, from the point of view of distinguishing it from weak selectionist theories, it is necessary to postulate population bottlenecks which have altered gene distributions at some unstudied time in the past.

These considerations suggest that the framework for discussion needs to be reassessed. The question why there is so much genetic diversity is a general one, and any answer will have to be general too. It is likely to come from examination of large data sets, predictions from computer simulations etc., and not from detailed case histories taken species by species. That point was realized at an early stage by the neutralists. The difficulty with the stepwise approach is its assymetry; a demonstration of selection shows that under some circumstances the locus is not neutral but failure to demonstrate selection does not imply neutrality. On the other hand, a general model may predict neutrality. An example is the case of the evolution of dominance, where the assumption that modifiers are unlinked polymorphic loci sets an upper limit to the primary selection which can act on them.

The approach should always be ecological genetic, however, in the sense that the investigator should always pay attention to how the environment shapes the phenotype. When this is done it is seen that selection may generally be expected to be density regulated. When environmental conditions are ameliorated selection is relaxed, and variant forms which previously were selected become functionally equivalent. Population size increases, and selection will again come into action. All alleles have the same status in this view, fluctuating from neutrality to selective constraint depending on environmental conditions and on gene combinations at other loci. The difference between selected and neutral genes is one of degree, and few mutants are likely to escape selection indefinitely.

The distinction between frequency-dependent and frequency-independent selection also becomes blurred, since most fitness values are to some degree density or frequency-dependent. Similarly, the problem of genetic load disappears. Species survive, flourish or fail in an ecological realm, and estimates of genetic load do no more than record how their genotypes equip them to do so.

Finally, we arrive at a rather uncomfortable conclusion. Many of the difficulties seem to result from trying to extract explicit solutions from the formal representations of population genetics. From the start it has been unclear what relation the representation of mean fitness has to real ecology. It is also unclear how one generalizes from single locus to multilocus systems, and whether the algebra of gene interaction is a reasonable way of describing genome organization. Representations such as those used above have only a limited value. They may show what is possible but cannot be used to test what is probable. For that, a larger number of parameters have to be considered together. The neutralist school avoided the problems by simplifying the algebra to the point where solutions can be obtained. The models then become unrealistic.

What are now required are simulations of evolving populations which are sufficiently complex to have some hope of providing insights about the real world. These must certainly include selection and finite, fluctuating population size. It will then be possible to match the predictions of the model to real data and to make critical comparisons between the various hypotheses. We would see whether the results obtained by the neutralists are model-dependent, or whether they would arise in selectionist models as well, and the robustness of the results under various sets of assumptions could be compared. The simulation approach also allows the problem of maintenance of diversity to be extended from the level of genetic polymorphism to that of the coexistence of interacting species. The result will be a much more comprehensive representation of evolution than those which we use at present.

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Ed K K N Nair K V Bhat J K Sharma &
K Swarupanandan Kerala Forest Research Institute
Peechi Kerala India

GENETIC DIVERSITY AND EVOLUTION

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ABSTRACT

Estimation of the amount of genetic variability in natural populations of living organisms is of such great interest that sharply divided opinion on the outcome of such estimation existed even before any reliable method of estimation was available The biochemical technique of enzyme electrophoresis has revealed an unexpectedly high level of genetic variability in a variety of organisms This technique suggests that organisms may be heterozygous for 6 to 15% of their loci and 15 to 50% of the loci may be polymorphic in any population The more recent technique of DNA restriction fragment length polymorphism (RFLP) has confirmed such high levels of genetic variability The debate now concerns, how such a high level of genetic variability is maintained The nature of this debate is bound to have profound implications both for evolution and for conservation Besides, recent discoveries in eukaryote genetics are likely to upset many of our traditional views about the genetics of evolution, and hence about its relevance for conservation

INTRODUCTION

The need for conservation

Our times have changed dramatically Today, no one dares to ask why we should conserve life forms on earth This may be more often due to fear of being ridiculed for asking an extremely unfashionable question rather than due to a clear understanding of the reasons behind the need for conservation The earth has been and continues to be a storehouse of a fantastic amount of biological diversity At least, a million and a half of living organisms have been catalogued and named The estimated number of species of living organisms has been increasing by leaps and bounds Not long ago, it was believed that the total number of species may be of the order of 5 to 10 million But recent studies of beetles in the canopies of tropical rainforests suggest that there may be as many as 30 million species of insects (Erwing, 1982, 1983; Stork, 1988). Even if we accept an estimate of about 30 million for the total number of species of living organisms, it is still only a fraction of the number of species which have gone extinct during the 3.5 billion years since life originated on this planet True, there are arguments to show that there has been a tremendous spate of extinctions in recent times and the trend is likely to continue But one may argue that there have been such spates of mass extinctions from time to time and there is nothing unusual about the present one.

There are however at least two compelling arguments in favour of conservation One is that the quality of human life and perhaps even our survival may depend on it The second, scientifically more interesting argument, is that we may be able to prevent at least some of the extinctions Michael Soul (1987a), has said that 'presumably, glacial and inter-glacial humans could have prevented the Pleistocene extinctions if they had our values, our knowledge of genetics, ecology, biogeography and our level of technology' This the author believes, is a sufficiently challenging argument to appeal even to someone who is completely unconvinced of the need for conservation of obscure forms of life

The need for knowledge of genetics and evolution

It is an undeniable fact that most cases of conservation require money political decisions and a certain amount of social work rather than a knowledge of genetics and evolution Nevertheless, there are at least a few species whose conservation may be aided by an application of the principles of genetics and evolution Species of carnivores as the cheetah (O'Brien *et al* , 1982) primates such as the Golden Lion Tamarin (Kleimann *et al.*, 1982), birds such as the California condor (Stewart, 1978; Newton and Chancellor, 1985) and the Hawaiian goose (Stewart, 1978) can be mentioned in this context where there is sufficient interest in saving these species and there are several programmes for their conservation including attempts to breed them in captivity and release them in the wild But, we may nevertheless be fighting a losing battle The processes of speciation and extinction are undoubtedly governed by genetic, demographic and evolutionary principles We may not yet have understood or discovered all of these principles but there is good reason to suspect that they exist One may, therefore, argue that conservation biology, the science of discovering and applying the principles of genetics and evolution in conservation efforts, should be vigorously pursued It is also true, however, that sometimes a species dwindles to such few numbers that we may be unable to apply the required biological principles These predicaments may be expressed as the following two conundrums of conservation biology:

If all is well, you often do not need the principles of genetics and evolution

If all is not well, you often cannot use the principles of genetics and evolution

In spite of this, there is room to believe that there are at least a few cases which are at neither extreme, so that the principles of genetics and evolution may help

GENETIC VARIABILITY IN NATURAL POPULATIONS

Definition of the problem

Nothing in biology makes sense except in the light of evolution, and evolution is brought about either by the force of natural selection or by random changes, the latter referred to as genetic drift Either way, genetic variability in natural populations is the raw material for evolution In Darwin's time, the nature of this variation was unknown But very early in this century, it was realized that alternative forms of genes caused by mutations are the source of genetic variability It is obvious, therefore, that any understanding of evolution requires a knowledge of the extent of genetic variability in natural populations

The struggle to measure variation

It turns out however, that genetic variation in natural populations is not easy to measure Nearly all of classical genetics depended on the recognition and study of mutants that manifested themselves as morphological variants These mutants were occasionally of spontaneous origin but were mostly induced by various mutagenic agents. Such mutants can hardly be expected to reflect the extent of natural genetic variation Besides, these mutants only become recognizable when they lead to sufficiently strong effects But, the stuff of evolution must be made of all those subtle variations which leave little or no trace in the external morphology of an organism This is the epistemological paradox of Lewontin (1974) that 'what we can measure is by definition uninteresting and what we are interested in is by definition unmeasurable'.

The 'Classical' and 'Balance' hypotheses

Long before there emerged an ability to determine the extent of genetic variability in natural populations, there were two diametrically opposed schools of thought about the outcome of such measurements The author strongly recommends a penetrating discussion on this issue by Lewontin (1974), who has argued that 'it is a common myth of science that scientists collect evidence on some issue and then by logic and intuition form what seems to them the most reasonable interpretation of the facts'. Instead, 'long before there is any direct evidence, scientific workers have brought to the issue deep-seated prejudices ...', so that 'schools of thought about unresolved problems do not derive from idiosyncratic intuitions, but from deep ideological biases, reflecting social and intellectual world views'.

According to the 'Classical' hypothesis which was largely due to Muller, two randomly chosen individuals from a population would be expected to be nearly identical at almost all their genetic loci, because so called *wild type* alleles would be expected to have gone to fixation at most loci One of them might occasionally have a mutant allele in place of one of its *wild type* alleles The mutant alleles are expected to be so rare that both the individuals are unlikely to have the same mutant allele. For the same reason, it would be rare to find an individual who would be homozygous for the mutant allele Mutant alleles are expected to arise by the rare phenomenon of mutation and are expected to be eliminated from the population because most mutant alleles are deleterious Such rare mutant alleles that are better than the *wild type* are expected to get fixed in the population, but then they would be called *wild types* In other words, most individuals are expected to be homozygous for the *wild type* allele at most of their loci and most loci are expected to be monomorphic. The concept of genetic load that concerned Muller so much and which refers to those deleterious mutant alleles that have not yet been eliminated from the population, can be traced to this 'classical' view.

The 'Balance' hypothesis which is largely credited to Th. Dobzhansky (1955) makes a very different prediction about two randomly chosen individuals from a population. It expects that a number of different alleles exist for each locus in the population so that for most loci, the two individuals are expected to have different alleles Even within the same individual, the two chromosomes may often have different alleles In other words, there is no such thing as a *wild type*. Many, if not most loci, are expected to be polymorphic and any individual is expected to be heterozygous at a substantial proportion of its loci Lewontin (1974) sees this 'Balance' hypothesis of people such as Th. Dobzhansky and E. B. Ford as reflecting the optimistic world view of natural historians that evolution is 'essentially progressive' and that it 'leads to increased harmony between living systems and the conditions of their existence'.

The electrophoretic revolution

The pioneering studies of Lewontin (Hubby and Lewontin, 1966; Lewontin and Hubby, 1966) and of Harris (1966) which used the technique of electrophoretic detection of enzyme variants called *isoenzymes* or *isozymes* have, for the first time, made it possible to make reasonable estimates of the extent of genetic variability in natural populations Many genes code for protein products and many proteins are enzymes that reside in the cytoplasm of the cell and contribute to one or more of the myriad steps in metabolism Proteins are polymers of amino acids which in turn are complex organic molecules that have a net charge in solution Although the three dimensional structure of a protein is complex and may bury many of the amino acids, the net charge of a protein molecule is usually a function of its amino acid composition and sequence Mutations, which are changes in the nucleotide sequences of DNA, often lead to a change in the amino acid sequence of the resultant protein This usually results in a change in the net charge of the protein molecule Enzymes different from each other by a single mutation can often be discriminated because of their charge differences resulting in different mobilities in an electrical field It is a well established technique today to remove enzymes from the cells, transfer them to a neutral matrix such as starch or polyacrylamide, separate them by passing electric current and visualize them by various staining procedures As this relatively simple technique has become available, hundreds of individuals belonging to a number of species have been surveyed for variations at a variety of enzyme loci Although all genes do not code for enzymes, and all mutations do not lead to detectable differences in the net charge of enzymes, this technique gives an approximate estimate of the genetic variability in natural populations

Most modern studies compute two quantities namely, *polymorphism* and *heterozygosity* from such electrophoretic data *Polymorphism* is defined as the proportion of polymorphic loci in any population of a species A polymorphic locus is usually defined as one in which the most common allele has a frequency no greater than 0 95 *Heterozygosity* is defined as the average frequency of heterozygous individuals per locus in a population which is equivalent to the average frequency of heterozygous loci per individual A recent survey (Ayala, 1982) indicates that 142 species have been studied and some 15 to 28 loci have been screened for each group of organisms such as fishes and amphibians The average polymorphism ranges from 0.145 for birds to 0.529 for *Drosophila* In general, the average polymorphism for invertebrates is 0 469, for vertebrates it is 0.247 and the plants have a value of 0 264 The average heterozygosity varies from 0.033 for self-pollinating plants to 0 151 for insects other than *Drosophila* and wasps In general, invertebrates have a heterozygosity of 0 134 and vertebrates have a heterozygosity of 0.060 while it is 0 046 for plants These results mean that 25 to 50% of the loci may be polymorphic and that individuals may be heterozygous at as many as 5 to 13% of their loci. This is a very high level of genetic variability indeed! Not only do these results demolish the concept of the *wild type* allele but quite clearly uphold the expectations of the 'Balance' school In recent years, several refinements in these techniques have been made to enable the detection of more subtle changes in the charge of protein molecules These techniques have led to a further increase, albeit a small one, in our estimates of genetic variability in natural populations.

The age of DNA

One problem with the estimates of genetic variability based on electrophoretic separation of proteins is that all DNA does not code for proteins, let alone enzymes. To obtain unbiased estimates of genetic variability, we will clearly have to look at the DNA itself. Techniques to reduced An equally obvious reason for the effective population size to be less than the actual population size is that different age structures of populations result in different number of individuals in the reproducing age class A somewhat less obvious factor that also reduces the effective population size is unequal fecundity of different individuals (Hartl, 1981).

Minimum viable populations

Many people dislike this phrase because it suggests that we can determine with certainty the minimum number of individuals that are required to prevent a population from becoming extinct Nevertheless, this is a useful concept because it allows one to begin to model processes that determine that number Managers of wildlife and game parks will find the phrase less offensive if they realize that the concept is more often used to help in modelling than as a firm recommendation for real life situations

It is useful to classify factors that might lead to the extinction of a population into two categories, namely, systematic factors and chance or stochastic factors Examples of systematic pressures on populations include deforestation, habitat destruction, hunting, etc. The principles of genetics and evolution are often of little use to mitigate such pressures on populations It is the stochastic factors which are more troublesome and which require the principles of genetics and evolution for their understanding and possible mitigation the stochastic factors which may drive populations to extinction, or more generally speaking, change population numbers, may be classified into four subheads (Shaffer, 1981) *Demographic stochasticity* arises from chance events that are inevitable in the survival and reproductive success of small numbers of individuals *Environmental stochasticity* arises from chance variations in environmental factors such as the presence of predators, parasites and diseases *Natural catastrophe* such as flood, fire and drought which may occur at unpredictable times, will also have somewhat unpredictable consequences for population sizes Finally, *Genetic stochasticity* results from changes in gene frequencies due to genetic drift, inbreeding, etc The purpose of the minimum viable population concept is to enable mathematical modelling of these stochastic effects on probabilities of extinction. To suit this purpose, Shaffer (1981) has proposed the following definition: 'A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1,000 years, despite the foreseeable effects of demographic, environmental and genetic stochasticity and natural catas-trophes'. Using such a definition and using all available data on the grizzly bear, Shaffer (1981) has calculated that populations consisting of less than 30 to 70 individuals occupying less than 2,500 to 7,400 km^2 area, have less than 95% chance of surviving even for 100 years The important point here is not to worry about the details of the definition of the minimum viable population because the definition can always be modified to suit particular requirements The important point is that Shaffer and others (Gilpin and Soul, 1986; Soul, 1987b) have been developing the methodology for being able to make such calculations based on available data

Optimum genetic relatedness to mates

It is widely recognized that *inbreeding*, defined as mating between close genetic relatives, has harmful consequences and is the main reason why small populations fail to survive for long The idea of the deleterious effects of inbreeding is now widely recognized because it

estimate genetic variability from restriction fragment length polymorphism (RFLP) data are being rapidly developed (Jefferys 1979; Nei and L [illegible] 197[illegible]. The methodology here is somewhat different. Restriction endonucleases are e[illegible] that [illegible] DNA at specific sites leading to a specific number of fragments of predicta[illegible] ze. Ch[illegible] in the sequence of DNA may abolish or create sites of recognition for th[illegible] alters the number and size of fragments that will be obtained u[illegible] A with restriction endonucleases. For example, Jeffery (1979) stud[illegible] ing to the globin genes of man in 60 unrelated individuals. An ex[illegible] 4 restriction sites corresponding to about 300 base pairs revealed th[illegible] that roughly one in a hundred base pairs is polymorphic. Studi[illegible] likely to further increase our estimates of the levels of genetic v[illegible] ons.

What maintains genetic variability?

Far from wondering where the genetic variab[illegible] to act upon, the electrophoretic revolution and the age of DN[illegible] other extreme of wondering as to why there is so much vari[illegible] what mutually exclusive hypotheses that attempt to explain the [illegible] variability. One is the theory of natural selection which claims th[illegible] is maintained because its bearers are fitter than those which c[illegible] approximately the reasoning of the 'Balance' school which [illegible] d on particular combinations of alleles.

Not surprisingly, many people find it har[illegible] ness difference associated with each variant. The so called ne[illegible] poses that most alleles are *neutral* and make no difference to [illegible] Mathematical models developed by neutralists show conv[illegible] alleles can be maintained in natural populations due to rand[illegible] and associated stochastic processes. The *selectionist - neutralist* controv[illegible] a number of years and neither has been successfully discarded (May[illegible] Clearly both processes are involved in different situations but this is no[illegible] biology. The implications for conservation biology of gen[illegible] ed by natural selection is quite different from the implicatio[illegible] ained by drift. Failure to attribute genetic variability unambigu[illegible] at least on a case by case basis, may turn out to be a [illegible] applying the principles of genetics and evolution to problem[illegible]

APPLIED GENETICS AND [illegible]
IN CONSERVATION — SOM[illegible]

Effective population size

It should be clear to any one that the fate of a p[illegible] e number of individuals comprising the population. Ho[illegible] als in the population is not what usually matters. What [illegible] *ation size* which may be equal to but it is often substanti[illegible] n size. A simple example will serve to show why the eff[illegible] h smaller than the actual population size. If the sex ratio [illegible] one sex, the actual number of individuals contributing [illegible] stantially has an apparently simple explanation Many harmful genes are recessive and thus go undetected in the heterozygous state But inbreeding is expected to result in homozygosity and thus lead to expression of these deleterious genes That inbreeding is harmful, has become something of a dogma Perhaps, this dogma is by and large justified. There is clear evidence that inbreeding leads to deleterious consequences in a variety of species (Ralls *et al*, 1979; Ralls and Ballou 1983) It is also well known that many species of birds and mammals avoid inbreeding (Ralls *et al*, 1986) Apart from inbreeding leading to homozygosity of deleterious alleles there is much evidence that heterozygosity *per se* increases the fitness of organisms (Allendorf and Leary, 1986; Ledig 1986). The problems with such generalizations, however, is that there are significant exceptions where inbreeding and/or homozygosity are prevalent Genetic polymorphism is virtually absent in many selfing plants, a population of elephant seal, a species of gopher, some lizards and an isolated snail population Nevertheless these populations are doing very well (Frankel and Soul, 1981). Ralls *et al.* (1986) concluded their review of inbreeding in birds and mammals with a statement that 'it is unjustified to conclude that close inbreeding non-incestuous inbreeding optimal inbreeding or, indeed, optimal outbreeding prevails in natural populations of birds or mammals'. The standard explanation for such results in animals and man is that inbreeding for many generations has already eliminated most deleterious genes so that further inbreeding can not lead to homozygosity of deleterious genes But most authors who make this suggestion are quick to add that such populations have no evolutionary potential and that they are doomed to extinction It should be noted, however, that this last statement is a matter of belief and can not easily be scientifically tested.

The problems associated with drawing general conclusions regarding inbreeding depression are illustrated by recent studies of human populations in Southern India The reference here is to studies being conducted at the Indian Institute of Science, Bangalore, by Appaji Rao and his colleagues Their major findings are: i. inbreeding has been and continues to be fairly high in South Indian populations, ii yet, there is no evidence that deleterious genes have been eliminated from these populations and iii nevertheless, there is little evidence of inbreeding depression because there are no significant consanguinity-related differences in the survival of new-born infants (Devi and Rao, 1981; Devi *et al.*, 1982; Bittles *et al.*, 1985; Bittles *et al*, 1987; Devi *et al.*, 1987; Rao *et al*, 1988)

If inbreeding and the consequent homozygosity is very often detrimental to the survival of a population, does it follow then that mates should be as distantly related as possible? Apparently, the answer to this is negative When individuals who are very unrelated to each other mate, one sees the phenomenon of outbreeding depression (Templeton, 1986) The reason usually attributed to this is that it breaks down certain combinations of genes which have evolved over long periods One may be tempted to conclude from this that there is an optimum genetic distance for selection of potential mates. Although, this idea has some followers (Bateson, 1983) it is unlikely that there exists any such universally optimum mating distance The consequences of inbreeding or outbreeding will almost certainly vary from species to species and even from population to population. There is likely to be no substitute therefore for basic demographic and genetic data on individual species and populations in need of conservation efforts

APPLIED GENETICS AND EVOLUTIONARY BIOLOGY IN CONSERVATION – CASE STUDIES

The Cheetah

The cheetah has been the subject of extensive studies by O'Brien (1985, 1987b) and his colleagues using both traditional and modern techniques. Today there are only two surviving natural populations of the cheetah one in South Africa and the other in East Africa. Both these populations appear to be extremely genetically impoverished and reproductively impaired. Seventy percent of the sperms produced by an adult male are abnormal, a condition that would certainly lead to the verdict 'infertile' in humans and other animals. The total sperm count itself is very low: it is about 10% of what is seen in domestic cats. There is also evidence of developmental abnormalities: the cheetah skulls show significantly more asymmetry than those of other species. There is also significantly more infant mortality in captive cheetah populations compared to captive population of other cats or mammals. Two techniques show that the cheetah is genetically impoverished. The most polymorphic locus in vertebrates is the major histocompatibility complex which is responsible for rejection of tissue grafts between any two individuals except identical twins. In cheetah however, skin grafts were accepted even from completely unrelated individuals (O'Brien *et al.*, 1985). Electrophoretic studies have led to estimates of polymorphism ranging from 0.02 to 0.04 and heterozygosity ranging from 0.0004 to 0.014. This makes the cheetah the least genetically varied species studied in the wild. From these studies O'Brien *et al.* (1987b) concluded that cheetah experienced an extreme bottleneck perhaps about 10,000 years ago and the East African population has gone through a second bottleneck within the last century.

This and other evidences can be thought of as being consistent with the idea that small populations undergo inbreeding which in turn leads to genetic impoverishment reproductive impairment and finally extinction. Such data are also being used to recommend outbreeding wherever possible for captive populations. For instance, it has been suggested that captive individuals derived from the South African population must be crossbred with those from the East African population. It is not clear whether such recommendations will always help. How do we know, for example, that some particular combination of genes has not been fixed in the East African population which is necessary for its survival? It should be remembered that the East African population of cheetah has survived in spite of being genetically impoverished for 10,000 years. In other words the question is how do we avoid the pitfalls of inbreeding depression on the one hand and that of outbreeding depression on the other? There can be no general solution to this problem and only detailed studies of individual species may provide some hints.

The Asiatic lion

O'Brien and his colleagues (O'Brien *et al.*, 1987a) have also conducted a similar study with the Asiatic lion which exists in the wild as a single population of about 250 individuals in the Gir Sanctuary in India. Like the cheetah and in contrast to African lion populations, the Gir population also appears to be genetically impoverished. All 46 genetic loci studied electrophoretically were found to be monomorphic ($p = 0.0$)! Like the cheetah, the Gir lions also show a high proportion of abnormal spermatozoa. There is independent evidence that the Gir population of lions has also undergone one or more bottlenecks in the recent past.

GENETICS IS FULL OF SURPRISES

The theme of this presentation has been that the principles of genetics and evolution can at least sometimes, be usefully applied to problems of conservation It would be unfair to make this statement without pointing out the many pitfalls involved in applying the principles of genetics and evolution to problems of conservation On the one hand attempts to develop appropriate methodology to apply even the most elementary principles of genetics and evolutionary biology are still in their infancy Most population genetic models require extremely simplifying assumptions and are usually dubbed as 'one-locus two-allele models On the other hand our knowledge of genetics has been growing by leaps and bounds throwing up the most unexpected surprises The following are some such important surprises that have come up as a result of recent research in genetics and molecular biology It must be emphasized that we are very far indeed from even understanding the implications of these new findings for conservation biology Perhaps some of these findings will make no difference to the way in which genetic principles are applied in conservation biology On the other hand there are at least some which bound to have profound implications for conservation biology But these are decisions which can only be made after much more thought is given to this topic Therefore, the discussion is on the most spectacular findings of modern genetics regardless of whether it appears today that they will alter the way we apply genetic principles to conservation biology Listed below are eight statements which had more or less become dogmas in genetics and which are being questioned today (Alberts *et al*. 1983; Lewin 1985; Rothwell, 1988)

Double stranded DNA is the genetic material

Double stranded DNA is indeed the genetic material in most living organisms But there are at least three kinds of exceptions to this that are known today Many bacterial viruses such as ΦX174 have single stranded DNA as their genetic material Many viruses have RNA (both double and single stranded) as their genetic material Most surprisingly of all, the so called slow viruses appear to have no nucleic acids at all in them!

Information flows from DNA to RNA to protein

This is often known as the 'central dogma of molecular biology' which was unchallenged until about 1969, when Howard M Temin discovered that information can also flow back from RNA to DNA This pheno-menon known as reverse transcription is now well established Once in few years we hear of a claim that information flow from protein to nucleic acids has been demonstrated So far these have all been false alarms but one gets the feeling that it may not be long before some form of information transfer from protein to nucleic acids is discovered.

The genetic code is universal

Genes code for the synthesis of protein by means of the genetic code which consists of triplets of nucleotides which are called 'codons' and which specify the sequence of amino acids in protein molecules The 'meaning' of each of the possible 64 codons had been deciphered in a number of organisms during the late 1960s. Much was made of the fact that the code was universal – each three-letter codon conveyed the same message in all organisms Among other things, the universality of the genetic code was [illegible] as evidence

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The one-gene one-enzyme hypothesis

It was believed for a long time that DNA is organized into discrete non-overlapping units called genes, each of which codes for a separate protein molecule It was soon discovered however, that some stretches of DNA did not code for either a protein or for a RNA molecule, but functioned in a structural fashion by binding to regulatory molecules This by itself was not a big surprise What is surprising, however, is that many genes especially in higher organisms, are not discrete non-overlapping units. Many genes have one or more stretches of 'unnecessary' sequences within them which are called 'introns'. In other words, different portions of a gene are located in several different places and have to be brought together before a protein molecule can be produced

There is an even more profound violation of what was expected from the one-gene one-enzyme hypothesis It was expected that the amount of DNA in an organism would be approximately equal to the amount required to code for the various proteins made by that organism. This seems to be true for a bacterium such as *Escherichia coli* The genetic material of *E coli* consists of a single mole-cule of DNA, 4 2 x 10^6 nucleotides long This much DNA can code for 1.4 x 10^6 amino acids Since an average protein in bacteria is about 350 amino acids long, the *E coli* DNA can code for about 4,000 different protein molecules There is evidence that *E coli* in fact, has about 4,000 different kinds of proteins, so that it seems to have just the right amount of DNA

If we move away from *E. coli* on either side of the complexity scale, this principle is violated ΦX174s a very simple bacterial virus whose genome consists of a single stranded DNA molecule, 5,400 nucleotides long This can code for 1,800 amino acids. Since the average weight of an amino acid is about 109, the ΦX174 DNA can code for a maximum of 2,00,000 daltons of protein However, this virus is known to produce 10 proteins with a total molecular weight of about 2,50,000 daltons In other words, this virus has less DNA than it needs. This is compensated by having overlapping genes so that some portions of the DNA are parts of two different genes and are read in different reading frames

When we look at organisms more complex than *E. coli*, we see a different kind of violation. The genome of the fruitfully *Drosophila melanogaster* has about 1.65 x 10^8 nucleotide pairs per haploid genome. This can code for 55 x 10^6 amino acids. Even if an average protein in *Drosophila* is 700 amino acids long, this amounts to about 78,000 proteins. However, the maximum number of functional genes (proteins) in *Drosophila melanogaster* is estimated to be about 5,000. The amount of DNA present is therefore in excess of an order of magnitude more than what seems to be required Similarly, the human genome consists of 3 x 10^9 nucleotide pairs per haploids genome. This much DNA can code for a billion amino acids Even if an average protein in man is 2,000 amino acids long, the human DNA can code for 0.5 million proteins. However, the estimated number of functional genes in man is 30,000 to 40,000. Thus, 90% of the genetic material of higher organisms has no known function and is variously labelled as repetitive DNA, satellite DNA, junk DNA and more recently, selfish DNA

DNA is a static blueprint

DNA is the blueprint which carries the master copy of nearly all the information required for the development and functioning of living organisms. It was reasonable to expect that this blueprint would not be tampered with and would remain completely unchanged throughout development and indeed throughout the life of the cell. It turns out, however, that DNA is a dynamic entity with mobile elements and jumping genes constantly moving from one location to the other and bringing about rearrangements in the blueprint itself.

The mitosis-meiosis dichotomy

It has always been believed that no genetic change takes place during mitotic cell division. It is only during meiosis that recombination and such other genetic reshuffling was expected to take place. Recent studies of plant cells in tissue culture have broken this myth. A variety of genetic changes have been detected in plant cells in tissue culture which are undergoing only mitotic cell division. Some of the genetic changes observed include aneuploidy, chromosomal rearrangements, gene introgression, sequence copy number changes, transposable element activation, new point mutations sometimes in the homozygous condition and altered expression of multi-gene families. These changes are labelled as *somaclonal variation* and have been put to much practical use (Larkin *et al.*, 1985; Larkin, 1987). Somaclonal variations in plants have been exploited to obtain increased seedling vigour in lettuce, jointless pedicels in tomato, improved rice protein content, salt tolerance and yield increase in flax, *Pseudomonas* and *Alternaria* resistance in tobacco, *Fusarium* resistance in alfalfa, etc. It is true that some of these more drastic genetic changes may be a response to the artificial conditions of tissue culture. But it is hard to believe that all of these changes are a response to tissue culture. It is reasonable to expect that at least some of these genetic changes also take place during mitotic cell divisions in plants. Genetic variability between parts of a plant such as different branches or leaves is poorly understood. But somaclonal variation seen in tissue culture should prepare us for profound genetic changes from one part of a tree to another.

Levels of natural selection

Most evolutionary arguments made are somewhat vague without precisely specifying the level at which natural selection was expected to act. The controversy over individual *versus* group selection in the last two decades has brought this problem into sharp focus and today, the individual organism rather than some higher level such as the group or the species, is thought to be the unit of natural selection. This has brought the much needed clarity in evolutionary arguments. However, it is only being realized more recently that natural selection can act on units smaller than the individual organism. To some extent, this was expected because, phenomena such as meiotic drive, gene conversion and non-reciprocal recombination have been known for some time. However, the ability of single genes or small stretches of DNA to replicate 'selfishly' at the expense and to the detriment of the organism which harbours them has come as quite a surprise. The most extreme example of such a selfish DNA is the so called paternal sex ratio factors (*psr*), which is transmitted to the zygote through the DNA in the sperms in the parasitic wasp, *Nasonia vitripennis*. Upon entering the zygote, it appears to dissociate itself from the paternal genome and selectively inactivate the rest of the paternal genome so that the zygote becomes haploid and develops into a male. This ensures that the selfish DNA can once again reach a zygote where it can repeat the act Populations carrying this factor thus keep on producing all-male progeny and may eventually go extinct, but laboratory stocks carrying the factor can be maintained (Warren *et al.*, 1981; Nur *et al.*, 1988)

Bottlenecks kill populations?

When a population is reduced to a very small number of individuals, it is said to have gone through a bottleneck. It is widely believed that populations that go through bottlenecks are doomed because inbreeding and other chance factors make them genetically impoverished during the bottleneck Edwin Bryant and his colleagues (Bryant *et al.*, 1986) set out to test this prediction by rearing populations of houseflies starting from 1, 4 and 16 male-female pairs. To everyone's surprise they found that at least in some of their populations, there was more and not less variation in the bottlenecked flies in such physical characters as size and shape of their wings Nearly all theoretical models had predicted the opposite. The simple fact is that nearly all models had assumed variance to be additive simply because it is easy to model mathematically. It appears, therefore, that non-additive variance may be more important and recent modelling efforts with non-additive variance effects come close to explaining Brayant's results To quote Bryant, 'what happened with theoretical analysis of bottlenecks is what often happens with mathematical representations of biology .... as often happens, you go from a simplifying process that gives you an approximate answer to thinking that you have got the answer' (Lewin, 1987). This is perhaps the single greatest danger in applying the principles of genetics and evolution in conservation biology

IMPLICATIONS OF MODERN GENETICS FOR CONSERVATION BIOLOGY

To spell out the implications of all these surprises that modern genetics has thrown up is beyond the scope of this paper. But it is obvious that at least some of these new findings such as the dynamic state of the genome, somaclonal variation, selfish DNA and the increased phenotypic variation resulting from population bottlenecks will have profound consequences for conservation biology. Predictions of the fate of populations and estimations of minimum viable populations are bound to be very significantly affected by such processes. The task of applying the principles of genetics and evolutionary biology to problems of conservation is bound to be long and tedious with few or no shortcuts But conservation biologists will do well to take note of the continuing advances in genetics and molecular biology

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COUNTRY REPORT : INDIA

BIOLOGICAL DIVERSITY AND NATURE CONSERVATION IN INDIA

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INTRODUCTION

India's land area of 3.29 million km^2, extending between 7^0 - 36^0 N and 70^0 - 96^0 E, encompasses a unique diversity of habitats ranging from snow-capped mountains through hot deserts and evergreen forests to coastal mangroves. The earliest evidence of agriculture in the Indian sub-continent is around 6000 BC, and by 2000 BC it had spread to most regions. Because of this intensive human interaction with the land since ancient times, it can be expected that only a fraction of the original landscape would remain unaltered. About 17% of India's land area is under some form of natural or modified vegetation cover. The history of land-use and its consequences for biological diversity in India has numerous lessons for conservation planning in many countries of the Old and New World tropics where a much larger proportion of land is under natural vegetation, but where development is depleting it rapidly during recent times.

Apart from lower plant groups and invertebrates, the plant and animal diversity of India has been relatively well documented. About 15000 species of flowering plants have been described from India. Estimates of other plant taxa include 5000 species of algae, 1600 lichens, 20000 fungi, 2700 bryophytes and 600 pteridophytes (Jain 1984). The animal species described include [illegible]00 insects, 4000 mollusca, 8500 other invertebrates, 1400 fishes, 140 amphibians, 420 reptiles, 1200 birds (but 2100 species and sub-species) and 340 mammals (Zoological Survey of India 1980a). Further exploration of the invertebrate taxa may increase the total to about 150,000 animal species (Gadgil and Meher-Homji 1986). Thus, about 200,000 species of living organisms may be present in the country. There is virtually no information on the rate at which this diversity is being decimated.

The diversity is, of course, not uniformly distributed. Certain habitats such as the evergreen forests of northeastern and peninsular India have far more species than the arid tracts. The different habitats are also protected to varying degrees through nature reserves (national parks NP and wildlife sanctuaries WS). Although there has been no consensus so far on the classification of the biogeographic regions of the country, the following categories are useful for describing the biological diversity: Western Himalaya, Eastern Himalaya - NE

India, Rajasthan - Gujarat, Central Highlands, Gangetic Plains, Deccan Plateau, Western Ghats, Coastal Region and Islands.

1 Western Himalaya

The Indian territory of the great Himalayan mountain chain is especially diverse in topography and vegetation. From the southern foothills at less than 1000 m altitude to cover 8500 m, the vegetation shows a diverse spread, including tropical moist deciduous and evergreen forests, subtropical dry evergreen sclerophyllous and chiprine forests, temperate oak and coniferous forests, subalpine altimontane forests, and alpine scrub, meadows and steppes

The fauna has Palaearctic and Indo-Malayan affinities. The Himalaya have more species of wild sheep than any other mountain range. Those which can be found within Indian territory include the urial and bharal. The goats and goat- antelopes seen here include wild goat, ibex, markhor, Himalayan tahr, serow and goral. Tibetan antelope and Tibetan gazelle may be found seasonally in Ladakh. Other notable mammals include red panda, Himalayan black bear, brown bear, spotted linsang, clouded leopard, snow leopard and the hangul deer which is endemic to Kashmir. The bird families endemic to the Himalaya include broadbills. Some of the rare Himalayan birds are the chir pheasant, Himalayan monal pheasant, Sclater's monal, Blyth's tragopan, Western tragopan and blacknecked crane.

The major conservation areas are Rajaji WS (247 km^2), Corbett NP (521 km^2) and Dudhwa NP (490 km^2) in the moist deciduous belt, Gulmarg (180 km^2), Dachigam NP (141 km^2) and Shikari Devi WS (213 km^2) with temperate forests and valley of flowers (90 km^2) in the alpine meadows. Certain other protected areas extend over a range of habitats - Govind Pasha Vihar WS (320 km^2, sub-tropical to alp. meadow), Kistwar NP (200 km^2, temperate to alpine steppes). Overa-Aru WS (212 km^2, temperate to alpine steppes), Kedarnath WS (478 km^2, temperate to sub-alpine forest) and Hemis High Altitude NP (150 km^2, sub-alpine to alpine steppes). The proposed Nanda Devi Biosphere Reserve would be vital for the conservation of the sub-alpine and alpine region.

2 Eastern Himalaya and NE India

The eastern Himalaya extending over North Bengal, Sikkim, Arunachal Pradesh and Assam, along with the associated hills of the northeastern states is one of the richest regions in biological diversity. The entire range of vegetation types seen in the Western Himalaya, from deciduous forest to alpine steppes is also found here. Because of the higher rainfall and lower latitude, the vegetation is more tropical and floristically more diverse than in the western Himalaya. The floristic richness of the eastern Himalayan region can be realized from the fact that over 50% of species described for the whole of India in certain plant taxa such as orchids (650 out of 1100 species described), bamboos (58 out of 100) and ferns (more than 500 out of 1000) are found here (Rao and Hajra 1986). Chatterjee (1939) made an estimate of 3000 endemic dicot plants in the Himalayan region of which a major proportion would be found in the east. This region is also one of the major centres in the world for the origin of cultivated plants. Wild relatives of banana, mango, citrus, pepper and cucurbits are seen here.

The primate fauna of this region is notably represented by hoolock gibbon (which is India's only ape), golden langur, capped langur and slow loris. The one-horned rhinoceros and thamin deer are endemic, while the largest population of wild buffalo is seen here. The goat-antelope takin is found in restricted numbers at high altitudes. Salim Ali (1977) has listed the species of birds for the eastern Himalaya.

Some important conservation areas are Manas WS (2840 km^2), Kaziranga NP (430 km^2) and Jaldapara WS (116 km^2) for rhinos, Keibul Lamjo NP (40 km^2) for the endemic thamin, and the proposed Namdapha Biosphere Reserve (233 km^2) in Arunachal for the rich subtropical and temperate forest.

3. Rajasthan and Gujarat

The hot arid desert belt in the northwest extends along the border with Pakistan, primarily in the states of Rajasthan, Punjab and Gujarat. Vegetation is mainly shrubby with species of *Calligonum, Prosopis, Salvadora, Capparis* and *Euphorbia*. Diversity is relatively low with only 550 species of flowering plants having been recorded. The vegetation over the interior Aravalli hills and Gir hills is dry deciduous forest.

Characteristic mammals of this region are the antelopes (chinkara four-horned antelope, blackbuck and nilgai), hyaena, wolf and various rodents (Prakash 1986). The wild ass is endemic to the Rann of Kutch, while only 200 Asiatic lions survive in the Gir forests of Gujarat. The Great Indian bustard is a highly endangered bird. The overall bird diversity is high; over 300 species of resident and migratory birds have been recorded in the wetlands of the famous Bharatpur sanctuary in Rajasthan. Forty-three species of reptiles have also been listed for the desert belt.

Major nature reserves in the arid zone are the Desert National Park (c 3000 km^2) in Rajasthan and the Wild Ass Sanctuary in the Rann of Kutch. The Gir Lion NP (1412 km^2) is the last refuge of the Asiatic lion, while Ranthambore NP (392 km^2) and Sarika WS (496 km^2) in the Aravallis are famous tiger reserves. The small Velavadar NP (18 km^2) harbours a large population of blackbuck.

4. Gangetic Plains

The natural vegetation has been depleted over most of the Gangetic plains. The wetlands and rivers have crocodiles (mugger and gharial), small numbers of Gangetic dolphin and over 20 species of fresh water turtles. The plains are also rich in water birds. There are no unique protected areas worth mentioning in this region.

5. Central highlands

The Vindhya and Satpura hills, Chota Nagpur plateau and other associated hills extend over Madhya Pradesh and parts of Maharashtra, Uttar Pradesh, Bihar and Orissa: Vegetation ranges from semi-arid to moist deciduous forest. The deciduous forests are mainly those of sal *Shorea robusta* associated with *Buchanania, Cleistanthus, Toona, Symplocos, Terminalia* and *Adina*. Plant diversity is moderate with 700 to 1000 species of angiosperms recorded within particular vegetation types.

There are no notable endemic mammals in this region. The fauna is largely Indo-Malayan with gaur, elephant, sambar and typically Indian forms such as blackbuck, nilgai and sloth bear. The region has one of the largest concentrations of tigers in the country. Small populations of wild buffalo and the hand-ground race of barasingha also occur here.

Protected areas include Bandavgarh NP (449 km^2), Kanha NP (98 km^2), Simlipal NP (303 km^2), Palamau NP (979 km^2) and Melghat WS (1591 km^2) tiger reserves, Kutru WS (2274 km^2) and Indravati NP (1258 km^2) harbouring wild buffalo, Tadoba NP (117 km^2), Nagzeri WS (136 km^2) and Nawegaon NP (133 km^2).

6. Deccan Plateau

The Deccan plateau lying in the rain shadow of the Western Ghats is a semi-arid region with vegetation consisting largely of dry thorn and deciduous forests, dominated by *Acacia, Anogeissus, Hardwickia* and Albizia. Certain associated hills of the plateau to the east may have patches of moist deciduous forest. The typical climax vegetation of the Deccan has almost completely disappeared. Less than 500 species of angiospherms have been recorded within the vegetation sub-types here.

Fauna is typical of semi-arid tracts. Blackbuck, sambar, gaur (in wetter belts), wolf, hyaena, sloth bear, leopard and tiger are seen. The grizzled giant squirrel survives in the dry forests along the Cauvery river in the Eastern ghats.

Ranebennur WS (119 km^2) protecting blackbuck and a few Great Indian bustards has little natural vegetation. Other major reserves include Nagarjunasagar Tiger Reserve (3568 km^2), Tungabhadra WS (112 km^2).

7. Western Ghats

The Western Ghats and associated hills of the peninsula are second only to NE India in biological diversity. Although the vegetation cover over the ghats in Maharashtra has largely disappeared, a good proportion of the range in Karnataka, Kerala and Tamilnadu is still forested. There are two major vegetation divisions in the Western ghats - a western portion enjoying very high rainfall and covered with evergreen forest, while the eastern belt in the rain shadow consist largely of deciduous forest. The evergreen forests are dominated by *Mesua, Palaquium, Cullenia, Hopea, Dipterocarpus, Persea, Holigarna, Diospyros, Memecylon* and *Syzygium*. The upper reaches of the ghats above 1500 m usually have grassland and stunted montane evergreen forest patches known as *sholas*. The dominant trees in the deciduous forests are *Tectona*, species of *Terminalia, Lagerstroemia* and *Anogeissus*. Typically, the evergreen sub-types contain 1500- 2000 species each, while the deciduous types have 700-1000 species. The Western Ghats as a whole harbour about 4000 angiosperm species from about 200 families (Nair and Daniel 1986). Of the 57 genera and 2100 species endemic to peninsular India (Nayar 1982) most of them are confined to the Western Ghats. The level of endemism is highest in the Agasthyamalai - Ashambu hills at the extreme south. The three most common families are Poaceae (400 species). Leguminosae (320 spp.) and Orchidaceae (250 spp. out of 1000 in India). The region is also rich in pteridophytes (148 spp. in Palani hills alone) and bryophytes.

The fauna is diverse, with many species endemic to this tract. Two primates (Nilgiri langur and lion-tailed monkey) are endemic to the Western Ghats. Other endemics are Nilgiri tahr, Nilgiri marten and Malabar civet, while the only viable population of grizzled giant squirrel is found in the Srivilliputhur hills. The Western Ghats also harbour relatively large population of elephant, gaur, sambar, wild dog, leopard, tiger and sloth bear. About 580 species and sub-species of birds are seen here with 57 endemic forms. A family (Uropeltidae) and 7 genera of reptiles as well as 5 genera of amphibians occur only in the Western Ghats.

The protected area network in the Western Ghats is impressive with most vegetation types being covered. Important reserves are Pushpagiri WS (38 km^2), Silent Valley NP (90 km^2), protecting the wet evergreen forests, Mukurti Peak WS (78 km^2) and Eravikulam NP (97 km^2) in the montane shola-grasslands, Dandeli WS (5729 km^2), Bhadra-Shettihally WS (827 km^2), Wynad WS (344 km^2) and Biligrirangaswamy Temple WS (324 km^2) in the deciduous forests. Other sanctuaries such as Anamalai WS (958 km^2), Periyar Tiger Reserve (777 km^2), Parambikulam WS (270 km^2) and Mundanthurai WS (520 km^2) protect a range of habitats from deciduous to evergreen forest. The

Nilgiri Biosphere Reserve (5520 km^2) comprising some of these existing sanctuaries and Reserve Forests is a pivotal conservation area in the Western Ghats

8 Coastal Region

The Indian coastline from Gujarat to West Bengal is about 5500 km^2 long. Only small fragments of the natural vegetation of the coastal tracts remain today. Remnants of the dry evergreen forest typical of the east cost can be seen in Tamilnadu, mainly in Guindy NP (2.7 km^2) and Point Calimere WS (17 km^2). These sanctuaries are important strong holds of blackbuck. Mangrove vegetation, characteristic of estuarine tracts, is seen at Pichavaram (4 km^2) and a portion of the Sundarbans Tiger Reserve (2585 km^2). The coastal belt is rich in bird fauna. The Rann of Kutch on the west coast is an important breeding ground for flamingoes. Along the east coast, Point Calimere, Pulicat lake and Chilka lake attract large numbers of shore birds. Coral reefs are seen in the Gulf of Kutch and Gul of Mannar (Wafar 1986).

The marine life includes a variety of algae, invertebrates, fishes, reptiles and cetaceans. Among the phytoplanktonn are 55 species of dinoflagellates, 35 diatoms and 100 cynanophytes and other flagellates in the Indian Ocean (Qasim and Kureishy 1986). Many sea turtles nest along the coastal belt. Special mention must be made of the dugong which can be seen in the Gulf of Mannar.

9 Islands

The two major groups of islands are the Laccadives & Minicoy in the Arabian Sea and Andaman & Nicobar islands in the Bay of Bengal. In the Andaman & Nicobar islands, the coast and estuarine belt has mangrove vegetation and coral reefs, while the islands themselves possess some of the best preserved evergreen forests of the country. Over 1000 species of flowering plants, including 220 endemics (Thothatthari 1984) including notable endemics such as Narcandom hornbill and Nicobar pigeon have been recorded. Conservation areas in the Andaman & Nicobar islands include Jayawa area NP (721 km^2), Saddle Peak NP (33 km^2), Mount Harriet NP (47 km^2) and a few small islands. The Laccadives & Minicoy islands are important for their coral reefs

10 History of nature conservation

Traditions of nature conservation, maintained through religious beliefs, are ancient in India. Many of these beliefs such as in sacred trees (the peepal

Ficus religiosa), animals (rhesus monkey *Macaca mulatta*) or biological communities (sacred groves and ponds) still persist. In fact, sacred groves still exist in regions as far apart as Kerala and Sikkim. In certain regions these groves are the only remnants of the original vegetation and, hence, may harbour very rare plant species (Nair and Mohanan 1981).

The edicts of Emperor Ashoka (3rd century BC) protecting a range of living creatures are well known. Kautilya's Arthasastra (c. 300 BC-AD 300) prescribed the elimination of elephants from river valleys which were to be cultivated, but it also urged setting apart forests along the periphery of the kingdom as elephant sanctuaries, where killing of elephants was prohibited.

Since the beginning of the Christian era, there are records of hunting prserves maintained by feudal lords and princes. This approach to conservation continued into 20th century India. The Moghul rulers (16th century), the princes of later periods and the British had their exclusive sanctuaries for sport hunting of big game. This did not, however, mean a demise of a more fundamental people's conservation movement. The sacrifice of the Bishnois of Rajasthan durinng the 17th century in protecting the *khejti (Prosopis cineraria)* trees of their village from being cut by the ruler of Jodhpur (for use as fuel wood in brick kilns meant to supply material for his palace) is well known. Even today they do not allow the uprooting of *Khejti* or the killing of animals such as blackbuck near their villages.

During the mid-19th century, the British organized the Forest Departments in the country. Large tracts of forest were declared as Reserve Forests for management by the government. The exploitation of timber was, however, thoroughly disorganized until 1920 - 1930, as revealed in the Forest Working Plans. Sport hunting was also permitted in most of the Reserve Forests.

The large scale slaughter of elephants in the Madras Presidency was reduced after the Elephant Preservation Act of 1873. The British set up the first National Park (now called Corbett . P) in 1936. At that time they own hunting preserves some of which such as Gir and Bandipur, are important National Parks today. After the Indian independence, the Indian Board for wildlife was constituted in . . . However, the earlier nexus between hunting and conservation meant that thee majority of protected areas, under the modern legal framework, were set up in deciduous forests where large mammalian herbivores and carnivores occur at high densities. The initial emphasis was also on endangered and endemic mammals such as rhino (Kaziranga and Manas Sanctuaries), hangul deer (Dachigam) and Asiatic lion (Gir). A few refuges for water birds were also created, notably Vharatpur, Ranganthitoo, Vedanthangal and Point Calimere Sanctuaries. In 1973 the government with the help of World Wide Fund for Nature (WWF) launched "Project Tiger" to save this species which had declined to an estimated 1800 animals from 40000 at the beginning of the century. Although there are uncertainties about exact population figures (the 1986 estimate is about 4000 tigers), project Tiger has been certainly successful in saving India's national animal from immediate extinction.

The protected areas catering to large mammals did conserve other components of the ecosystem. But the emphasis on deciduous forests and grasslands meant a general neglect of other biomas and of the overall biological diversity of the country. There were a few exceptions; for example, the Sunderbans Tiger Reserve had a significant proportion of mangrove habitat During the 1970s, the importance of conserving the entire spectrum of biological diversity was realized. Based on the well-known biogeographic classification of Unvardy (1975), 12 sites were identified as potential sites for Biosphere Reserves in accordance with the concept evolved by UNESCO. These include the Nilgiris (representing Western Ghats), Nanda Devi (Himalaya), Rajasthan desert (Thar desert), Gulf of Mannar (marine) and Namdapha (NE India). Apart from emphasizinng conservation of the overall biological diversity of a country or region, the biosphere reserve concept also seeks to reconcile sustainable development with conservation. India's first biosphere reserve, the Nilgiri Biosphere Reserve, was established in September 1986 Covering a forested area of 5520 km^2, the reserve encompasses a diversity of vegetation types (including dry thorn, deciduous and evergreen forest) and many mammals endemic to Western Ghats such as Nilgiri tahr, Nilgiri langur and lion-tailed macaque.

People's conservation movements also came of age during the 1980s The Kerala Sastra Sahitya Parishad, a people's science movement, successfully spearheaded a battle to save a tropical evergreen forest in the Silent Valley from a proposed dam project Another grass roots movement, the Chipko (hug the tree) Andolan in the Himalaya came into the limelight with their adapted unconventional methods in saving trees from the axe of commercial interests.

Protected area network

In 1980 there were 17 national parks and 95 wildlife sanctuaries in India (UN List of Reserves). By 1987 this jumped to 1 biosphere reserve, 54 national parks and 372 sanctauries covering over 109000 km^2 or 3.3% of India's total land area or 13% of India's forest area (Rodgers and Panwar 1988).

There have been three recent attempts to relate the network of nature reserves with the biogeographic zones/biomes/vegetation types of India. Mackinnon and Mackinnon (1986) have reviewed the protected area system in the Indo-Malayan Realm. Their review of the Indian sub-continent is based largely on the biogeographic calssification of Rodgers (1985) which, in turn, is a modification of the widely used Udvardy system. A summary of their review is given in Table 1. For each "biounit" they have also given a detailed break up by vegetation types.

Gadgil and Meher-Homji (1986a, 1986b) have identified the conservation status and key localities in 43 major vegetation types described by other sources. A summary is provided in Table 2. More recently, Rodgers and Panwar (1988) have prepared a very detailed report on the protected area network in the country (summarized in Table 3).

Table 1

Biounits	Original area km^2	Remaining natural area km^2	% original area protected	% remaining area protected
1. Western Ghats	186000	61380	5.6	17.2
2. Bengal/Assam	442700	84110	1.1	6.2
3. North india	1532000	245120	2.8	17.6
4. S. Himalayas	331600	159170	3.6	7.6
5. Eastern Ghats	94600	34060	4.9	13.8
6. Coromandel	26000	2860	3.9	36.0
7. Deccan plateau	284000	45440	0.3	1.9
8. Thar/Indus (incl. Pakistan)	618920	123780	4.7	23.8
9. Laccadives	?	?	0	0
10. Andamans	6430	4370	4.1	6.2

Based on MacKinnon and MacKinnon (1986)

Table 2.

Zone	Potential areal km^2	Area of primary forest km^2	Area of all forest km^2	Area of Nature Reserves km^2	Nature Reserves as percentage of all forest
Arid	481300	0	2200	8200	a
Semi-arid	670000	17600	31400	7800	a
Peninsular deciduous	1291200	195500	283300	50000	17.6
Peninsular evergreen	62000	14100	16400	3600	21.9%
Himalaya	290500	112300	129000	100900	8.4%
Andaman and Nicobar	6800	5500	5500	5500	14.5%

a - The Desert National Park includes a large area without any vegetation cover.
Based on Gadgil and Meher-Homji (1986a).

Table 3.

Zone	Protected area			
	Size sq.km	No	Area km^2	Percentage
Trans-Himalayans	186,200	2	800	..
Himalayan	236,300	56	12,908	6.0
Desert	225,000	5	8,897	4.0
Semi-Arid	508,000	53	11,723	2.3
Western Ghats	159,000	44	15,935	10.0
Deccan Peninsula	1,421,000	115	48,110	3.4
Gangetic Plain	359,400	25	4,524	1.3
North-East India	171.400	17	1,882	1.1
Islands	8,507	100	710	8.3
Coasts	..	17	4,433	..
Total Country	..	•	109,652	3.3

Based on Rodgers and Panwar (1988).

Factors depleting biological diversity

Historically, the natural vegetation cover of the country has been depleted primarily by the expansion of agriculture to feed the burgeoning human population. About 44% of India's land area is cultivated. Traditionally, permanent agriculture of food crops was confined mainly to the Indo-Gangetic plains and the Deccan plateau and coastal belts. Since the later part of the 18th century, cultivation in the form of tea and coffee plantations invaded the moist forest regions of Western Ghats and Eastern Himalaya. This has been accompanied by monoculture plantations of teak, eucalypts, wattle and rubber. the area under tea, coffee and rubber in the Western Ghats of Kerala, Karnataka and Tamilnadu alone is 460 thousand hectares. This has resulted in a significant loss of the natural evergreen and moist deciduous forest cover. Teak, eucalypts, wattle and certain other softwood plantations occupy 10-15% of the forest area in the Western Ghats.

Shifting cultivation is a major cause of forest loss in certain eastern states such as Orissa, Meghalaya, Arunachal Pradesh, Manipur, Mizoram, Nagaland and Tripura. In these states between 25% and 50% of the forest land in under shifting cultivation or in fallow. Short rotation cycles have depleted soil fertility and kept the vegetation arrested in early successional stages with only grasses and weeds. Unlike other states in the country, only a minor proportion of the forests, varying from 24% in Arunachal to 9% in Meghalaya, in these predominantly tribal states are government Reserve Forests, the rest being village forests, privately-owned forests or unclassed state forests belonging to the district councils

Developmental projects such as irrigation and hydro- electric dams and mining have also significantly depleted the biological resources all over the country. India is one of the major dam builders in the world. In 1979, there were in the country 1554 dams classified as large by the Central Board 400 thousand hectares of forest land were submerged by dam projects. Examples of the devastation caused to forests by mining are the uneconomical iron are mining at Kudremukh in the Western Ghats of Karnataka and bauxite mining at the Amarkantak in Central India.

The new Forest Protection Act of 1980 brings forests under the concurrent list, whereby the permission of the central government has to be obtained before any Reserve Forest land is released for non-forestry purposes. This has largely put the brakes on "legal" deforestation. Ironically, in 1987 the central government itself cleared the massive Narmanda River Valley Project which envisages the construction of 329 large dams and 450 medium-sized projects, submerging 375 thousand hectares of land including prime deciduous forests in central India (CSE 1985).

Poaching has been a serious threat to the survival of numerous vertebrates. A lucrative illegal trade continues in ivory (from male elephants), horns (rhino), furs (snow leopard, tiger, panther, lynx etc.), skins (snakes), musk (musk deer) and feathers (peacock). The trade in love fauna is mainly in birds such as hill mynahs. The export of primates for use in medical research was halted in 1978. Plants are not immune; orchids are especially sought after. India signed the convention on International Trade in Endangered Species of Flora and Fauna (CITES) in 1976. Under the Wildlife Protection Act, 69 species of mammals, 40 of birds and 22 of amphibians and reptiles are listed as highli endangered or rare.

Air pollution is certainly a problem in urban India and in the vicinity of industries in rural regions. But no information is available on its impact on the natural vegetation of the country. On thee other hand, water pollution has depleted fish populations in various regions and affected the health of people consuming fish.

Future plans for conservation of India's biological diversity should expand the biosphere reserve network, reconcile development with conservation and expand the protected network, reconcile development with conservation and expand the protected area network in deficient regions such as the Deccan, Eastern Himalaya-NE India and Gangetic plains. In this regard, the proposals of Rodgers and Panwar (1988) to increase the protected area coverage to 4.6% of country's geographical area merit serious consideration.

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research reports

ASSOCIATIONS AMONG THE MODES OF POLLINATION AND SEED DISPERSAL—ECOLOGICAL FACTORS AND PHYLOGENETIC CONSTRAINTS

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Pollination – Seed dispersal – Clutch size – Phylogeny

Abstract

We argue that specific modes of pollination and seed dispersal tend to be associated (co-occur) in plants and that the pollination and seed dispersal modes adopted by the plant shapes reproductive features including clutch size and unit of dispersal. We tested these predictions using the data on the flora of the British Isles. We found that more often than expected wind-pollinated species tend to have wind-dispersed seeds and insect-pollinated species to have either passive (including explosive) or animal-dispersed seeds. Wind-dispersed species also tend to have a smaller clutch size with the fruit as a unit of dispersal, while passively dispersed species tend to have large clutch sizes with seeds as the unit of dispersal. We discuss the role of phylogenetic constraints and ecological factors in shaping these associations.

Introduction

Evolution of pollination modes and associated features in plants is generally viewed independently to that of the dispersal modes of fruits and seeds. The reasons may partly be traced to the botanical tradition of studying the morphology of flowers and fruits in isolation, disregarding their functional association. But as Van der Pijl (1982) points out, the morphology of flower components is highly influenced not merely by adaptation to pollination, but also by the modes of dispersal of seeds and pods and seedling establishment. Yet the possibility of associated evolution of pollination and dispersal modes due to their dependence on common morphological syndromes and vectors has only occasionally been proposed (Cronquist, 1962; Ridley, 1930).

Recently, Primack (1987) argued that due to the morphological continuity between flower, fruit and seed development, several features of these phases of reproduction should be closely related. Demonstrating positive associations among the features of flower, fruit and seed development, he suggested that their evolution may be closely interlinked or integrated. However, he did not consider the possibility of associations among the modes of pollination and dispersal and the consequent effects on the reproductive features.

In this paper, we develop the argument that in plants, evolution of the modes of pollination and dispersal are interlinked because of (a) the morphological continuity of flower and fruit (Primack, 1987), and (b) the possibility that selection favours adaptation of plants to the most commonly available vector of their habitat for both events.

We base our argument on the generally accepted assumption that dispersal of gametes and zygotes (seeds) is advantageous and that selection favours features that enhance or facilitate such dispersal. Dispersal of gametes (pollen grains: pollination) and seeds depends upon vectors. The 'types' of vectors or modes are few and common, namely, abiotic (wind or water), and biotic (insects or animals). Hence, selection can be expected to favour adaptation of plants to the same mode (vector) for both events.

There are several reasons for this. The inflorescence structure and plant architecture evolved to facilitate wind-pollination in a species might also predispose it for the wind-dispersal of its seeds or fruits (e.g. Gramineae). Similarly, the display features of a plant evolved to attract insects or animal pollinators can be extended to attract animal dispersers also. Simultaneous adaptation would also result in more economic usage of reproductive resources. Thus, species with a specific mode of pollination would be selected to adapt to the same mode for seed dispersal. This is especially likely when a particular vector is predominant in a habitat, since using the most abundant vector for both pollination and dispersal would help avoid competition and risks that otherwise arise by adapting to the scarce vector. In open-dry-habitats where wind movement is unhindered, competition for scarce vectors (insects or animals) favours both pollination and dispersal through wind. In contrast, in closed forest habitats where insect or animal density is high and wind movement is hindered, selection favours pollination and dispersal through insects/animals rather than through wind. It follows from the above that over a wide range of taxa, strong associations should exist among the various modes of pollination and dispersal. Wind-pollination is expected to be associated wih wind-dispersal and insect or animal-pollination with animal or passive (see below) dispersal.

The mode of dispersal of a species also shapes several of its reproductive features, such as clutch size and the unit of dispersal (Ridley, 1930; Uma Shaanker *et al.*, 1988; Ganeshaiah and Uma Shaanker, 1988). Species which disperse their fruits either through wind or water generally have a small clutch compared to those which disperse their seeds either explosively or through vectors (Ridley, 1930; Uma Shaanker *et al.*, 1988).

If, as argued above, the pollination and dispersal modes are associated, there should also exist associations among the different clutch sizes and pollination modes. Over a wide range of taxa it should therefore be possible to identify associations among specific modes of pollination and dispersal, clutch size and unit of dispersal. Here we test these predictions and discuss the importance of phylogenetic constraints and ecological factors in shaping these associations.

Materials and methods

Data on modes of pollination and dispersal, unit of dispersal and ovule number per ovary (clutch size) of 920 dicotyledonous species belonging to 92 families were collected from the 'Flora of British Isles' (Clapham *et al.*, 1952) where a comprehensive description of the species is provided. Information on the mode and unit of dispersal of species for which data were not provided was either obtained from other sources (Ridley, 1930) or derived from pod features. Monocotyledonous species were excluded from the study because the data provided on them was insufficient. Data on pollination modes were grouped into wind (and water), self- and insect-pollinated. Data on dispersal modes were grouped into wind (and water), passive (including explosive) and animal-dispersed. Data on clutch size were grouped into low (1–4), medium (5–10) and large (>10 ovules per ovary). The species with passive or explosive dispersal cannot by definition have fruit as the unit of dispersal and hence might have introduced an artefact into the analysis. However in some species the whole fruit detaches as a unit and then disperses its seeds passively (e.g. *Albizzia* and *Acacia*). These have been regarded as passive dispersal systems with fruit as the unit of dispersal. A four-way contingency table of these characteristics was set up and subjected to log-linear analysis to test for the independence of the distribution of attributes in each cell (Sokal and Rohlf, 1969).

Results

The four-way analysis indicated that all of the characteristics are significantly associated; their association was also evident on two- and three-way tests of independence (Table 1). However, for the sake of clarity and further discussion, the data are recast into two-way contingency tables (Tables 2–6). The following findings emerged.

(1) Wind-pollinated species, more often than expected, tend to be wind-dispersed (Table 2). Insect- or animal-pollinated species were more frequently animal or passively dispersed and less often through wind. Self-

Table 1. *G*-values of log linear test of independence for four-, three- and two-way analyses

Variable	df	*G*-value	*P* levels
D×P×U×C	46	966.8	<0.0001
D×P×U	12	684.49	<0.0001
D×P×C	20	260.50	<0.0001
D×U×C	12	693.14	<0.0001
P×U×C	12	299.00	<0.0001
C×U	2	152.86	<0.0001
C×P	4	93.98	<0.0001
C×D	4	110.74	<0.0001
P×U	2	83.06	<0.0001
P×D	4	140.76	<0.0001
D×U	2	482.18	<0.0001

D, dispersal modes; C, clutch size classes; P, pollination modes; U, unit of dispersal.

Table 2. Distribution of species into classes of dispersal and pollination modes

Pollination mode		Dispersal mode		
		Wind	Animal	Passive
Wind	Obs.	73	7	14
	Exp.	(33)	(17)	(45)
Self	Obs.	25	10	49
	Exp.	(26)	(13)	(35)
Insect/animal	Obs.	186	126	322
	Exp.	(225)	(112)	(304)

$\chi^2 = 91.16$; $P < 0.001$; df = 4.
$N = 812$; the remaining species (108) were not included in the analysis for lack of data.
Values in parentheses are those expected from random distribution.

Table 3. Distribution of species into classes of clutch size and modes of dispersal

Dispersal mode		Ovule number per ovary		
		1–4	5–10	>10
Wind	Obs	243	15	55
	Exp	(147)	(25)	(141)
Animal	Obs.	68	15	59
	Exp	(71)	(12)	(68)
Passive	Obs.	90	39	271
	Exp	(188)	(32)	(180)

$\chi^2 = 219.83$; $P < 0.001$; df = 4.
$N = 855$; the remaining species (65) were not included in the analysis for lack of data
Values in parentheses are those expected from random distribution

Table 4. Distribution of species into classes of dispersal modes and units of dispersal

Unit of dispersal		Modes of dispersal		
		Wind	Animal	Passive
Seed	Obs	73	5	423
	Exp	(180)	(74)	(247)
Fruit	Obs.	244	125	13
	Exp	(137)	(56)	(187)

$\chi^2 = 421.9$; $P < 0.0001$; df = 2.
$N = 883$; the remaining species (37) were not included in the analysis for lack of data
Values in parentheses are those expected from random distribution

pollinated species tended to be passively dispersed. Thus, as predicted, specific associations exist among the various modes of pollination and dispersal.

(2) Wind-dispersed species were associated with low (<4) clutch size and passively dispersed with large clutch size (>10; Table 3). The animal-dispersed species distributed randomly over all the three clutch size categories.

(3) In wind- and animal-dispersed species the unit of dispersal was usually the fruit, while in those with passive dispersal it was usually the seed (Table 4). The association between the modes and units of dispersal was made clear when only wind-dispersed species were considered; about 77% of them had fruits as their dispersal units.

(4) Species with small clutch size dispersed their offspring in fruits while those with large clutch size dispersed them individually (Table 5); 75% of the species with small clutch size had fruits as units while 84% of species with large clutch size had seeds as the units of dispersal.

Table 5. Distribution of species into classes of ovule number per ovary and units of dispersal

Unit of dispersal		Ovule number per ovary		
		1–4	5–10	>10
Seed	Obs.	100	47	316
	Exp	(217)	(40)	(206)
Fruit	Obs	297	27	61
	Exp.	(180)	(34)	(171)

$\chi^2 = 269.94$; $P < 0.001$; df = 2.
$N = 848$; the remaining species (72) were not included in the analysis for lack of data
Values in parentheses are those expected from random distribution

Table 6. Distribution of species into classes of ovule number and modes of dispersal

Pollination mode		Ovule number/ovary		
		1–4	5–10	>10
Wind	Obs.	68	6	11
	Exp.	(32)	(9)	(44)
Self	Obs.	32	5	47
	Exp.	(32)	(8)	(44)
Insect	Obs.	167	70	306
	Exp.	(203)	(54)	(276)

$\chi^2 = 85.89$; $P < 0.001$; df = 4.
$N = 712$; the remaining species (208) were not included in the analysis for lack of data
Values in parentheses are those expected from random distribution

(5) Like the wind-dispersed species, wind-pollinated species also had small clutch size (1–4; Table 6). Significantly more wind-pollinated species than expected had small clutch size (1–4), while more insect- or animal-pollinated species had large clutch size (>10).

Discussion

The results show that several features of pollination and dispersal in flowering plants are closely associated and that specific modes of pollination and dispersal tend to co-occur. Either as a consequence, or independently of this, emerge other associations among several features of dispersal and modes of pollination.

As argued earlier, the associations among pollination and dispersal modes can arise due to the simultaneous adaptation of plants to the predominant vector of the habitat by both these life history traits. Alternatively, the association could be due to the adaptation of one of the life history traits to the predominant vector of the habitat, the other having been shaped as a pleiotropic consequence. Association due to pleiotropy is particularly likely in plants because there is a morphological continuity in flowering and fruiting (Primack, 1987) and a strong association exists among the flower, pod and seed features (Gottlieb, 1984; Primack, 1987).

The adoption of a specific mode of dispersal shapes several reproductive features such as the clutch size (Uma Shaanker *et al.*, 1988) and the architecture of the plant (Ridley, 1930) that predisposes it to adapt to the same mode for pollination also (see below) and vice-versa.

Associations among the modes of pollination and dispersal could also arise due to phylogenetic constraints. For example, if the clutch size is consistently small in a set of related taxa, it might predispose such species to adapt to wind for both dispersal and pollination. Conversely, if the clutch size is large in a set of related taxa (e.g. Solanaceae), selection might favour in them pollination and dispersal through animals. In certain tribes such as *Faboidae*, *Mimosoidae* and *Caesalpinoidae*, where the clutch size varies considerably (Dudick, 1981), phylogeny *per se* may not contribute to such associations. In fact some plants exhibit plasticity in clutch size within their lifetime (e.g. *Impatiens*; Schemeske *et al.*, 1980). In a few other species, the phylogenetically-determined clutch size is reduced by the prevention of fertilization of ovules (Sedgeley, 1981; Uma Shaanker and Ganeshaiah, 1989) or by abortion of the developing embryos (Mogensen, 1975; Stephenson, 1981; Casper and Wiens, 1981; Wiens, 1984; Ganeshaiah and Uma Shaanker, 1988; Uma Shaanker *et al.*, 1988) Thus selection can break phylogenetic constraints and hence uncouple the modes of pollination and dispersal. In other words, although phylogenetic constraints may contribute to these associations, the extent to which it does so is limited by the degree of phylogenetic invariance of the characteristics. However, since it is rare to find mosaics of related taxa with similar traits, the influence of phylogenetic constraints on such associations is unlikely to be substantial. Rather, the predominant vector of the habitat may constitute the major factor shaping the observed associations.

The associations among modes of dispersal, unit of dispersal and clutch size can be explained by the trade-off between the cost of packing the seeds and benefit due to dispersal. In species where seeds are individually dispersed (either passively or through wind) packing many of them in a fruit will also reduce the packing cost per seed (Uma Shaanker *et al.*, 1988). But in species where the *fruit* is the unit of dispersal, either through wind, water or animals, the packing material *per se* (pulp or pod coat) aids in its dispersal and hence dispersal efficiency is positively related to the packing cost (pulp to seed ratio in animal-dispersed species: Howe and Vande Kerchkhove, 1980; Janzen, 1982; Jordano, 1984; and pod coat to seed weight ratio in wind-dispersed species: Augspurger and Hogan, 1983; Garrison and Augspurger, 1983; Ganeshaiah and Uma Shaanker, 1988). In these species, dispersal could be increased by reducing the seed number, thereby increasing the ratio of pulp to seed or pod coat to seed weight although it leads to an increase in the cost of packing the seeds. Thus, large clutch size would be selected in species which are passively dispersed and small clutch size in species where fruit is the unit of dispersal

Associations among the modes of pollination and clutch size can be explained by the pollen transfer units specific to each pollination mode. In wind-pollinated systems, pollen grains are dispersed individually and their deposition on the receptive surface of the stigma is a random event. In contrast, in insect- or animal-pollinated systems where pollen grains are always transferred in clumps (Cruden and Jensen, 1979) or as polyads and pollinia (Kenrick and Knox, 1982), the stigmatic surface receives them *en masse*. Hence the stigmas in insect-pollinated systems receive a high load of pollen grains if they are visited and none at all if they are not. Thus the average number of pollen grains per stigma in the pollinated (visited) flowers is higher in insect- than in wind-pollinated systems (Uma Shaanker and Ganeshaiah, 1990). Packing too many ovules per ovary in wind-pollinated species might lead to pollen grain limitation and too few in insect- or animal-pollinated species to an inefficient harvesting of pollen grains. Pollen loads on the stigma as a selective force should therefore favour small clutch size in wind-pollinated system and large clutch size in insect- or animal-pollinated systems.

The observed associations among the pollination and dispersal features might constrain the range of phenological patterns the species can adapt to and thus indirectly affect the life history of the plants. The studies on phenological patterns which abound with controversies regarding the selective forces involved, might benefit greatly by considering these associations. This might help in identifying meaningful patterns in and providing alternative explanations for otherwise apparently random phenological patterns.

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INSECT SPECIES DIVERSITY IN THE TROPICS : SAMPLING METHODS AND A CASE STUDY[1]

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(With ten text-figures)

The tropical regions of the world generally have a richer store of biological diversity than other regions of the globe. But most tropical habitats face a significant threat of destruction. Yet, little is known about tropical biotic communities. Suspecting that at least part of the reason for the poor documentation of tropical insect communities is the lack of appropriate research methodology, we have endeavoured to standardize a package of methods for quantitative sampling of insects, suitable for tropical ecologists with modest research budgets. This methodology includes the use of a small light trap as well as net sweeps, pitfall traps and scented traps. The methods have been used to sample insect species diversity patterns in three replicate one hectare plots each in twelve selected sites in the Uttara Kannada district of Karnataka, India. During this case study we have encountered 16,852 adult individuals belonging to 1,789 species, 219 families and 19 orders of insects. Here, we provide evidence that this methodology is adequate for sampling insects and differentiating habitats on the basis of the distribution of insect species. Some interesting biological problems that tropical ecologists can study with the data generated from the application of these methods are also briefly illustrated.

INTRODUCTION

One of the few relatively undisputed generalizations in community ecology is a latitudinal gradient of increase in biological species richness and diversity from the temperate regions to the tropics (see Krebs 1985, Colinvaux 1986). Apart from being something of a rule in community ecology this means that those of us who live in the tropics enjoy a biologically rich environment. Recent work suggests that the richness of the tropical insect fauna is beyond all earlier expectations (Erwin and Scott 1980, Erwin 1983 and Stork 1988). It is equally undisputed, however, that most tropical organisms are poorly studied and the little that we do know about any group of organisms comes largely from studies of temperate species. This is expressed most dramatically in the statement that the number of biologists is negatively correlated with the number of biological species in different regions of the globe (Robinson 1978). The poor state of our understanding of tropical biology may be partly attributed to the relative economic backwardness of tropical countries, the lack of facilities for research and sometimes to the lack of the tradition of modern scientific work.

We suggest, however, that at least sometimes this is due to the lack of appropriate research methodology suitable for tropical conditions. Studies on insect species diversity and the long term monitoring of insect species and populations in different habitats are good examples. Almost all the major long term insect monitoring programmes are based on light trap catches, a method that requires uninterrupted supply of electricity, often in the mid-

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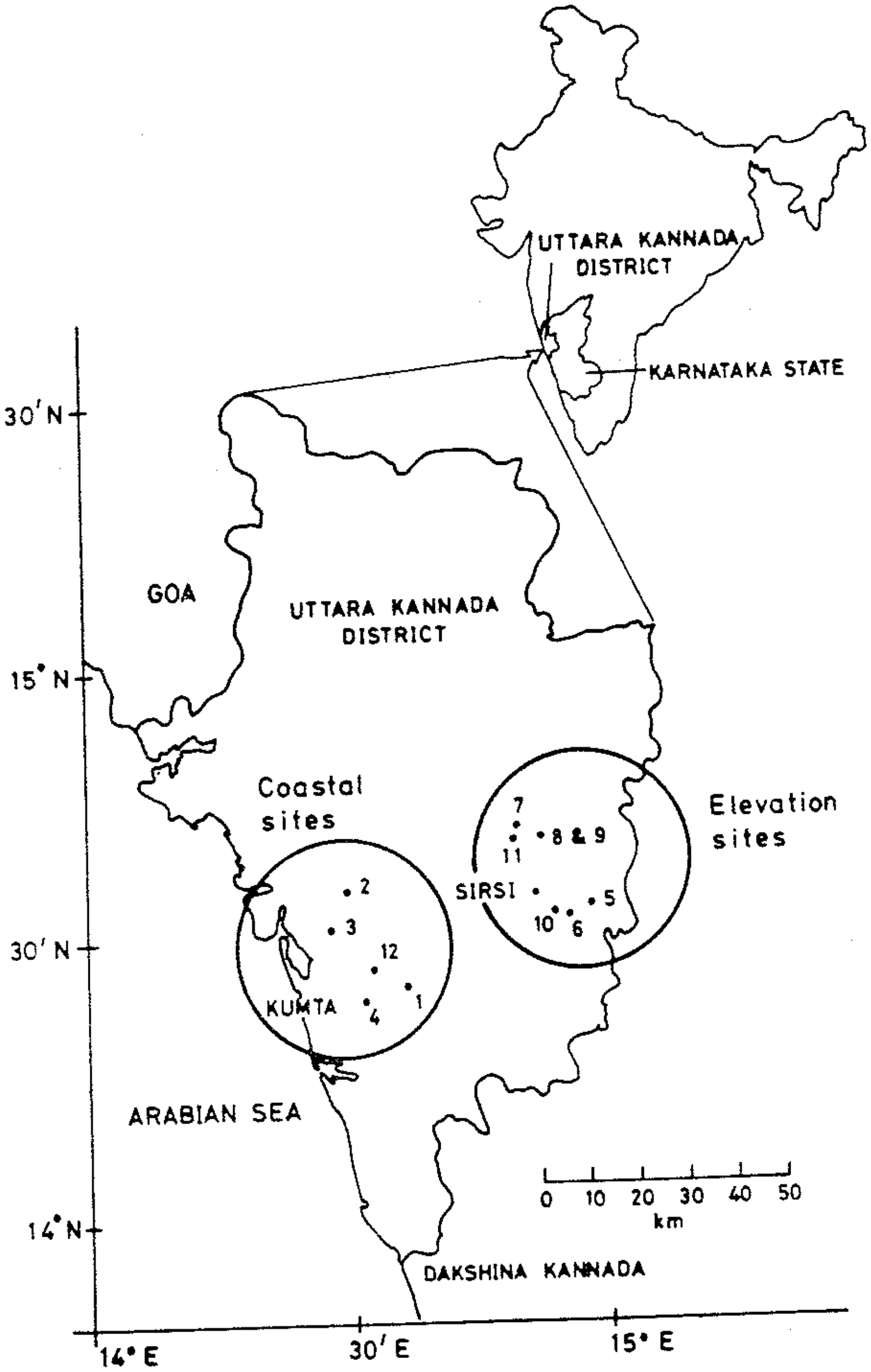


Fig 1. Map of Uttara Kannada district showing the 12 sites used in the study.
1. Santagal R.F., 2. Nagur R.F., 3 Mirjan M.F., 4. Chandavar M.F. 5. Bengle M.F, 6 Bidaralli R.F. 7. Sonda R.F. 8 Bhairumbe M.F, 9 Betta land. 10. *Eucalyptus* plantation, 11. Teak plantation, 12. *Areca* plantation

dle of a forest (Holloway 1983, 1987; Taylor 1978, Taylor *et al.* 1976, Wolda 1983a, b; Wolda and Roubik 1986) Sometimes the light traps are operated for years together without interruption. In most tropical situations, uninterrupted supply of electricity is nearly impossible even in cities and towns, let alone in the middle of a forest. The establishment and long term maintenance of electricity generating devices is prohibitively expensive for most ecologists working in tropical countries

Suspecting that this has prevented many tropical ecologists from undertaking insect species diversity studies (see Wolda 1981a), we have attempted to standardize a package of methods for quantitative sampling of insects, suitable for tropical ecologists with modest research budgets. Our methodology is based on the use of a small light trap using routinely available dry batteries but substantially supplemented by other methods such as net sweeps, pitfall traps and scented traps. We show here that such a methodoloy is adequate for sampling insects and differentiating habitats on the basis of insect species distribution. We also briefly illustrate some interesting biological questions that ecologists in tropical countries can begin to ask with the data generated from such methodology.

MATERIALS AND METHODS

Study sites: All our study sites were located in the Uttara Kannada district of the state of Karnataka, India (Fig. 1). The forested study sites fall broadly into two categories reflecting different levels of disturbance, namely, the Reserve Forests (R.F.) (relatively less disturbed) and the Minor Forests (M.F.) (relatively more disturbed). Sites representing both these categories were chosen in the coastal plains as well as at higher elevations (approximate altitude 600 m)

Selection of study sites in this manner ensured that these sites represent habitats under different environmental conditions and levels of disturbance. In addition to these forested habitats, three monoculture plantations (Pl.) and a leaf manure forest (Betta land) were also chosen for the study. At each of these sites, sampling was carried out in three one hectare plots. Thus a total of 36 one hectare plots from 12 habitat types were sampled (Table 1). A brief description of each study site is given in Table 2. All sampling was carried out during December, January, February and March which is part of the dry season in these localities

Sampling methods: To develop a package of methods for quantitative sampling of insect species, collections were made using four different methods which were standardized after extensive field trials.

1. **Light trap:** A portable light trap which can be easily assembled and dismantled was fabricated using locally available inexpensive material. The light trap uses a fluorescent light source (Eveready Fluorolite 7.5 inch; 6 watts) powered by routinely available battery cells. The main framework of the trap consists of four iron legs, an aluminium roof and two aluminium baffles, between which the light source is placed. Insects attracted to the light were collected through a funnel in a cyanide jar, below the light. One light trap was placed in the centre of the plot. The light was switched on at dusk and allowed to burn itself out as the batteries drained after about seven hours. The insects trapped in the jar were collected the next morning and preserved in 70% alcohol.

2. **Net sweeps:** Net sweeps were carried out to collect insects off the vegetation. The nets used in systematic sweeping of the ground level vegetation were made of thick cotton cloth with a diameter of 30 cm at the mouth and a bag length of 60 cm

For carrying out net sweeps the plot was divided into 100 quadrats, measuring 10 m x 10 m each. Six such quadrats were chosen at random and the entire ground level vegetation in the chosen quadrat was covered during the sweeping. Net sweeps were always done between 1000 h - 1200 hrs. The insects collected from each quadrat were transferred into polythene bags containing a cotton wad dipped in chloroform. Insects were later separated from the litter and preserved in vials containing 70% alcohol

3. **Pitfall traps:** The pitfall traps consisted of a 2.5 litre plastic jar with an opening of 9 cm in diameter, buried at ground level and protected from rain by a tripod stand carrying a plastic plate of about 30 cm diameter at a distance of about 15 cm above the ground. One pitfall trap was placed in each of five randomly chosen 10 m x 10 m quadrats. Each jar carried 25 ml of 0.05% methyl parathion. The traps were set up between 1500 and 1700 hrs and were collected the next morning. Insects trapped in the jars were preserved in 70% alcohol.

TABLE 1
STUDY SITES, PLOTS AND SAMPLING PERIOD

	Reserve forest	Minor forest	Plantations	Leaf manure forest
Coastal sites	Santagal R.F. (Plot Nos. 1-3) March 1984	Chandavar M.F. (Plot Nos. 10-12) January 1984	*Areca* Pl. (Plot Nos. 34-36) January 1985	
	Nagur R.F. (Plot Nos. 4-6) February 1984	Mirjan M.F. (Plot Nos. 7-9) December 1984		
Elevation sites	Bidaralli R.F. (Plot Nos 16-18) December 1983	Bengle M.F. (Plot Nos. 13-15) December 1983	Teak Pl. (Plot Nos 31-33) December 1984	Betta Land (Plot Nos. 25-27) January 1985
	Sonda R.F. (Plot Nos. 19-21) December 1983	Bhairumbe M.F. (Plot Nos. 22-24) January 1984	*Eucalyptus* Pl. (Plot Nos. 28-30) December 1984	

TABLE 2
BRIEF DESCRIPTION OF STUDY SITES

Sites	Vegetation type	Dominant tree genera	Remarks
Santagal R.F.	Evergreen	*Cinnamomum*, *Bischofia* and *Diospyros*	Thick tree canopy, understorey of cane breaks.
Nagur R.F.	Evergreen	*Holigarna* and *Hopea*	Thick tree canopy, understorey of sapling
Mirjan M.F.	Scrub	*Ixora*, *Buchanania* and *Terminalia*	Highly degraded semi-evergreen.
Chandavar M.F.	Semi-evergreen	*Ixora*, *Aporosa* and *Hopea*	Degraded, understorey of frequently lopped saplings
Bengle M.F.	Moist deciduous	*Terminalia*	*Degraded, thick undergrowth of* grass and annual herbs.
Bidaralli R.F.	Moist deciduous	*Terminalia*, *Xylia* and *Lagerstroemia*	Undergrowth of herbs and shrubs, *mainly Clerodendrum.*
Sonda R.F.	Moist deciduous	*Terminalia*, *Xylia* and *Aporosa*	Understorey mainly of *Psychotria* spp.
Bhairumbe M.F.	Moist deciduous	*Careya*, *Ziziphus* and *Randia*	Degraded, undergrowth of *Chromelina*.
Betta land	Moist deciduous	*Terminalia* and *Lagerstroemia*	Cleared of all undergrowth, maintained for leaf manure.
Eucalyptus Pl.	Monoculture	*Eucalyptus*	Thick undergrowth of grass and herbs surrounded by extensive moist deciduous forest.
Teak Pl.	Monoculture	*Tectona grandis*	Little or no undergrowth except *Lantana* and *Chromelina*
Areca Pl	Monoculture	*Areca catechu*	Plantations in valleys, surrounded by evergreen forest on hills.

4 **Scented traps:** A plastic jar of 2.5 litre capacity was used to fabricate a scented trap. The mouth of the jar was shielded from rain water using a plastic plate allowing a gap of 6 cm between the mouth of the jar and the plastic plate so that insects could freely move into the jar. The trap was baited with 200 ml of saturated jaggery (unrefined cane sugar) solution with two tablets of baker's yeast, 0.05% (final concentration) methyl parathion and 0.5 ml of pineapple essence. The traps were hung at about 1 m from the ground on a wooden peg. Five such traps were used, one each in the centre of a randomly chosen 10 m x 10 m quadrat. The scented traps were also set between 1500 -1700 hrs and collected the following morning. Insects trapped in the jaggery solution were filtered, washed and preserved in 70% alcohol

Thus one light trap placed in the middle of a one hectare plot working for about 7 hours (1900 to 0200 hrs), net sweeps in 6 randomly chosen 10 m x 10 m quadrats, 5 randomly placed pitfall traps and 5 randomly placed scented traps, both working for about 18 hrs each constituted one sampling unit. Each of the 36 plots were subjected to one such sampling unit

PRESERVATION OF SPECIMENS AND DATA RECORDING

All insects (except large moths) were stored in alcohol for future sorting. The insects were identified up to the family level and within each family, recognizable taxonomic units (RTU) were separated based on morphological differences. For convenience, the RTUs will be referred to as species hroughout this paper. Each such specimen was iven a serial number within that family. For each lot, site and quadrat, information on the order, amily, serial number, number of nymphs or larvae nd the number of adults were recorded. Only data n the adult insects are presented here.

anopy cover index: It was obvious from our reliminary results that a subjective classification of abitats into more disturbed and less disturbed ategories is insufficient to discern any relationship etween patterns of diversity and levels of disturnce. An attempt was therefore made to develop an dex to quantify levels of disturbance. One of the ajor causes of disturbance in tropical forests is a e fall, either man made or natural, which leads to ge scale changes in the understorey vegetation. The extent of canopy cover could thus be one good measure of disturbance.

A relative estimate of the extent of canopy cover was obtained by the presence or absence of canopy at randomly chosen points in the study plots. 50 such points at the corners of 10 m x 10 m quadrats were chosen to make observations on the canopy cover. At each of these points the observer counted the number of trees whose canopy intersected his line of sight immediately above his head Shrubs, tree branches and leaves obstructing the line of sight at less than about 3 m from the ground were not counted The number of trees which formed a canopy over these 50 points was used to obtain a mean value for the plot, which we call the Canopy Cover Index.

Data analysis:

1. **α Diversity:** Several indices of alpha (within site) diversity such as the Shannon Weiner index (Margalef 1958), Simpson's index (Simpson 1949), Hill's diversity indices N_1 and N_2 (Hill 1973, see also Gadagkar 1989), S_m (Hurlbert 1971, Wolda 1983a and α of the log series Fisher *et al.* 1943) were computed. For the sake of brevity only results using α of the log series are given in this paper. α of the log series was computed by an iterative procedure using the equation,

$$S = \alpha \log_e (1 + N/\alpha)$$

where S is the number of species in the sample, N is the number of individuals in the sample, and α is the index of diversity. The standard deviation of α was estimated as α /-log (1-X) where X = N/(N +α) (Anscombe 1950). Using this standard deviation, significant differences in diversity between habitats were judged by a z test.

2. **β Diversity:** β (between site or between method) diversity was estimated as coefficients of similarity given by the Morisita-Horn Index (after Wolda 1981b),

$$C_\lambda = \frac{2\,\Sigma\,(n_{1i}.n_{2i})}{(\lambda_1 + \lambda_2)\,N_1\,N_2}$$

where,

$$\lambda_j = \frac{\Sigma\, n^2_{ji}}{N_j^2}$$

where n_{ji} is the number of individuals of

TABLE 3
SUMMARY OF CATCH DATA ✓

Site	Plot number j	No. of orders	No. of families	No. of species	No. of individuals	Alpha of log series
Santagal R.F.	1	7	36	77	144	67.31
Santagal R.F.	2	8	33	73	231	36.77
Santagal R.F.	3	9	36	88	199	60.36
Nagur R.F.	4	10	33	59	247	24.55
Nagur R.F.	5	5	28	64	265	26.81
Nagur R.F.	6	8	30	65	213	31.88
Mirjan M.F.	7	8	40	87	950	23.31
Mirjan M.F.	8	9	48	102	874	29.93
Mirjan M.F.	9	10	44	88	1085	22.61
Chandavar M.F.	10	9	52	99	529	35.93
Chandavar M.F.	11	8	37	79	757	22.20
Chandavar M.F.	12	10	45	103	407	44.42
Bengle M.F.	13	12	77	164	496	85.58
Bengle M.F.	14	5	46	110	445	46.74
Bengle M.F.	15	10	68	171	590	80.79
Bidaralli R.F.	16	10	71	144	322	100.02
Bidaralli R.F.	17	12	67	157	539	74.44
Bidaralli R.F.	18	12	53	111	445	47.44
Sonda R.F.	19	8	35	78	204	46.15
Sonda R.F.	20	6	30	73	173	47.61
Sonda R.F.	21	4	35	67	256	29.53
Bhairumbe M.F.	22	10	30	67	175	39.69
Bhairumbe M.F.	23	9	29	58	177	30.05
Bhairumbe M.F.	24	7	43	77	301	33.44
Betta land	25	7	46	122	539	49.15
Betta land	26	10	40	100	304	51.97
Betta land	27	7	33	87	262	45.56
Eucalyptus Pl.	28	12	66	204	659	101.14
Eucalyptus Pl.	29	12	68	239	1331	84.95
Eucalyptus Pl.	30	8	52	176	1191	57.04
Teak Pl.	31	7	29	55	145	32.30
Teak Pl.	32	9	24	43	128	22.73
Teak Pl.	33	7	29	46	86	40.22
Areca Pl.	34	7	45	99	862	28.87
Areca Pl.	35	7	36	102	721	32.42
Areca Pl.	36	7	42	106	600	37.37
Total		19	219	1789	16852	506.06

species i in sample j and n_j is the number of individuals in sample j. The index was computed with data logarithmically transformed as ln $(n_{ij}+1)$. Cluster analysis was performed using a single-linkage algorithm.

RESULTS

Summary of catch data: A summary of the insect catch data in the form of the number of orders, families, species and individuals and α of the log series as an index of diversity for each of the 36 plots are shown in Table 3. In any given plot we encountered from 4-12 orders, 24-77 families, 43-239 species and 86-1331 individuals. In all the 36 plots put together we encountered 19 orders, 219 families, 1789 species and 16,852 individuals. Some patterns in this data are immediately apparent. The highest number of individuals, species and the highest diversity were seen in one or more of the *Eucalyptus* plantation plots, while the lowest number of individuals, species and the lowest diversity were seen in one or more of the teak plantation plots. Natural forest plots, including relatively less as well as the relatively more disturbed ones, were between these two extremes shown by the monoculture plantations.

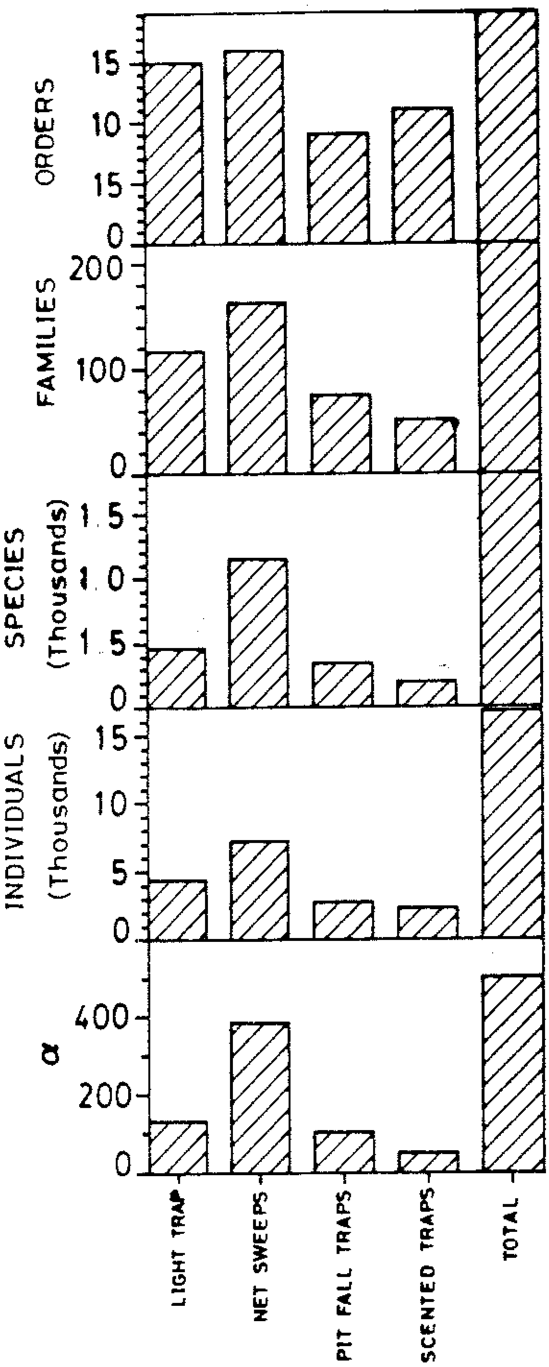


Fig.2 Numbers of orders, families, species, individuals and diversity of insects trapped by different methods.

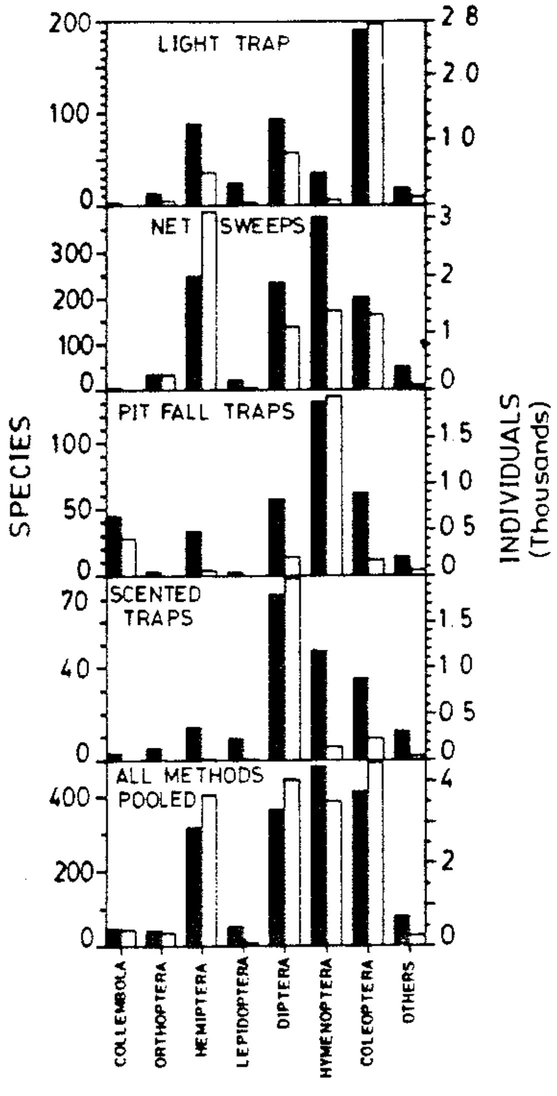


Fig.3. Taxonomic break up of insects trapped by different methods. Closed bars = species , open bars = individuals

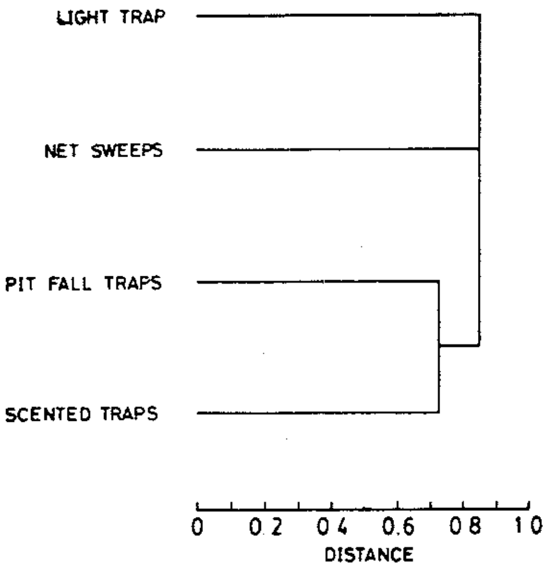


Fig.4. Dendrogram comparing insects caught by different methods (Distance = 1 – Morisita-Horn Index of Similarity). Data pooled from 36 plots.

Comparison of methods of collection: Net sweeps yielded not only the maximum numbers of orders, families, species and individuals but also the highest diversity of insects. But the remaining three methods, namely, the light trap, pitfall traps and scented traps together accounted for at least 50% of the catch (Fig. 2). The light trap yielded more Coleopterans than any other method. Most of the Hemipterans caught were in the net sweeps although net sweeps yielded an equally rich collection of Hymenopterans and Dipterans. Pitfall traps yielded more Hymenopterans than any other order while scented traps caught more Dipterans (Fig. 3).

Comparison of different species and their abundance among catches by different methods using the Morisita-Horn Diversity Index shows that each method yielded quite a different sample of insects. The similarity coefficient between any two methods ranges between 0.13 and 0.28. The consequent large distance (defined as 1 – coefficient of similarity) between insect samples obtained by different methods are shown in Fig 4.

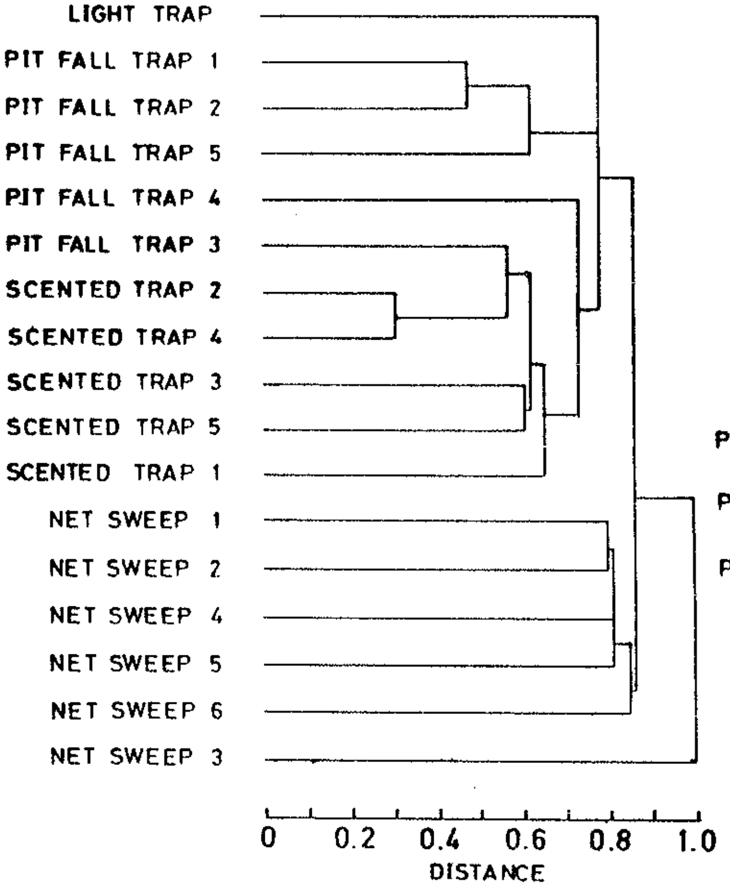
Since one light trap, 6 net sweeps, 5 pitfall traps and 5 scented traps were employed in each plot, we can compare the catches between different replicates of the same method. Employing the Morisita-Horn Similarity Index, we find that catches from different replicates of the same methods were by and large more similar than catches by different methods. It is important to note, however, that there

TABLE 4

COMPARISON OF DIVERSITY IN DIFFERENT CAPTURE SITES

Pairs of sites that are significantly different from each other in their levels of insect diversity as measured by α of the log series. A '+' in any cell indicates that the site mentioned in the row is significantly more diverse than the site mentioned in the column ($p < 0.05$). Numerals (1) to (12) in row and column headings refer to different sites. The mean and standard deviation of α for each site are given in the row titles. Names of sites in row titles and column titles are ordered according to diversity.

		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1)	Bidaralli R.F. 142.89 ± 7.851				+	+	+	+	+	+	+	+	+
(2)	*Eucalyptus* Pl. 140.32 ± 6.66				+	+	+	+	+	+	+	+	+
(3)	Bengle M.F. 136.10 ± 7.37				+	+	+	+	+	+	+	+	+
(4)	Santagal R.F. 106.97 ± 7.60							+	+	+	+	+	+
(5)	Betta Land 97.53 ± 6.23							+	+	+	+	+	+
(6)	Sonda R.F. 87.93 ± 6.46									+	+	+	+
(7)	Bhairumbe M.F. 76.12 ± 5.80											+	+
(8)	Chandavar M.F. 74.09 ± 4.83											+	+
(9)	*Areca* Pl. 69.60 ± 4.47												+
(10)	Teak Pl. 60.36 ± 5.58												
(11)	Nagur R.F. 58.03 ± 4.72												
(12)	Mirjan M.F. 53.91 ± 3.67												



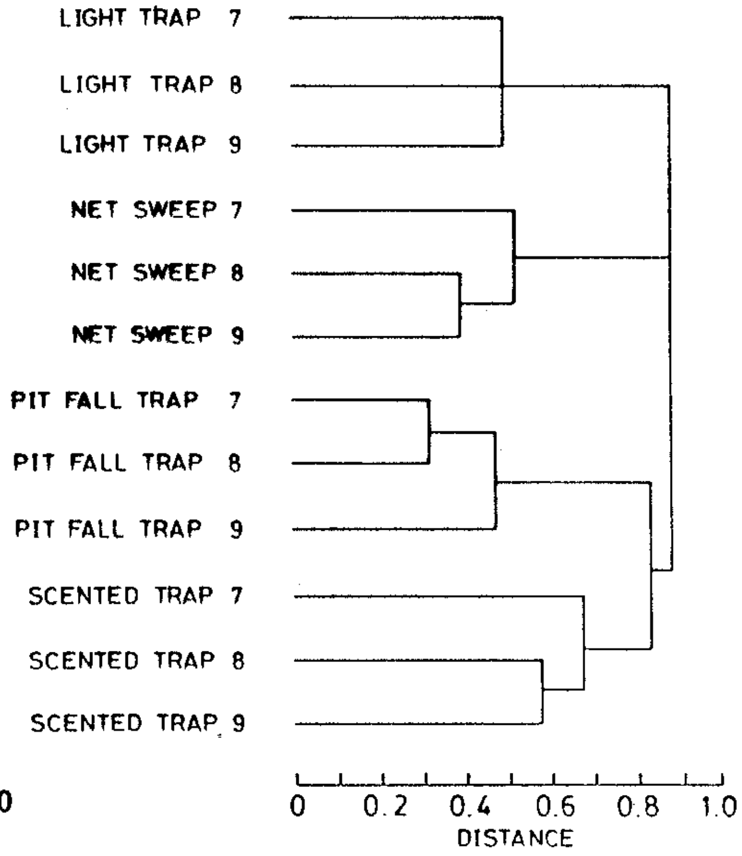
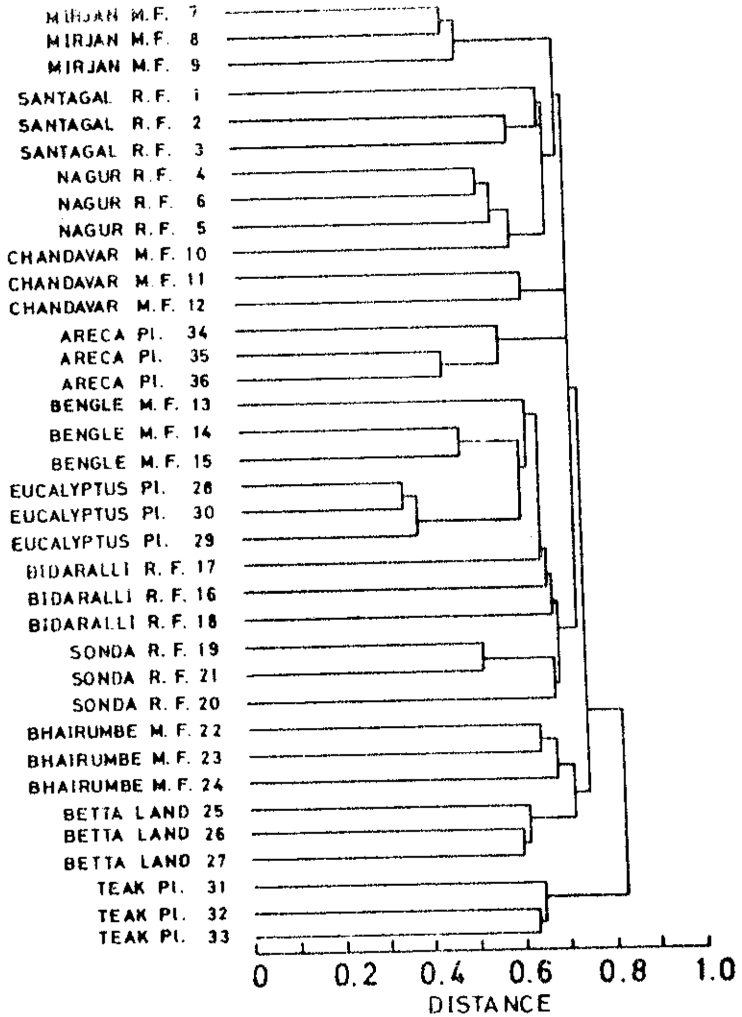


Fig.5. Dendrogram comparing insects caught by traps within a plot.
In general insects caught by the same method had greater similarity among themselves than insects caught by different methods. But insects caught in pitfall trap no. 3 were similar to those caught in the scented traps rather than those caught in other pitfall traps. Insects caught in nets weeps 3 were very different from all other insects caught in this plot. Data from plot 1.

Fig. 6. Dendrogram comparing insects caught by different methods in different replicate plots of the same site. Insects fall into four neat clusters depending on the method of trapping. Data from plots 7, 8 and 9 in Mirjan M.F.



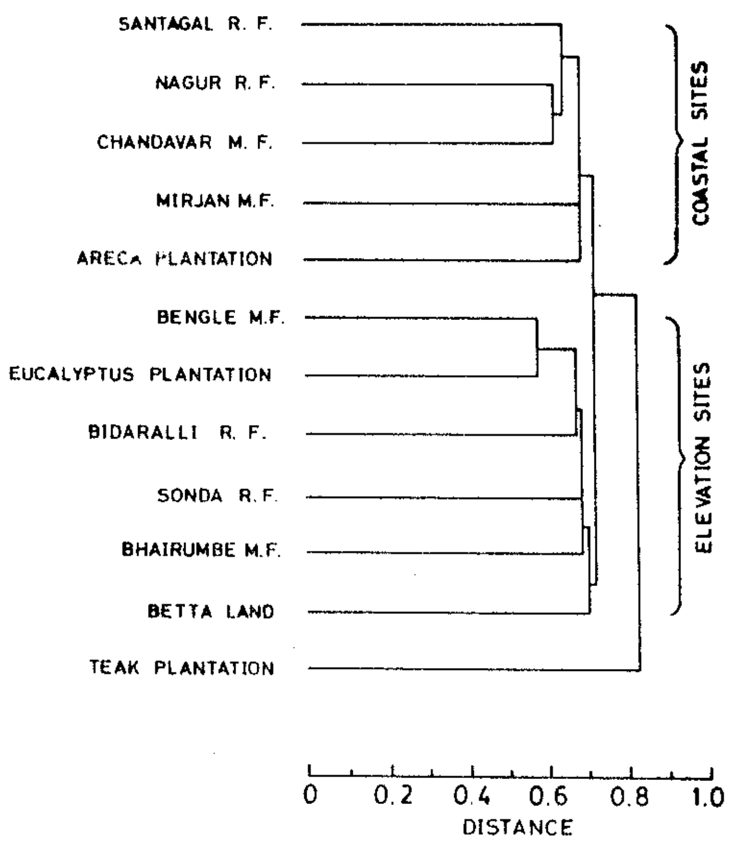


Fig. 7. Dendrogram showing similarity of insects caught in each of the 36 plots.
With the exception of Chandavar, Bengle and Bidaralli similarity between replicate plots of a site is greater than that between plots of different sites.

Fig. 8. Dendrogram showing similarity between different sites.
With the exception of the teak plantation all the down-ghat sites form one cluster and the up-ghat sites a different cluster.
Data pooled from three replicate plots for each site.

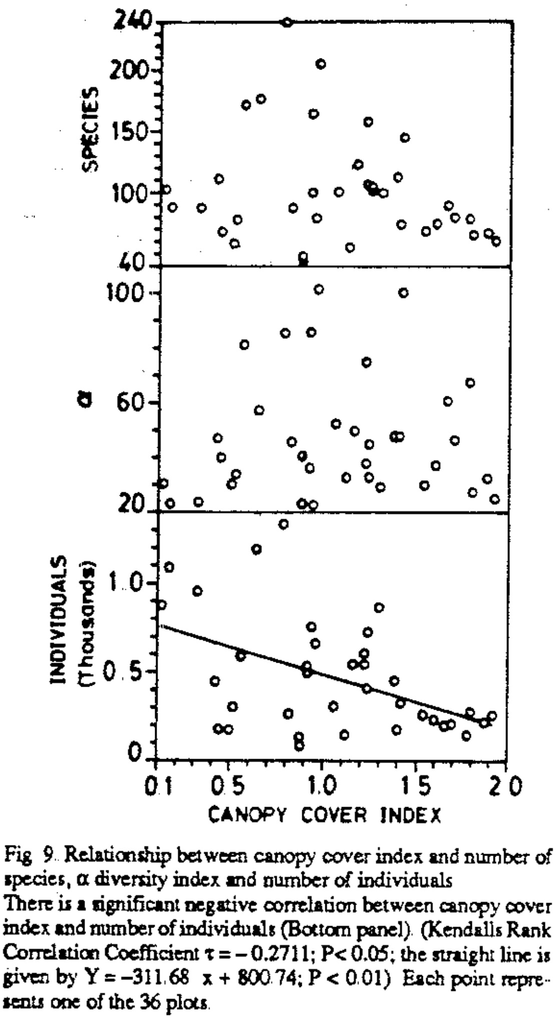


Fig 9. Relationship between canopy cover index and number of species, α diversity index and number of individuals
There is a significant negative correlation between canopy cover index and number of individuals (Bottom panel). (Kendalls Rank Correlation Coefficient $\tau = -0.2711$; $P < 0.05$; the straight line is given by $Y = -311.68\ x + 800.74$; $P < 0.01$) Each point represents one of the 36 plots.

are occasional exceptions. This is illustrated in an example of comparison of the 17 traps employed in plot number 1 (Fig 5). The catches from pitfall traps 1 and 3 have a greater similarity to catches from scented traps than to catches from the remaining pitfall traps. Similarly the catch from netsweep 3 stands out as being different from everything else. These anomalies may be on account of random fluctuations in the small samples of insects caught in each individual trap.

Pooling the insects from each replicate of the same method (except of course in the case of the light traps where only one was employed in each plot) leads to fewer anomalies. This is illustrated by comparing data from each method across the three replicate plots within a study site. For most sites the pattern is as distinct as in the example shown in Fig 6 for plots 7,8 and 9 in Mirjan M.F. It is thus clear that relatively similar insects are caught by repeating the same method in different replicate plots while relatively different insects are caught by different methods. This is by and large the pattern we find in all sites although there are some minor exceptions in some plots.

Comparison of plots and sites: Pooling catch data from all 17 traps in each plot, the 36 plots may be compared using the Morisita-Horn Similarity Index. Generally, the 3 replicate plots in each site are similar to each other and form a cluster before they "join" other clusters. This pattern was seen in 9 out of 12 sites, namely, Santagal R.F., Nagur R.F., Mirjan M.F., *Areca* Plantation, *Eucalyptus* Plantation, Sonda R.F., Bhairumbe M.F., Betta land and Teak Plantation. But there are some exceptions such as Chandavar M.F. and Bidaralli R.F. where at least one plot had greater similarity to plots from some other site than to other plots from the same site (Fig 7).

Insect catches pooled from all methods and from the three replicate plots constitute a combined sample for a site. Such combined samples permit comparison between the habitats represented by different sites. Because the variances of α can easily be computed, it is possible to conclude that the insects caught in Bidaralli R.F. are significantly more diverse than those caught in Santagal R.F. and all other sites of lower diversity (Table 4, $P<0.05$). Similarly, insects caught in Santagal R.F. are significantly more diverse than those caught in Bhairumbe M.F. and all other sites of lower diversity (Table 4, $P<0.05$). The 12 sites are ordered according to diversity and all pairs of sites that are significantly different from each other in diversity are shown in Table 4. Pooled catch data for each site can also be used to compare the sites using the Morisita-Horn Index. This leads to the remarkable result that with the exception of teak plantation, all coastal sites form one cluster and all elevation sites form a separate cluster, although it is not clear whether this result is statistically significant (Fig. 8).

Effect of canopy cover: Reserve forests, minor forests and plantations were initially chosen because they were expected to represent different levels of disturbance. To obtain a more objective and continuous index of disturbance, however, we have measured the extent of canopy cover in each plot. This was achieved through the canopy cover index, which is the mean number of trees whose canopies overlap with each other at any given point in the plot (see methods). Clearly, canopy cover is only one of the many factors that must affect the distribution and abundance of insects on the floor of the forests. This is reflected by the considerable scatter in points when we plot the number of species, and diversity or number of individuals as a function of the canopy cover index (Fig. 9). Nevertheless there is a statistically significant inverse correlation between the canopy cover index and the number of individuals ($P< 0.02$).There is also a suggestion that both the number of species and diversity are more variable and can reach very high levels at intermediate levels of canopy cover while relatively fewer species and lower diversity are obtained at very high or very low value of canopy cover index.

Sampling strategy: Our sampling strategy, aimed at making the methods quantitative and unbiased, involved three steps. First, we employed 5-6 replicates of each method within each plot (except in the case of light trap). Second, we employed four methods (light trap, net sweeps, pitfall traps and scented traps) within each plot. Finally, we sampled from three replicate one hectare plots within each site or habitat type (Twelve sites drawn from two elevations were sampled but this was meant to apply the underlying methodology).

In an attempt to evaluate each of these steps in our strategy, we have performed a nested ANOVA and partitioned the variance in the number of individuals of each species into the following compartments: (1) between replicates of the same method within a plot, (2) between methods within a plot, (3) between replicate plots of the same habitat type, (4) between different habitat types and (5) between elevations. Repeating this analysis separately for each of the 1,789 species, we present the minimum, maximum, mean and standard deviation of the percentage variance at each level in Table 5. On an average, 73.6% of the variance is seen between replicates of the same method within a plot, 23.7% between different methods within a plot, 1.7% between replicate plots of the same site or habitat type and a negligible amount of variance is seen between habitat types and between elevations. We conclude from this that the two most important steps in our sampling strategy required to ensure the collection of a wide variety of insects from each locality are to use replicate traps of each method within a plot and to use different methods to trap insects within each plot. Sampling from replicate plots of each site, on the average, adds only a minor component of the variance but we nevertheless recommend at least some replication of plots because in specific cases such replicate plots may be useful. For instance, in Chandavar M.F., Bengle M.F. and Bidaralli R.F. one of the three replicates was quite different from the other two (Fig. 7.)

Habitat "*Specializations:*" Comparing the relative contributions of different insect orders both in terms of number of species and in terms of number of individuals, we find that in some sites a very large proportion of the spelcies or individuals belong to one insect order and the dominant order varies from site to site. While some sites are so "specialized" others appear to be more "generalized" with a fairly even distribution of species and individuals across 4 or more orders.

A few of the relatively clear examples of this phenomenon are shown in Fig. 10. 75% of all insects caught in Mirjan M.F. belonged to Coleoptera. 58% of all insects caught in Chandavar M.F. belonged to Diptera whereas in Bhairumbe M.F. 28% of the insects belonged to Hemiptera, 25% to Coleoptera, 22% to Hymenoptera and 17% to Diptera. Similarly 40% of all species caught from Mirjan M.F. belonged to Coleoptera, 38% of all species caught in the *Eucalyptus* plantations belonged to Hymenoptera but in Bengle M.F., 25% of the species belonged to Hymenoptera, 25% to Diptera, 22% to Hemiptera and 19% to Coleoptera

Trophic structure of insect communities: Since all specimens are identified up to the family level, it is possible to determine the approximate trophic structure of the insect communities encountered in this study. Most insect families can be assigned to any one trophic level such as phytophages, predators, parasites and scavengers. The greatest difficulty in doing this was encountered in the family Formicidae. The ants have therefore been set aside as a separate category. The relative contributions of different trophic levels vary enormously. As in the case of the distribution of orders, we find that in some sites a very large proportion of the species or individuals belong to a particular trophic level and that

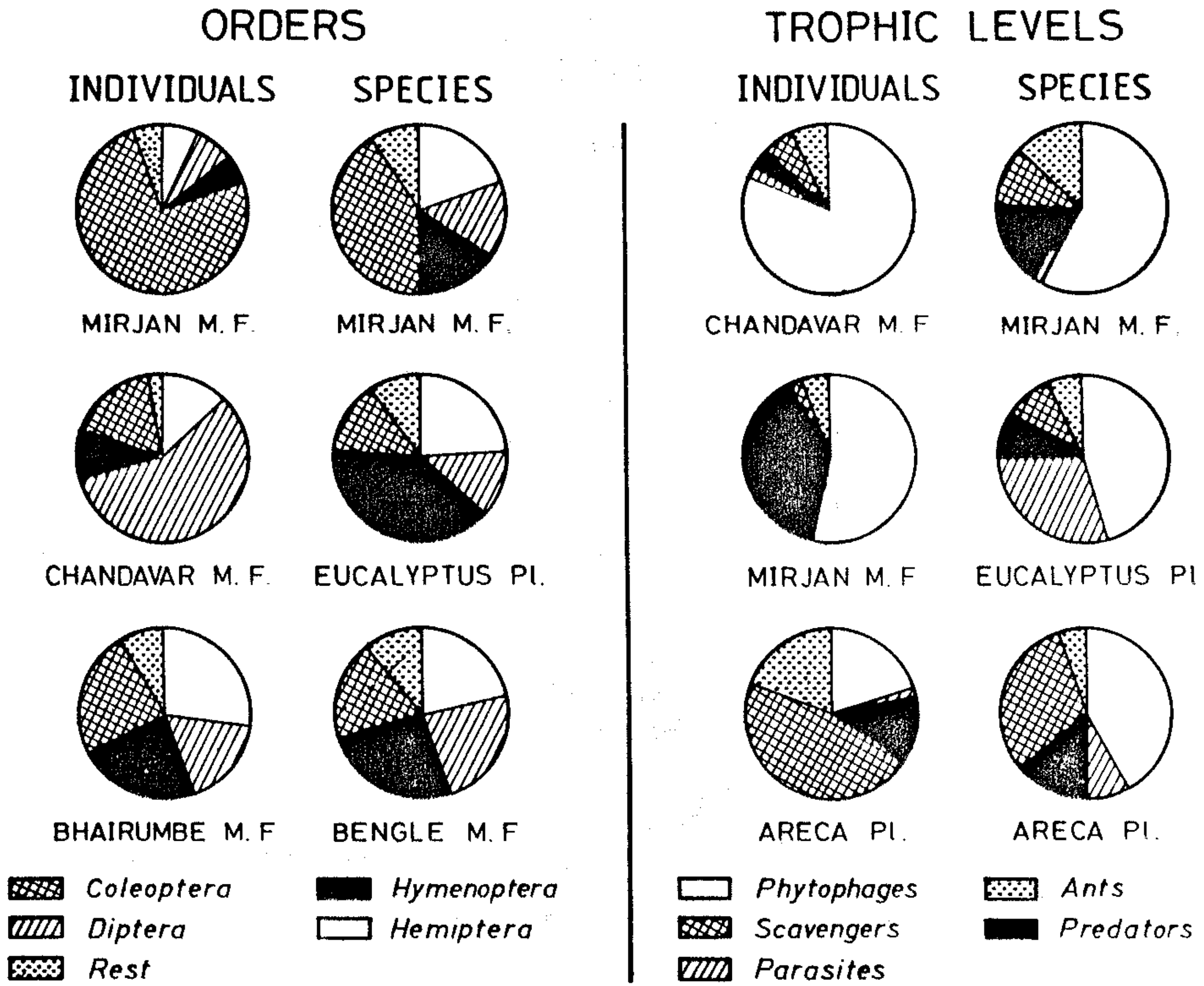


Fig. 10. Pie-charts showing the proportion of individuals and proportion of species belonging to different orders and different trophic levels in some selected sites.

TABLE 5
NESTED ANALYSIS OF VARIANCE TO PARTITION VARIANCE BETWEEN DIFFERENT COMPONENTS OF THE SAMPLING STRATEGY

	Distribution of variance (%)			
	Minimum	Maximum	Mean	Standard deviation
Between replicates of the same method in a plot	0	99.7	73.6	37.7
Between different methods within a plot	0	100	23.7	38.4
Between replicate plots of the same habitat type	0	18.6	1.7	1.7
Between different habitat types	0	33.8	0.9	2.6
Between elevations	0	10.1	0.1	0.4

the dominant trophic level varies from site to site. A few clear examples of this are shown in Fig. 10. Nearly 82% of all insects caught in Chandavar M.F. were phytophages, nearly 54% of insects caught in Mirjan M.F. were phytophages whereas in *Areca* plantation only 20% were phytophages. Instead, scavengers account for 47% of the individuals caught in the *Areca* plantation. Ants constituted only 7% and 5% respectively of the individuals caught in Chandavar M.F. and Mirjan M.F. but constituted as much as 19% of the insects caught in *Areca* plantation.

Similar patterns can be illustrated with reference to the number of species rather than the number of individuals. Less than 2% of the species caught in Mirjan M.F. were parasites whereas nearly 29% of the species caught in the *Eucalyptus* plantation were parasites. Just as in the case of individuals, scavengers constituted a very large proportion of the species (31%) in the *Areca* plantation.

DISCUSSION

We have outlined here a strategy for quantitative sampling of insects in forested habitats and plantations that is likely to be useful to tropical ecologists with modest research budgets and minimal facilities. We argue that methods requiring the operation of a light trap continuously for months or years and especially in forested sites are inaccessible to most ecologists living and working in the tropical countries of the world. On the other hand it is studies of tropical communities that are most urgently needed and most likely to provide adequate field data required for understanding the principles of community ecology. We have therefore standardized a package of methods involving a small, portable, dry battery operated light trap and supplemented with other methods such as net sweeps, pitfall traps and scented traps. In an effort to make the methods reproducible, we have, by careful standardization, attempted to hold the sampling intensity or effort constant. One sampling unit thus corresponds to one light trap operated for a fixed number of hours in the middle of a one hectare plot, 6 net sweeps performed by a standardized method in 6 randomly chosen 10 m x 10 m quadrats, 5 pitfall traps and 5 scented traps placed at randomly chosen positions for 18 hours in a one hectare plot. Such a sampling exercise can be completed in 24 hours and therefore may be repeated every day by the same people and the same equipment. We have shown that such a sampling method yields a collection of insects which may be said to broadly represent that site. The method could thus be used to compare insect communities in different habitats or across different seasons and can also be used for long term monitoring of changes in tropical habitats (See Hammond 1990 and Stork and Brendell 1990 for similar efforts).

Traditional methods based exclusively on operating powerful light traps every night represent a very intense level of sampling compared to our methods. The result is that it is impossible to use all the insects caught in these light traps Most investigators are forced to discard the bulk of the catches and concentrate their attention on one or a small group of insect species. The methods we describe sample insects at a much lower intensity making it necessary and possible to use all the insects collected Clearly, this is a more efficient procedure and leads to minimal destruction of natural populations of insects Undoubtedly, the traditional powerful light trap method is more convenient – little or no work is required on the part of the investigators and sorting and identifying insects belonging only to a small, selected, familiar group is relatively easy. Our method requires more work on the part of the investigators both in terms of preparation and laying out the traps and more significantly in sorting all the insects belonging to different and often unfamiliar groups Tropical ecologists will inevitably have to pay some price for not always being able to set up well organized research stations and obtain large budgets. We believe that the price in terms of man-power required by the methods we describe is small and a requirement of man-power is one price that tropical countries can pay relatively easily Besides, the methods we have used will also help detect community level changes in the insect fauna This is not usually achieved when only a selected group of species is monitored.

Because of the low intensity of sampling and the consequent need to include all insects collected in any analysis, we thought it best to use a variety of different trapping methods so as to attract different kinds of insects Our finding that the catches for each of the 4 methods are quite different from each other justifies this. Because of the low intensity of sampling and the consequent small numbers of insects caught in each trap leading to random fluctuations, we thought it necessary to include several traps of the same kind in each plot and to use at least 3 replicate plots in each habitat site Although the insects caught by the same method have greater similarity to each other rather than to insects caught by other methods in the plot, there are a few exceptions Similarly, although the insects caught in different replicate plots of a site have a greater similarity to each other rather than to insects caught in some other site, again there are a few exceptions These exceptions justify the inclusion of replicate traps and replicate plots, but the relative rarity of these exceptions suggest that the extent of replication is fairly adequate.

In the process of standardizing these methods, we applied them to 12 carefully selected sites representing diverse habitat types so that, if the methods were successful, we might have something to say about the habitat types. We believe that the methods are successful and we therefore rank the chosen sites in their order of diversity values. The range of diversity values obtained is sufficient to permit us to make these comparisons with statistical significance

Another interesting result we have is that with the exception of the teak plantation, the coastal and the elevation sites form 2 different clusters, suggesting that geographical separation and altitudinal variation override even extreme differences in levels of disturbance We obtained this result in spite of including relatively undisturbed reserve forests, relatively disturbed minor forests as well as monoculture plantations both among the coastal as well as elevation sites. This is not to say that there was no difference among the various sites in one region. Several statistically significant differences in levels of diversity between sites in the same geographical region and altitude were obtained And yet similarity between sites within one geographical and altitudinal region was greater than similarity across geographical or altitudinal regions In addition to providing a method of understanding and comparing tropical habitats we believe that such a method, if applied on a large scale, will permit tropical ecologists to generate substantial field data relevant to current ecological theory.

For example, we have made an attempt to understand the factors affecting the distribution of diversity and abundance of insects Using the canopy cover index as an objective and continuous measure of levels of disturbance, we have shown that the number of individuals is inversely correlated with the canopy cover index As the canopy is opened up, we find many more insects in the forest understorey This result is further evidence that the insects we trap are at least loosely associated and therefore characteristic of a given region Canopy cover is clearly only one of the many factors that must affect distribution of insects. Despite the resultant scatter in the data, we have an indication that insect diversity can reach high levels at intermediate levels of canopy cover. When the canopy is closed there is little understorey vegetation and hence, little insect activity. When the canopy is completely opened up, it results in nearly dry and barren land It is at intermediate levels of canopy cover that a rich mosaic of habitat types can form in the forest understorey and lead to high levels of insect diversity.

The sites we have studied are different from each other in many ways. One of the more interesting differences lies in the proportional representation of species or individuals belonging to different insect orders While some sites are "generalized" in that they have a fairly uniform distribution across 4 or more orders, others are more "specialized". For instance, Mirjan M.F. is a Coleoptera "specialist", Chandavar M.F is a Diptera "specialist". Similarly, some sites are dominated by phytophages while others are either dominated by other trophic levels or have a relatively even representation of different trophic levels Some sites have few ants or parasites while others have a large number of these. Why is there such a pattern in the distribution of insects ? Data of this kind will help formulate specific studies intended to understand the factors governing insect distribution We believe that these methods will be equally useful for monitoring seasonal and long term changes in tropical habitats Work is in progress to apply these methods in that direction

It is now widely recognised that tropical habitats face a much greater threat of destruction than other regions of the globe This makes the study of tropical insect communities both urgent and challenging It is also true that the economic conditions of most tropical countries make a certain amount of developmental activity inevitable. For this reason, ecologists are being increasingly called upon to make assessments of the impact of such developmental projects on tropical biotic communities. We hope that the methods described here will contribute towards meeting these challenges

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CHAPTER IX

THE AMPHIBIAN FAUNA OF KARNATAKA: WHAT DOES IT SUGGEST?

R.J. Ranjit Daniels[*]

INTRODUCTION :

Of all vertebrates, the amphibians are considered biologically the most unique and ecologically, the best indicators of environmental health These animals owe their repute to their 1) bimodal life - a dependence on both land and water, 2) sensitive, permeable skin which has to be moist for efficient gas exchange, 3) cold bloodedness - as a result being able to survive on low energy and 4) requirement of rather stable surrounding temperature viz., 20-30°C to which they are best adapted (Duellman & Trueb, 1986; Duellman, 1989; Blaustein & Wake, 1990).

In a recent discussion on declining populations of amphibians, Blaustein and Wake (1990) have said that these animals are being reduced in numbers all over the globe While there is evidence that habitat destruction has played a significant role in this regard at least in the equatorial countries, biologists are perplexed by the disappearance of amphibians from seemingly protected areas as well. Some possible, though not readily discernible, reasons for the decline are natural such as random fluctuations in the populations. However, in marginal and isolated habitats, these fluctuations can eliminate species and often permanently, as amphibians are poor dispersers Of the others, industrial and pesticide pollution and direct harvest by man are noteworthy

Declining amphibian populations could have a major impact on other organisms including humans Amphibians are integral components of many ecosystems, often contributing the highest fraction of vertebrate biomass. Moreover, amphibians are top carnivores and are major consumers of invertebrates especially insects They are also eaten by predators such as fish, snakes, birds and mammals Thus the loss of amphibians in any ecosystem could profoundly affect the populations of the animals that they eat and the animals that eat them.

As mentioned earlier, amphibians are also excellent indicators of environmental stresses. Their bimodal life exposes them to both aquatic and terrestrial pollutants - and they are particularly sensitive because of their highly permeable skin which can rapidly absorb toxic substances. Further, the egg stage is extremely susceptible to chemical pollutants, and exposure to high concentrations of certain chemicals can result in developmental abnormalities. The growth rate of frogs and toads may be significantly affected by even short-term exposures to acid conditions (Blaustein & Wake, 1990)

The general biology and ecology of amphibians thus suggest that they are to be looked at more carefully in any environmental monitoring programme. Unfortunately, as in many other tropical countries, these animals have been neglected for a long time in India. Few have looked at Indian amphibians form the point of view of conservation of biological diversity (Daniels, in press a) Therefore in the discussion that follows I would bring out some of the little known facts about the diversity, status and ecology of the amphibians of Karnataka with special reference to those found in the west where much of its biological diversity lies.

AMPHIBIANS OF KARNATAKA :

The state of Karnataka is one of the 5 major states that share the biological wealth of the Western Ghats. At least 7 districts in Karnataka viz., Uttara Kannada, Dakshina Kannada, Shimoga, Chickmagalur, Hassan Kodagu (Coorg) and Mysore (to a lesser extent) are hilly and preserve a significant proportion of the natural vegetation of the Western Ghats For instance the Uttara Kannada district with about 70% of its area under forest is easily the most forest-covered district in south India It is therefore not surprising that 50% of the amphibian fauna of the Western Ghats are known from Karnataka alone.

The Western Ghats are considered as the richest in amphibian species in the whole of tropical Asia. There are 117 species of frogs, toads and caecilians (legless amphibians) hitherto described from the Western Ghats (Table 1). This narrow biogeographical province is also remarkable for the amphibian fauna unique to it

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in that 86 species (including 14 caecilians) are endemic; many being forest and hill stream specialists (Boulenger, 1890; Daniel, 1963 & 1975; Daniel & Sekar, 1989; Inger & Dutta, 1986; Chanda & Ghosh, 1989; Das, 1990).

There are 58 species of amphibians reported from Karnataka (Table 1; Appendix). Thanks to the efforts of early workers such as Professor C.R.N Rao (1937) many species of amphibians have been described from Karnataka. Thus Karnataka as a state stands next only to Kerala in its wealth of amphibian species. However, when smaller areas are compared, it turns out that the Kodagu-Hassan - Dakshina Kannada forests hold the maximum number of species in the entire Western Ghats (Daniels, unpublished manuscript).

Some of the amphibians of interest include the Malabar torrent toad *(Ansonia ornata)*. This little known toad is restricted to the forests of Kodagu and Dakshina Kannada in Karnataka and has not been discovered elsewhere in the past 100 years (Daniels, in press b). The tadpoles of this colourful toad are found in clear, torrential streams clinging to the slimy rocks against the water current. The only other species of torrent toad known from the Western Ghats is *Ansonia rubigina* discovered recently from Silent Valley in Kerala (Pillai & Pattabiraman, 1981). Another amphibian partial to the torrential streams is the frog *Micrixalus saxicola*. This species was first known from Kerala and nowhere considered common. However, it is common in a few streams in the hills of Dakshina Kannada and Chickmagalur showing a preference for perennial, fast flowing streams strewn with boulders and bordered by lush vegetation (Daniels, pers. observ.)

Frogs in the genera *Ranixalus*, *Nannobatrachus* and *Nictibatrachus* are endemic to the Western Ghats. *Ranixalus gundia*, the sole representative, of the genus is exclusive to Karnataka. Species of *Nannobatrachus* are probably the smallest amphibians on the Western Ghats. Of the 2 species hitherto described in this genus, *N. kempholeyensis* is known only from the Hassan district. Species of *Nyctibatrachus* are rather flattened frogs with diamond-shaped pupils. Of the 8 species so far known to science, 5 occur in Karnataka. They vary in size from less than 3.0 cm *(N. aliciae)* to 8.0 cm *(N. humayuni)*. *Nyctibatrachus* aliciae was described for the first time by Robert Inger and colleagues (1984) from southern Kerala and *N. humayuni* was first reported by Bhaduri and Kripalani (1955) from Uttara Kannada-Goa forests. It is therefore interesting to note that these two species coexist in the forests of Neria in Dakshina Kannada (Daniels, pers. observ.).

That there is a poor representation of caecilians in Karnataka is not surprising. These legless amphibians are burrowing and very secretive. Hardly anything is known of their patterns of distribution and ecology. More efforts would certainly unearth a few more species in Karnataka. For instance, between 1990 and 1991, I discovered a handful of toad and frog species including *Bufo parietalis*, *Rana keralensis*, *Nyctibatrachus* spp, *Micrixalus saxicola* and *Polypedates cruciger* for the first time in the forests of Dakshina Kannada. *Polypedates cruciger* is a treefrog which was considered to be endemic to Sri Lanka till this time (Daniels, in press a & c). However whether many species have perished undiscovered already in recent times and would others wait to be discovered is a major issue that should cause some concern to the environmentalists.

Much of what has been discussed above point only to the biogeographical and evolutionary history of the amphibians of Karnataka. What is probably more important is their ecological requirements such as habitat structure, species interactions and predator pressure and the array of human threats that they are facing today. Hence, in what follows, I briefly discuss these aspects.

HABITAT STRUCTURE :

All amphibians can be simply grouped based on habits into 1) aquatic, 2) terrestrial, 3) arboreal and 4) fossorial. Depending on the habitat type any one of these 4 groups can dominate in biomass. For instance in any agricultural ecosystem such as paddyfields, there is an abundance of aquatic species including *Rana tigerina*, *Rana cyanophlyctis*, *Rana hexadactyla* and *Rana limnocharis*. Fossorial species spend most of their time underground such as *Microhyla rubra*, *Kaloula pulchra* and the balloon frogs *Uperodon* spp, which are all in the family Microhylidae. These are common in the more seasonal habitats such as deciduous and scrub jungles. Terrestrial and arboreal amphibians are the most abundant in the moist forests. The evergreen forest environs often afford shelter to amphibians in all the 4 groups and thus are very rich in species. This is a more general trend and has been related to the more stable microclimatic conditions under the forest canopy in the humid tropics (Duellman, 1989).

The amphibians of Karnataka are no exceptions to the general pattern of habitat selection. Of the 34 species that I have observed, 25 were found in the moist forest environs. At least 20 of these species were found in leaf litter on the forest floor. Preliminary studies in the forests of Dakshina Kannada have suggested that an extensive canopy cover and higher density of trees are the two major structural attributes that determine the overall microclimate of the forests. A closed canopy helps preserve moisture in the leaf litter even during the short dry season in the Western Ghats of Karnataka. Hence these forests abound in treefrogs, especially *Philautus* (Table 1) Species of *Philautus* are exceptional in that they deposit their eggs in moist litter where they develop till young frogs emerge without any free-living tadpole stage.

Dense evergreen forests also ensure the continued presence of ground water and hence we find swamps and springs often associated with these forests. Permanently wet habitats are much sought after by most amphibians and particularly by those with peculiar breeding habits One example may be *Rana beddomi* a common litter frog in forests of Karnataka. This species breeds on slimy rock faces well protected by overhanging vegetation. The tadpoles which appear glassy develop in a thin film of clear water on the rock's surface where they are remarkably adept in skittering away at the approach of any predator. Such safe nurseries are however not easily available outside the limits of the humid evergreen forests

Forests also prevent soil erosion and ensure a constant flow of cool, clear and well aerated water in the smaller streams along the hills Many species require such waters for successful development of tadpoles The adults of *Micrixalus saxicola* and *Nyctibatrachus* spp , are extremely sensitive to turbidity and the resultant warming of water (Daniels, pers observ).

SPECIES INTERACTIONS AND PREDATOR PRESSURE :

When more than one species coexist there has to be some sort of interaction Interactions can be simple between predator and prey or more complex when more than one species compete for the same set of natural resources. Where there are less than 10 species such as in an agricultural ecosystem, the interactions are simpler than in evergreen forests in Karnataka where often 13-18 species of amphibians coexist Interactions can be across classes of animals as well. For instance in all our forests there is an abundance of large terrestrial invertebrates such as spiders, scorpions and centipedes which besides preying on smaller amphibians expel them from under logs and rock crevices that are commonly available on the forest floor.

Pit vipers *(Agkistrodon* and *Trimeresurus)* prey on terrestrial frogs on the forest floor as do keelback water snakes (Natricdae) in aquatic habitats The bullfrog *Rana tigerina* is an important amphibian predator Any thing smaller in size is food for this species Measuring 16 cm and weighing not less than 500 g adult bullfrogs are a natural threat to all smaller amphibians wherever they are found In general forest floor amphibians are 2 5-3.5 cm and weigh less than 5.0 g These are safe as bullfrogs do not generally exist within dense evergreen forests However, they are found along the edges and very easily invade the disturbed and secondary forests. I have seen bullfrogs breeding alongside other forest amphibians in hill streams flowing through secondary forests. Juvenile bullfrogs devour any smaller frog within reach. And as there are no dangerously toxic species of amphibians as there are in Central and South America, all smaller frogs are in danger of being devoured by larger frogs and other vertebrates.

THREATS TO AMPHIBIANS :

The most significant threat is large-scale destruction of habitats especially the evergreen forests This has been felt world wide and requires no further emphasis However, the less obvious forms of habitat destruction have not gained the publicity they require For instance, while treefalls and the resultant gaps created are normal in forests, opening the canopy deliberately in the process of selective logging can lead to exposure of forest floor Dessication of the forest floor and litter are serious problems and are deleterious to the terrestrial amphibians Many small swamps and springs which are perenial are rendered seasonal due to openings in the canopy Soil and silt particles in the runoff water reaching streams cause the water to be turbid which in turn makes the water warmer and deficient in oxygen Many species of amphibians including *Nyctibatrachus* perish in such waters

A second form of habitat disturbance is removal of leaf litter from the forest floor. This is a common practice in parts of Karnataka, especially in Uttara Kannada. Leaf litter collected from the forest floor go into betelnut gardens Large areas of the forest floor are swept clean of litter and amphibians as well. Forests may appear intact superficially but the most vital component, the leaf litter, is lost

Fire is another serious threat to terrestrial amphibians. While this is not so much of a problem in the evergreen forests and other wet habitats, it is a common disaster in the drier forests. There are not many species of terrestrial and litter amphibians in the drier forests. However, a few species of treefrogs (Rhacophoridae) and others like the fungoid frog *Rana malabarica*, the balloon frog *Uperodon systoma* and the little known toad *Bufo hololius* often stay dormant within barks at the base of trees or under rotting logs and pieces of wood on the forest floor during the dry season. Uncontrolled fires on the forest floor would simply roast such unfortunate animals alive.

Constant human interference such as deepening or widening of hill streams by removing the bordering vegetation, particularly reeds *(Ochlandra)*, not only destroy breeding sites of many species of treefrogs but also expose the small frogs to predators like *Rana tigerina*. Random check-dams across flowing waters often made to trap fish and left as such stagnate the water making it muddy and poorly aerated.

It is important to mention again that for any amphibian to survive there should be appropriate habitats available for both tadpoles and adults. The bicoloured frog *(Rana curtipes)* for instance, is a common litter frog in the forests of Karnataka. The tadpoles of this species are exceptionally large in size and swim in characteristic schools in large streams and tanks adjacent to forests. The adults are however rarely seen near water and the juvenile frogs stay briefly near water after metamorphosis and disperse into the adjacent forests. This is just one of the many species which show such dependence on 2 major and different habitat types for their survival.

Having discussed some of the physical and biological threats to amphibians let us consider some of the chemical threats. The most serious problems are industrial and factory wastes draining downstream in both hills and plains. In southern parts of the Western Ghats, wastes from rubber factories have probably affected the populations of species of stream-breeding frogs including the common species *Rana temporalis*. This species used to be common in the south about 20 years back where I first saw it. Today it is practically absent in those streams which drain all the wastes from rubber and tea factories. Incidentally, *Rana temporalis* is very common along the streams in Silent Valley and parts of Dakshina Kannada (Daniels, in press a).

Heavy metal and other synthetic toxicants are often found in high concentrations in urban and suburban sewage. On the Indian Institute of Science campus at Bangalore, for instance, all open drains that flow continuously are polluted with a variety of such chemicals. There are at least 7 species of frogs and toads in this campus. However, even the most common species viz., the paddyfield frog *(Rana limnocharis)* avoids these drains. Cities in Karnataka, suburbs and even rural plains are not exempt from polluted waters flowing through. Pollutants from cities draining downstream continue to remain at dangerous concentrations even at a distance of 100 km from the source (Thomas Burton, pers. commun.).

Pesticides in the neighbourhood of hill estates and agricultural areas directly and indirectly destroy amphibians. Direct poisoning is common both in water and land. Indirect poisoning by consuming poisoned insects is very likely in all cultivated areas. Whereas DDT holds a world wide repute as being the most dangerous and persistent environmental toxicant, many other more dangerous insecticides are being passed as 'safe'. In any agricultural areas, especially where commercial crops are grown, organophosphorous insecticides such as Nuvacron, Metacid, Rogor and Metasystox are often excessively used. I have witnessed in parts of Tamilnadu insectivorous birds fall dead after consuming poisoned insects rising from cotton fields treated with one or more of these insecticides. Slow release granular pesticides such as Furadon and Thimmet are commonly applied to soil in rice and sugarcane fields to prevent root and shoot pests. Amphibians are directly exposed to these poisons.

Fertilizers can be equally dangerous in water. Excess nitrate salts in water suffocate even adult frogs. Frogs including *Rana tigerina* kept in plastic or glass jars are soon suffocated in their own nitrate rich excrement. Nitrified water give rise to excessive algal blooms rendering the habitat largely unfit for breeding amphibians. Much of the hill streams in the Western Ghats including those in Karnataka are subject to nitrate rich runoff water from estates and plantations uphill. A well protected patch of forest downstream would be under such indirect stresses and hence it may not be readily obvious why amphibians are disappearing from even 'seemingly well-protected areas'.

The last form of threat is that posed by humans directly. Frog-legs and the so-called scientific quest have together eliminated tonnes of frogs locally. While export of frog-legs has at least been temporarily banned, collections in the name of science continue. Year after year frogs are being dissected to serve no real purpose. *Rana hexadactyla* the green frog has been the unfortunate victim in this mission of education. Its a large frog. And as size is the only criterion for local collections, adult females (which are often gravid) including other larger species such as *Rana tigerina* and *Rana cyanophlyctis* indiscriminately reach biology laboratories. 'Scientific expeditions' are no better. Hundreds of specimens have been simply removed from forests for the sake of museums and other private collections. However since all these are done in the guise of 'exploratory science', they are passed (Daniels, in press a)

CONCLUDING REMARKS :

The state of Karnataka has a very diverse amphibian fauna. However, very little research efforts have been directed on these rather gentle and delicate animals. Whatever information that exists suggest that amphibians are very sensitive to environmental changes and their disappearance from any ecosytem should warn us of the more dangerous consequences. That new species are being discovered each day only indicates that the diversity is much more than expected. There is therefore a need to do more intensive studies on amphibians. It would be best if scientists felt the urgency involved as many species are being threatened with extinction even as they are being discovered

Habitat management is essential. For instance removal of leaf litter from the forest floor might be curbed during the nonrainy season. Specimen collection and indiscriminate killings must be discouraged. While it is often required to collect a few individuals of any new species for the sake of identification and documentation, massive collection expeditions can be avoided. Scientists should resort to non-destructive field studies of amphibians. After all, if we are to preserve more species they should be living where they ought to be and not pickled in bottles

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Table 1: Taxonomic breakup of the amphibian fauna of the Western Ghats and Karnataka

Order	Family	Genera	Number of species	
			W.Ghats	Karnataka
Anura (Frogs and Toads)	Bufonidae	Ansonia	2	1
		Bufo	10	7
		Pedostibes	1	-
	Microhylidae	Kaloula	1	1
		Melanobatrachus	1	-
		Microhyla	2	2
		Ramanella	6	4
		Uperodon	2	2
	Ranidae	Micrixalus	6	1
		Nannobatrachus	2	1
		Nyctibatrachus	8	5
		Rana	25	14
		Ranixalus	1	1
		Tomopterna	6	3
	Rhacophoridae	Philautus	24	12
		Polypedates	2	2
		Rhacophorus	4	1
Gymnophiona (Legless amphibians/Caecilians)	Ichthyophidae	Ichthyophis	7	1
		Uraeotyphlus	4	-
	Caecilidae	Gegeneophis	2	-
		Indotyphlus	1	-
Total 2	6	21	117	58

Appendix : A list of amphibians known from Karnataka

Bufonidae

Ansonia ornata
Bufo brevirostris
Bufo fergusoni
Bufo hololius
Bufo melanostictos
Bufo microtympanum
Bufo parietalis
Bufo stomaticus

Microhylidae

Kaloula pulchra
Microhyla ornata
Microhyla rubra
Ramanella minor
Ramanella mormorata
Ramanella triangularis
Ramanella variegata
Uperodon globulosum
Uperodon systoma

Ranidae

Micrixalus saxicola
Nannobatrachus kempholeyensis
Nyctibatrachus aliciae
Nyctibatrachus humayuni
Nyctibatrachus major
Nyctibatrachus sanctipalustris

Nyctibatrachus sylvaticus

Rana aurantiaca/bhagmandlensis
Rana beddomi
Rana curtipes
Rana cyanophlyctis
Rana hexadactyla
Rana intermedius
Rana keralensis/verrucosa
Rana leithii
Rana limnocharis
Rana malabarica
Rana sauriceps
Rana temporalis
Rana tenuilingua
Rana tigerina
Ranixalus gundia
Tomopterna breviceps
Tomopterna dobsonii
Tomopterna leucorhynchus

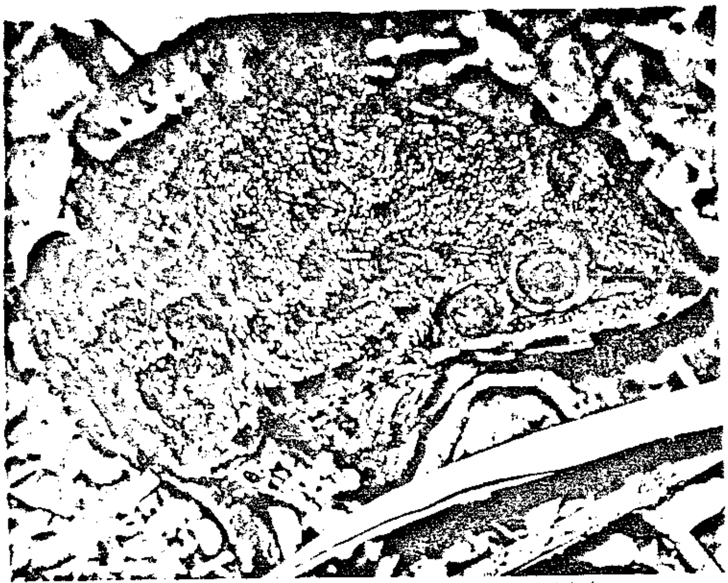
Rhacophoridae

Philautus charius
Philautus crni
Philautus elegans
Philautus femoralis
Philautus hassanensis
Philautus kottigeharensis
Philautus longicrus?
Philautus melanensis
Philautus montanus?
Philautus narainensis
Philautus swamianus
Philautus temporalis
Polypedates maculatus
Polypedates cruciger
Rhacophorus malabaricus

Ichthyophidae

Ichthyophis beddomi

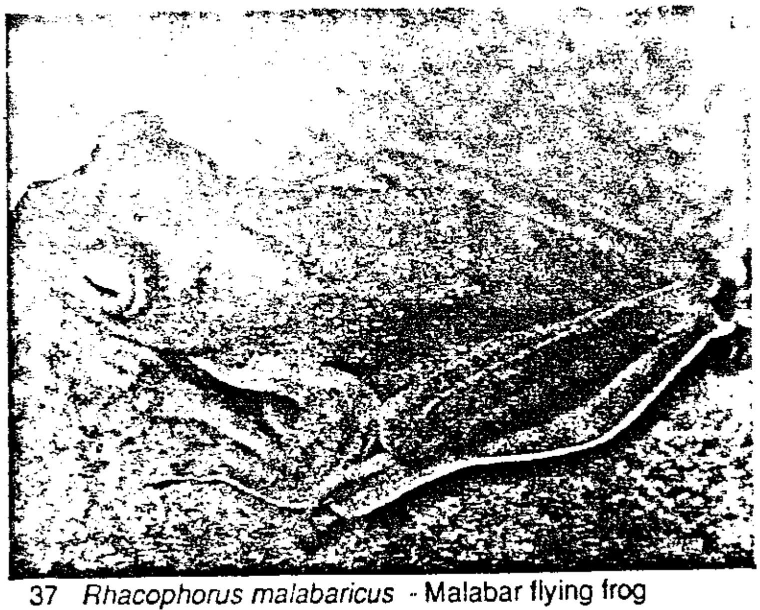
FROGS IN KARNATAKA



34 *Rana tigerina* - largest **carniverous**amphibian sought after by laboratories and restauranters

35 *Polypedates cruciger* - tree frog from Karnataka
A new record for India

36 *Bufo parietalis* - forest toad in leaf litter of evergreen forests in Dakshina Kannada



37 *Rhacophorus malabaricus* - Malabar flying frog strikinglycoloured amphibian in Western Ghats of Karnataka

38 *Rana hexadactyla* - the green frog - sought afte
its size by industries and laboratories

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Changes in the Bird Fauna of Uttara Kannada, India, in Relation to Changes in Land Use over the Past Century

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ABSTRACT

The hilly district of Uttara Kannada (13°55′N–15°32′N Latitude and 74°5′E–75°5′E Longitude) with an area of 10 200 km² is one of the most forested tracts of south India although the total area under forest has been reduced from 80% to 70% over the past century Excellent documentation of the bird fauna exists from the 1890s and 1980s with a shorter survey conducted in 1938 An analysis of these three surveys suggests that the size of the total bird fauna has remained constant around 465 ± 20 taxa over this period However most of the thirty-one resident bird taxa recorded earlier but not sighted in the recent survey, as well as nine taxa observed only recently are notable habitat specialists Only a few of these specialists that have probably been lost over this period are forest birds the majority being characteristic of the drier cultivation and scrub areas. Recent invaders seem to prefer aquatic ecosystems and it is suggested that this may be a more general pattern It is therefore vital that more attention be paid to conservation of the biological diversity of the semi-arid tracts of the Indian subcontinent

INTRODUCTION

While loss of biological diversity, especially in the developing countries of the tropics, has become a matter of worldwide concern, there are relatively

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few good field data to support this. Most of the available information is either based on rather incomplete surveys or more complete investigations of relatively restricted areas such as individual islands or forest reserves (Leck, 1979; Brash, 1987; Whitten *et al.*, 1987). The Indian subcontinent is amongst the biologically better known parts of the tropics and its bird fauna has been extensively documented, from Jerdon's (1862–64) pioneering investigations to Ali & Ripley's (1983) authoritative handbook. However, an investigation of the regional changes in India's bird fauna in some depth against the background of a massive increase in the human population, extensive deforestation and substantial changes in the pattern of land use, has not been possible until now as there have been very few long-term studies of the bird fauna of any region within India, most being based on surveys lasting from a few weeks to a few months and being obviously very incomplete. An important exception to this is Davidson's (1898*a*, *b*) account of the birds of Uttara Kannada (earlier known as North Kanara/Canara) based on five years' careful observations and collection between 1888 and 1896. The northern part of the same district was resurveyed over a period of three months in 1938 by Koelz (1942). We therefore have an excellent historical record almost precisely from a century and half century ago of the birds of this district. The field studies of R.J.R.D., ranging over a five-year period from 1983 to 1988, provide the most complete regional study of the current bird fauna of India. These three data sets are therefore an excellent basis on which to examine whether there have been significant changes in the bird fauna of this region, and if so what its implications are for a long-term strategy of conserving India's heritage of biological diversity.

THE LOCALITY

The district of Uttara Kannada (13°55′ to 15°32′ N Latitude and 74°5′ to 75°5′ E Longitude), with an area of 10 200 km^2, lies at the centre of India's west coast where the hill range of Western Ghats, parallel to the coast, is at its lowest and broadest, running all the way to the sea, but hardly ever rising to over 600 m in altitude. The annual rainfall ranges from 350 cm near the coast to 500 cm at some places on the crestline of the hills, but decreases to 120 cm on the eastern edge where the hills merge with the Deccan plateau. Only 1000 km^2 of the total area are cultivated and 130 km^2 are orchards. Of the rest, 7000 km^2 are in different stages of degraded forest and the remainder villages and townships, reservoirs and barren hill tops (Gadgil *et al.*, 1985–86). The forests are well distributed and, except for the heavily settled narrow coastal strip, 80% of the 5 km × 5 km grids into which the district may be divided still retains some forest cover (Pascal, 1984, 1986).

The major transformation undergone by the region over the last century is a reduction in total forest cover from over 8000 km^2 (Campbell, 1883) to around 7000 km^2 (Pascal, 1984; Gadgil *et al.*, 1985–86; Kamath, 1985), this land being converted to townships, mines and hydroelectric projects or reservoirs. These changes have largely occurred in the hilly regions away from the coast which were earlier malarial and almost totally under forest cover interspersed with very small enclaves of cultivation and orchards. The first major saw mill was opened in this hilly tract in 1917 followed by a plywood factory in 1944 and a paper mill in 1955. Manganese and iron-ore mining also began in 1955, and by 1983 266 km^2 of forest land had been cleared. A hydroelectric project along the river Kalinadi in the north of the district has since 1970 destroyed 145 km^2 of forest. Along the coast more than 25 km^2 of land was planted with cashew *Anacardium occidentale* and, in the drier eastern parts, at least 70 km^2 with the Australian blue gum *Eucalyptus* spp. since the 1960s (Kamath, 1985).

Campbell (1883) mentions that there were more than 7000 ponds and tanks in the district, 60% of which were used for irrigation. However, these were all small and shallow and went dry during summer. Furthermore, due to non-availability of cultivators because of the malarial conditions, a 'great deal' of the more than 1000 km^2 of available cultivable land was lying barren. The development of major irrigation projects since 1956 has brought more than 130 km^2 of this area from the drier eastern belt under irrigation. The number of wells fitted with electric irrigation pumps has also risen from 39 in 1971 to 5385 at present. As a consequence, what were dry scrub and fallow lands a century ago are now under irrigated cultivation and there are large perennial reservoirs in the driest parts of the district (Kamath, 1985; Gadgil *et al.*, 1985–86; Gadgil & Subash Chandran, 1988).

METHODS

Davidson (1898*a*), though he spent most of his spare time collecting (by shooting) and identifying birds all over the district, mentions that his list is 'incomplete'. For every bird listed, clear details are provided of geographic distribution, some mention of abundance, commonness and rarity, habitat preference, nesting season and migration. Koelz (1942), on the other hand, collected and identified birds from a small portion (a triangle of *c.* 25 km on each side) in the north of the district between January and March 1938. Within this short period he listed 232 taxa, most of which are forest-dwellers. For these birds, he recorded some information on geographic distribution, habitat preference, abundance, commonness and rarity, although not as detailed as Davidson's. Koelz did not visit the coastal marshes and seashores, and thereby almost totally omitted the waders, ducks and other common waterfowl that frequent the district

The recent survey done by R J R D was more systematic. Between 1983 and 1988, the entire district was traversed. Birds were sight-recorded during the first two years on 36 1-ha plots distributed over a few localities. The latter part of the survey involved sampling on more than a hundred 600-m long transects laid all over the district, representing most of the major habitat types. In addition, systematic records were kept since 1983 of every bird taxon opportunistically encountered outside the sample limits and while travelling. For each of the 343 taxa encountered during the 5-year period, details of geographic distribution and habitat preference are available. The district was divided into about 500 5 km × 5 km grids and the present patterns of distribution of these birds and the major habitat types were mapped. It seems appropriate in this context to treat a species and subspecies of bird alike. Therefore, the term 'taxon' has been used throughout the text to refer generally to a species or subspecies of bird

RESULTS

Our basic data set is the sighting of 341 taxa by Davidson (D), 232 by Koelz (K) from a part of the district and 343 by R J R D (R). These data are analysed, first for all birds, and then for all birds except the saltwater taxa not seen by Koelz (Table 1). There are three possible reasons as to why some taxa were recorded by one of the observers but not by one or more of the others: (1) The taxon was present, but the other observer/s failed to record it; (2) the taxon was not present at the time, but this was a part of the normal turnover of the total bird fauna unrelated to any change in the habitat; or (3) the taxon was not present because its preferred habitat was not available

TABLE 1

Number of Bird Taxa Recorded by Davidson and or Koelz[a] and or R J R D from Uttara Kannada District

	Observers							*Total*
	DKR^b	$DK\bar{R}^c$	$D\bar{K}R$	$D\overline{KR}$	$\bar{D}KR$	$\bar{D}K\bar{R}$	$\overline{DK}R$	
All taxa	195	9	95	42	17	11	36	405
All taxa except salt-water birds	195	9	76	35	17	11	18	361

[a] Koelz spent only 3 months on his survey whereas Davidson and R J R D spent 5 years each
[b] Seen by all three observers
[c] Seen by D & K but not by R and so on

Preston (1979) suggests a simple model for estimating the number of bird taxa that any particular observer fails to record. He assumes the visibilities of all taxa to be equal and the chances of detecting a given bird by any observer to be the same. If the total number of taxa present in the locality is N, then Np^n would be the number seen by n observers. This model failed to fit ($\chi^2 = 47$) the birds of Uttara Kannada, excluding those of salt water. We then relaxed two of the assumptions of this model: (1) that the three observers were equally efficient in detecting different taxa, since Koelz spent only three months against the five years by the other two observers, and Davidson collected birds, while R.J.R.D only sighted them; and (2) that the chances of all taxa being recorded were equal. We assumed then that the chance of the ith taxon being recorded by jth observer was

$$1 - (1 - V_i)E_j$$

where V_i is the probability of a bird being recorded, and E_j the efficiency of the observer. We further assumed that V was uniformly distributed between 0 and 1, i.e. if the total number of species was N, then the chance of the ith taxon being recorded was i/N. We then have four unknown parameters, E_D, E_K, E_R and N to be estimated from the 7 data points of the second row of Table 1. This model can be fitted to the data ($\chi^2 = 8{\cdot}3, p < 0{\cdot}05$); as follows: $E_D = 3{\cdot}27$, $E_R = 2{\cdot}99$, $E_K = 1{\cdot}31$, $N = 409$. As expected $E_D > E_R > E_K$. This N excluded salt-water birds. Using the values of E_D, E_R, we can estimate the number of salt-water taxa to be 56. Thus the total avifauna of Uttara Kannada, including those not recorded by any of the three observers, is 465 ± 20, with a confidence interval at 95% level. This is a plausible estimate. Apart from the 405 taxa recorded by the three observers, there are 14 isolated records in the skin collection of the Bombay Natural History Society or in unpublished checklists of amateur birdwatchers. It is also likely that another 14 taxa recorded from the neighbouring states of Goa, Maharashtra and Kerala, but not yet recorded from Uttara Kannada, may also occur here (Ali, 1969; Grubh & Ali, 1976; Abdulali, 1981). This brings the total number to 433, very close to the lower limit (445) of our estimate.

Therefore, at this level of analysis of the regional bird fauna as a whole, there is no reason to suspect any significant decline in the total number of taxa of birds or change in the composition of the bird fauna. The taxa not recorded in various surveys might have been missed simply because of the necessary incompleteness of the surveys. If this is accepted, however, it follows that those missed are most likely to be those with rather low probabilities of being recorded, namely by being highly cryptic or with small localized populations. In this context it is reasonable to exclude winter visitors from consideration, since many of these visit only occasionally. Thus in 1986, a large flock of about 2000 demoiselle cranes *Anthropoides virgo* wintered in Uttara Kannada, almost certainly for the first and only time over the century. Similarly a single individual of the greyheaded lapwing *Vanellus cinereus* was recorded in the northeastern part of Uttara Kannada (15° 10′ N Lat.) in February 1987, this being its first record south of 25° N Lat. If we therefore omit the wintering species from the analysis of taxa recorded earlier and not recorded by R.J.R.D. and *vice versa*, this leaves us with 31 and 9 taxa respectively (Table 2) of locally resident birds, analysed in Table 3

TABLE 2

List of the 31 Taxa of Birds Not Sighted during the Recent Survey but Recorded Earlier by Davidson and/or Koelz (DUK $\overline{R}$) and the 9 taxa Only Recorded Recently by R.J.R.D. ($\overline{DUK}$ R)

DUK $\overline{R}$	$\overline{DUK}$ R
1. *Gyps indicus*	1. *Ardea alba*
2. *Icthyophaga icthyaetus*[a]	2. *Threskiornis melanocephala*
3. *Gorsachius melanolophus*[a]	3. *Platalea leucorodia*
4. *Pseudibis papilosa*[a]	4. *Glareola lactea*
5. *Coturnix coromandelicus*	5. *Sterna aurantia*
6. *Perdicula erythrorhynchus*	6. *Bubo coromandus*
7. *Perdicula asiatica*	7. *Alauda gulgula*
8. *Turnix suscitator*	8. *Estrilda amandava*
9. *Turnix sylvatica*	9. *Lonchura kelaarti*
10. *Turnix tanki*	
11. *Rallus striatus*	
12. *Rallina eurizonoides*	
13. *Sypheotides indicus*	
14. *Rostratula benghalensis*	
15. *Burhinus oedicnemus*	
16. *Cursorius coromandelicus*	
17. *Treron bicinctus*	
18. *Streptopelia decaocto*	
19. *Streptopelia orientalis erythrocephala*	
20. *Psittacula eupatoria*	
21. *Strix leptogrammica*	
22. *Taccocua leschenaulti*	
23. *Centropus toulou*	
24. *Picus myrmecophoneus*	
25. *Mirafra javanica*	
26. *Mirafra assamica*	
27. *Turdoides striatus somervillei*	
28. *Turdoides caudatus*	
29. *Dumetia hyperythra*	
30. *Zoothera dauma*	
31. *Aethopyga siparaja*	

[a] Recently resighted by amateur birdwatchers

TABLE 3

Attributes of Birds Recorded in terms of being Habitat Specialists (S), Rare (R) or Cryptic (C)

Attributes[a]	$DUK\,\overline{R}$[b]	$\overline{DUK}\,R$[c]
SRC	8	1
$SR\overline{C}$	9	1
$S\overline{R}C$	6	NIL
$S\overline{RC}$	1	4
$\overline{SR}C$	2	1
$\overline{S}RC$	1	NIL
$\overline{S}R\overline{C}$	4	2
$\overline{SRC}$	NIL	NIL
Total	31	9

[a] SRC taxon that is a habitat specialist, rare and cryptic; $SR\overline{C}$, taxon that is a habitat specialist and rare but not cryptic, and so on

[b] Recorded by Davidson and/or Koelz but not by R J R D

[c] Recorded by R J R D but not by Davidson and Koelz

according to habitat specialization, cryptic characteristics and rarity. Rarity is defined here as species not seen more than four times, always in very small numbers or in highly localized populations

Table 3 reinforces the conclusion that being rare or cryptic, and consequently not being recorded, could largely account for the apparent changes in the bird fauna. Nevertheless, it is also apparent that habitat specialization is the single most significant attribute of those birds not recorded at any time. It is thus likely that there have been some actual changes in the composition of the bird fauna of the Uttara Kannada, over and above those that can be attributed to some taxa being missed. Such a change could be due to normal turnover of the taxa, in which case the habitat specialists and generalists utilizing the different habitats would be represented amongst those recorded only earlier or only recently in the same proportion as in the overall bird fauna. Tables 4 and 5 make such an analysis of the resident taxa. It is evident from Table 4 that habitat specialists are represented comparatively more frequently amongst those which have been recorded either only earlier or only recently as compared to the rest. This suggests that transformation of some specific habitat types may be responsible for the observed changes. Table 5 strengthens this conclusion, showing that taxa utilizing dry cultivation and dry rocky hillocks with scrub are represented in a higher proportion amongst the birds recorded only earlier, and those utilizing aquatic ecosystems are represented much more

TABLE 4

Number of Habitats Utilized by Those Resident Birds which have either been Recorded Only Earlier (DUK $\overline{R}$) or Only Recently ($\overline{DUK}$ R) as Compared to the Remaining 376

Number of habitats utilised	*All birds except DUK $\overline{R}$ & $\overline{DUK}$ R*	*DUK $\overline{R}$*	*$\overline{DUK}$ R*
1	49 (13)	8 (26·7)	0
2	118 (31·5)	12 (40·0)	1 (11·1)
3	74 (19·7)	4 (13·3)	5 (55·5)
4	61 (16·3)	4 (13·3)	2 (22·2)
5	36 (9·6)	1 (3·3)	1 (11·1)
6	12 (3·2)	0	0
7	9 (2·4)	1 (3·3)	0
8	6 (1·6)	0	0
9	3 (0·8)	0	0
10	3 (0·8)	0	0
11	0	0	0
12	1 (0·3)	0	0
13	0	0	0
14	1 (0·3)	0	0
15	0	0	0
16	0	0	0
17	0	0	0
18	1 (0·3)	0	0
19	0	0	0
20	1 (0·3)	0	0
21	0	0	0
Total	375[a]	30[a]	9

Percentages are given in parentheses.

[a] For two of the 416 taxa of Uttara Kannada birds no specific habitat description has been given in Ali & Ripley (1983), the basis on which this analysis and that given in Table 5 have been made

amongst the birds recorded only in the recent survey As mentioned above, dry scrub/secondary thickets and grasslands were amongst the habitats relatively common in the cultivated tracts of the low-rainfall eastern areas as a result of poor irrigation facilities and cultivation practices at the times of the Davidson and Koelz surveys (Campbell, 1883; Davidson, 1898*a*; Koelz, 1942). These have subsequently been transformed through extensive irrigation of cultivated lands and planting of other areas by exotic xerophytic species such as *Eucalyptus* and, recently, *Acacia auriculiformis*. At the same time, the district now has a series of reservoirs developed either for irrigation or power generation, greatly increasing the habitat available for birds dependent on larger water bodies. It is therefore likely that the disappearance of species such as the ring dove ***Streptopelia decaocto*** and

TABLE 5

Utilization of the Different Habitats by those Resident Birds which have been Recorded either Only Earlier (DUK $\overline{R}$) or Only Recently ($\overline{DUK}$ R) as Compared to the Remaining 376

Habitat	*All birds except DUK $\overline{R}$ & $\overline{DUK}$ R*	*DUK $\overline{R}$*	*$\overline{DUK}$ R*
1 Humid/wet rocky cliffs/hilltops	14 (3·7)	—	1 (11·1)
2 Humid/wet/mixed/semi-evergreen/ secondary evergreen forests	133 (35·4)	9 (30·0)	—
3 Humid grasslands	42 (11·2)	8 (26·6)	2 (22·2)
4 Humid/moist degraded/open forests-thickets	150 (40·0)	8 (26·6)	2 (22·2)
5 Humid betelnut/coconut/cocoa banana/mixed plantations	20 (5·3)	—	—
6 Humid/moist exotic tree plantations (*Casuarina Anacardium occidentale Acacia*)	15 (4·0)	—	—
7 Freshwater marshes/tanks reservoirs/paddy fields	121 (32·2)	3 (10·0)	7 (77·8)
8 Freshwater hill streams	28 (7·5)	1 (3·3)	—
9 Freshwater rivers	36 (9·6)	1 (3·3)	6 (66·7)
10 Beaches	53 (14·1)	—	3 (33·3)
11 Offshore (pelagic)	14 (3·7)	—	—
12 Estuaries/mangrove/saltpans, etc	74 (19·7)	1 (3·3)	5 (55·6)
13 Coastal coconut	7 (1·9)	1 (3·3)	—
14 Moist dry teak plantation	37 (9·9)	1 (3·3)	—
15 Moist teak-type deciduous forest	49 (13·1)	—	—
16 Moist dry *Eucalyptus* plantations	18 (4·8)	1 (3·3)	—
17 Dry deciduous forest	46 (12·3)	3 (10·0)	—
18 Dry rocky hillocks with scrub	92 (24·5)	14 (46·7)	—
19 Dry cultivation	121 (32·3)	15 (50·0)	2 (22·2)
20 Moist dry bamboo facies	29 (7·7)	3 (10·0)	—
21 Human settlements habitation	136 (36·3)	3 (10·0)	2 (22·2)

Percentages are given in parentheses Since a single taxon may use more than one kind of habitat the percentages add up to more than 100%.

common babbler *Turdoides caudatus* may be related to the loss of habitat It is also possible that species such as the white ibis *Threskiornis melanocephala* and skylark *Alauda gulgula* are new additions to the bird fauna of the district due to the creation of extensive areas of suitable habitat

DISCUSSION

Birds utilizing the forest habitat in the Uttara Kannada district appear to be little affected by the changes that have taken place over the last century, including a decline in the area under forest cover from about 80% to 70% accompanied by an increase in the size of cultivated enclaves and habitation within the forest. Thus, we resighted the single localized population of about 20 birds of the Wynaad laughing thrush *Garrulax delesserti*, a subspecies endemic to the Western Ghats, in the same locality near Castle Rock as had been noted by Davidson and Koelz. Five forest taxa which have apparently disappeared, i.e. the Nilgiri thrush *Zoothera dauma*, the large Indian parakeet *Psittacula eupatoria*, the little scaly-bellied green woodpecker *Picus myrmecophoneus*, the orange-breasted green pigeon *Treron bicincta* and the yellow-backed sunbird *Aethopyga siparaja*, were all rare. Uttara Kannada represents the northern fringe of distribution of *Z. dauma*, and the southern limit for *A. siparaja* (Ali & Ripley, 1983). It is possible that small populations of these species still exist in Uttara Kannada and have been overlooked. By and large, the forest bird fauna of the district has not fared too badly over the last century. The raptors, often noted as most likely to suffer extinction, have also all persisted during the period, the only resident species not recorded by R.J.R.D.—the fishing eagle *Ichthyophaga ichthyaetus*—having been recently resighted by amateur birdwatchers (Bruno Boedts, pers. comm.). As in Java, the raptors appear able to adapt to living in smaller habitat fragments (Thiollay & Meyburg, 1988).

Birds on the fringes of their geographical distribution, those with special habitat preferences, birds of larger size and birds hunted by man for food have been noted to be particularly susceptible to extinction (Diamond, 1971, Terborgh, 1974). Apart from the thrush *Z. dauma* noted above, the ring dove *S. decaocto*, a very conspicuous bird for which the Uttara Kannada district constitutes the western fringe of its distribution, seems now to be extinct. Of the scrub/dryland birds which have apparently disappeared, the lesser florican *Sypheotides indicus*, the Indian courser *Cursorius coromandelicus* and the sirkeer cuckoo *Taccocua leschenaulti* as well as *S. decaocto* are all amongst the largest of the scrub/dryland specialists. They also all happen to be hunted by man for food.

King (1978) notes that of the birds on decline in the world 67·2% are forest birds, 16·8% scrub and grassland birds and 12·7% frequent wetlands. For Uttara Kannada the second category seems clearly to be the most threatened. This is likely to be true also of the country as a whole for, as Table 6 shows, the natural vegetation of the semi-arid and arid tracts of the country has been subject to the highest level of degradation. Consequently, the list of threatened bird forms of the Indian subcontinent as it appears in the recent compilation by the World Conservation Monitoring Centre (1988) includes six taxa characteristic of scrubland habitat, prominent amongst which are the Great Indian bustard *Choriotis nigriceps*, Bengal florican *Eupodotis bengalensis* and the Jerdon's courser *Cursorius bitorquatus*. While some serious thought has been given to the conservation of the desert

TABLE 6

Extent of Potential Area, Closed Canopy Forest, Forest Including Degradation Stages and Nature Reserves in Major Zones in India

Zone	*Attributes*	*Potential*	*Closed canopy*	*All forest*	*Nature reserves*
Arid	Area[a]	481·3	0	2·2	8·2
	Percentage[b]	17·2	0	0·1	10·0
	Ratio[c]	—	0	0·006	0·6
Semi-arid	Area	670·0	17·6	31·4	7·8
	Percentage	23·9	5·1	6·7	9·6
	Ratio	—	0·21	0·28	0·4
Peninsular deciduous	Area	1 291·2	195·5	283·3	50·0
	Percentage	46·1	56·6	60·7	61·6
	Ratio	—	1·23	1·32	1·34
Peninsular evergreen	Area	62·0	14·1	16·4	3·6
	Percentage	2·2	4·1	3·5	4·4
	Ratio	—	1·86	1·6	2·0
Himalaya	Area	290·5	112·3	129·0	10·9
	Percentage	10·4	32·6	27·7	13·4
	Ratio	—	3·13	2·66	1·29
Andaman and Nicobar	Area	6·8	5·5	5·5	0·8
	Percentage	0·2	1·6	1·3	1·0
	Ratio	—	8·0	6·5	5·0
Total	Area	2 801·8	345·0	467·8	81·2
	Percentage[d]	—	12·3	16·7	2·9

[a] 1000s of km^2.
[b] % of total area in that column.
[c] % of actual to potential habitat
[d] % of total area (Gadgil & Meher-Homji. 1986)

biota with the establishment of a Desert Biosphere Reserve, we believe that the semi-arid regions deserve the most urgent attention of those concerned with the conservation of India's biological diversity.

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Assigning Conservation Value: A Case Study from India

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Abstract: *We assign conservation values to ecological zones, habitat types, and specific localities of the south Indian district of Uttara Kannada on the basis of occurrence of bird taxa. This is a two-step process, assigning values first to individual bird taxa and second to spatial elements based on the occurrence of birds. The attributes of bird taxa considered are geographical distribution at four levels, habitat preference, taxonomic position, and degree of endangerment. The criteria translating the attributes into values are based on the assumption that the rarer, more taxonomically unique, or more endangered the taxon, the more valuable it is. The conservation value of a given bird taxon is thus a point in a seven-dimensional space. We reduce this to three dimensions by using internal correlation and clumping of values. Each spatial element may then be assigned a conservation value based on number of taxa and the total and mean conservation value along the three dimensions. The*

Resumen: *Hemos asignado valores de conservacion a zonas ecológicas, tipos de hábitat, y localidades específicas de Uttara Kannada, que es un distrito sureño de la India, en base a la presencia de los grupos taxonomicos de aves. Este es un procedimiento en dos etapas. Primero se le asignan valores a taxa individuales de aves y segundo a los elementos espaciales basados en la presencia de las aves. Las características de los grupos taxonómicos de aves considerados son, la distribución geográfica en cuatro niveles, hábitat preferido, posición en la taxonomía, y nivel de riesgo. Para transformar estas características en cifras, se parte de la base de que los grupos taxonómicos más valiosos son los más raros, los que tienen características taxonómicas más especiales, o los que corren mayor riesgo. El valor de conservación de un grupo taxonómico dado es, por lo tanto, un punto en un espacio de siete dimensiones. Hemos reducido estas dimensiones a tres, mediante el uso de correlaciones internas y agrupamientos de valores. Cada elemento espacial recibe un valor de conservación basado en el número de taxa, y el valor total y promedio del valor de conservación a lo largo de los tres ejes. Los valores totales están altamente corre-*

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total values are highly correlated with number of taxa, permitting a simplification of the problem at the level of spatial elements to four dimensions. The analysis provides a basis for assigning specific conservation values to five ecological zones of the district, to fifteen natural, quasinatural, and manmade habitat types, and to 107 specific localities. Our analysis shows that degraded evergreen forests, exotic tree plantations, and urban settlements have low conservation value; the other habitat types considered rank high along one or more dimension. We also identify 12 different sets of 20 localities each that would maximize either the diversity of bird taxa or conservation value along the different dimensions. We thus attempt to synthesize diversity and quality of taxa to generate conservation prescriptions, whereas the existing methods tend to emphasize either rare or endangered taxa or total diversity. Such prescriptions would be one useful input into working out an overall conservation strategy for a geographical region.

lacionados con el número de grupos taxonómicos, lo cual permite una simplificación del problema de los elementos espaciales a cuatro dimensiones. El análisis sirve para asignar valores específicos de conservación a cinco zonas ecológicas del distrito, a 15 tipos de hábitat naturales, seminaturales y artificiales, y a 107 localidades específicas. Nuestro análisis demuestra que los bosques perennes degradados, las plantaciones de árboles exóticos, y las colectividades urbanas tienen un valor de conservación bajo; los otros tipos de hábitat considerados tienen un valor alto en una o más dimensiones. También hemos identificado 12 juegos diferentes de 20 localidades cada uno que podrian incrementar ya sea la diversidad de los grupos taxonómicos de aves o el valor de conservación a lo largo de distintas dimensiones. Así hemos tratado de sintetizar la diversidad y la calidad de los grupos taxonómicos para generar recomendaciones sobre la conservación. En contraste, los métodos actuales tienden a enfatizar los grupos taxonómicos raros o de alto riesgo, o la diversidad total. Dichas recomendaciones podrian ser útiles al elaborar una estrategia de conservación general para una región geográfica.

Introduction

Conservation action demands value judgments because such action often involves a choice among a set of alternatives. Some alternatives must therefore be considered to be of higher priority than others. It is useful to make explicit such a process of forming value judgments to help reduce the chance that arbitrary actions will be based on some momentary emotional appeal or compromise. This is the motivation underlying a number of recent attempts to assign specific conservation values to biological and landscape elements. The elements in consideration may vary from an isolated population of a plant species to a major biome such as the tropical rain forest (Nature Conservancy 1983; Usher 1986). We present here an attempt to assign conservation values, and we describe their use in deriving specific conservation prescriptions. Our work pertains to valuation of ecological zones, habitats, and specific localities in the Uttara Kannada district of the state of Karnataka in South India based on the presence and absence of bird taxa.

Study Area and Methods

The Uttara Kannada district along with the adjoining taluk (= county) of Hangal from Dharwad district (13° 55′–15° 32′ N; 74° 05′–75° 05′ E) is located centrally on the Malabar biogeographic province. The Malabar, c 160,000 km^2 in extent, comprises of a narrow coastal strip 5 to 100 km in width along with the hill chain of Western Ghats running north-south parallel to the west coast between 8° and 20° N lat. (Fig. 1). The hill chain is a long band 50–100 km in width ranging in altitude between 400 and 2680 m. It is broken by just one narrow gap, the Palghat gap, over its entire length of 1600 km. The annual rainfall in this province averages 2000 mm, but it is as high as 6000 mm on the crest and as low as 600 mm in the eastern rain-shadow region. Its range of habitats includes beaches; estuaries; low-, medium-, and high-elevation tropical wet evergreen forests; and moist and dry deciduous forests and scrub (Subramanyam & Nayar 1974). There are a number of manmade habitats too. Ali and Ripley (1983) and Daniels (1989) record 586 taxa of birds (which includes 515 full species, some of which exist as two or more distinct subspecies in the Malabar) and broadly distinguish 24 major habitat types for the Malabar province.

The study area (Fig. 2) of 11,000 km^2, characterized by low hills with only a few peaks above 600 m, has a great diversity of habitats, including 21 of the 24 habitat types described for the Malabar province (Daniels 1989). Based on rainfall, vegetation, the extent of human interference, and the pattern of diversity and distribution of birds, the district may be divided into five ecological zones: the coast, the northern less-disturbed evergreen forest, the southern more-disturbed evergreen forest, the moist deciduous forest, and the dry deciduous forest and scrub (Pascal 1982, 1984, 1986; Daniels 1989).

The bird fauna of Uttara Kannada is relatively well known. Davidson (1898a,b) published detailed notes on distribution and habitat preference of birds of the district based on collections from 1888 to 1896. Subsequently Koelz (1942) published a supplementary list based on a 3-month survey. Daniels (1989) maintained detailed notes on bird taxa throughout the district over

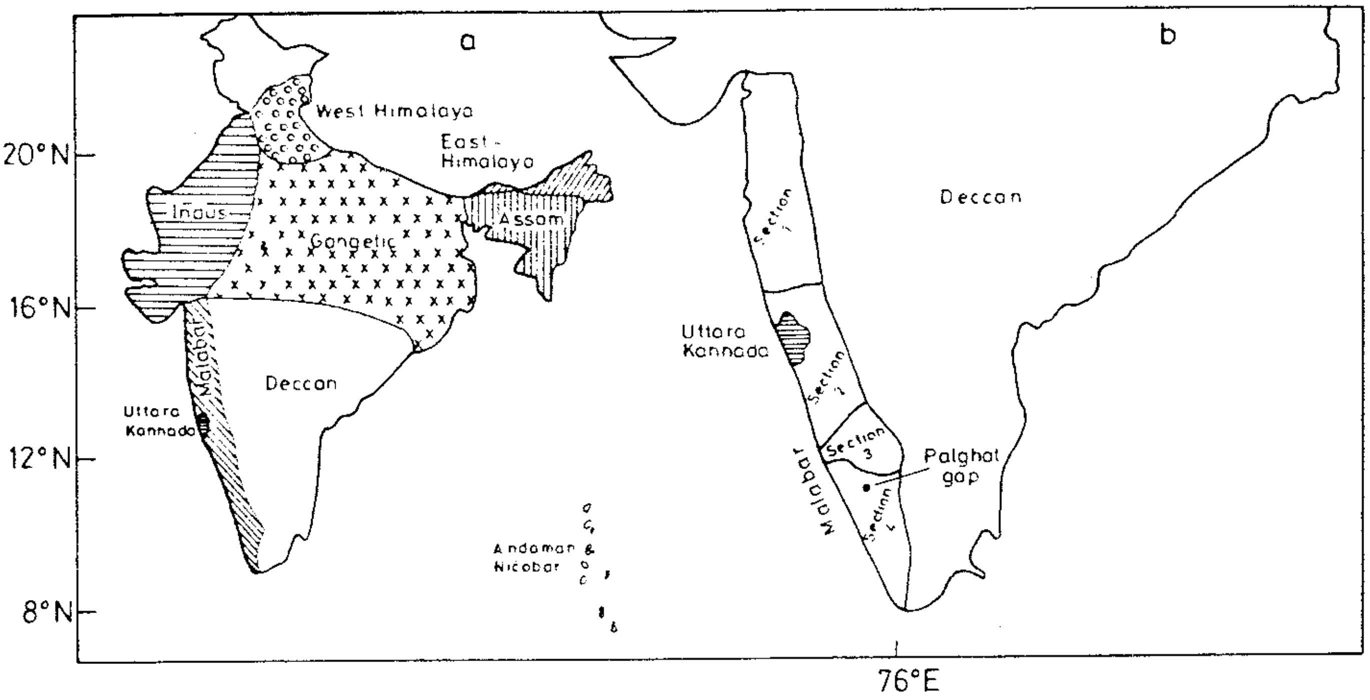

Figure 1 The Uttara Kannada district in relation to the major biogeographic provinces of the Indian subregion (a) and the four sections in the Malabar province (b)

a 5-year period involving 1018 days of field observation During this period he visited 237 localities scattered over the district and recorded the presence and absence of bird taxa For the sake of mapping the spatial distribution of each taxon of bird, the district was divided into 498 grids of 5 km × 5 km Using the vegetation maps (1:250,000; Pascal 1982, 1984) and the Survey of India toposheets (1:250,000 & 1:50,000), the distribution of the major habitats of the district was mapped onto these grids.* Notes were maintained on the presence or absence of each taxon by grids and by habitat types during the 5 years of field work This information was used to assign the different taxa of birds to the respective zones and habitats These data have been supplemented by systematic 2-hour, 600-×-200-m strip transect samples from 107 localities These localities were chosen to encompass the total range of variation in climate, topography, and habitat types over the district The transects were covered on foot between 8 00 and 10.00 hours in forests and associated habitats and between 7 30 and 9 30 hours in nonforest and open habitats such as marshes during the nonrainy seasons (November–May) of 1986–1988. Additional information made available by three amateur naturalists on birds in this district has also been utilized The total was 420 taxa of birds (402 full species and more than one subspecies of some of these species) recorded over the century from this district. Daniels et al (1990*a*) analyze the changes in the bird fauna over the time span that these records reveal

Assigning Conservation Values

Conservation value is assigned to an element such as a taxon or a locality with reference to an *attribute,* for instance, the extent of geographical distribution of a given bird taxon or the number of resident bird taxa in a given locality The different states of such attributes are then assigned values based on a *criterion.* Thus we may decide that the more restricted the geographical distribution of a taxon, the greater the *value* of the taxon, or the larger the number of taxa present in a locality the more valuable the locality is The actual values may either be ranks along a scale or a specific number (Nature Conservancy 1983; Usher 1986)

In the endeavor contemplated here the conservation values would be one of the inputs for identifying a set of protected localities The values are computed on the basis of the presence and absence of different bird taxa in particular localities, habitats, or ecological zones We set this up as a 2-step process, assigning values to (1) individual bird taxa, and (2) localities, habitats, or zones based on the values of the bird taxa occurring therein

Step One: Bird Taxa

The attributes of bird taxa of the Malabar considered are the extent of their geographical distribution, their habitat preference, their taxonomic position, and their degree of endangerment The criteria translating the attributes into values are based on the assumption that the

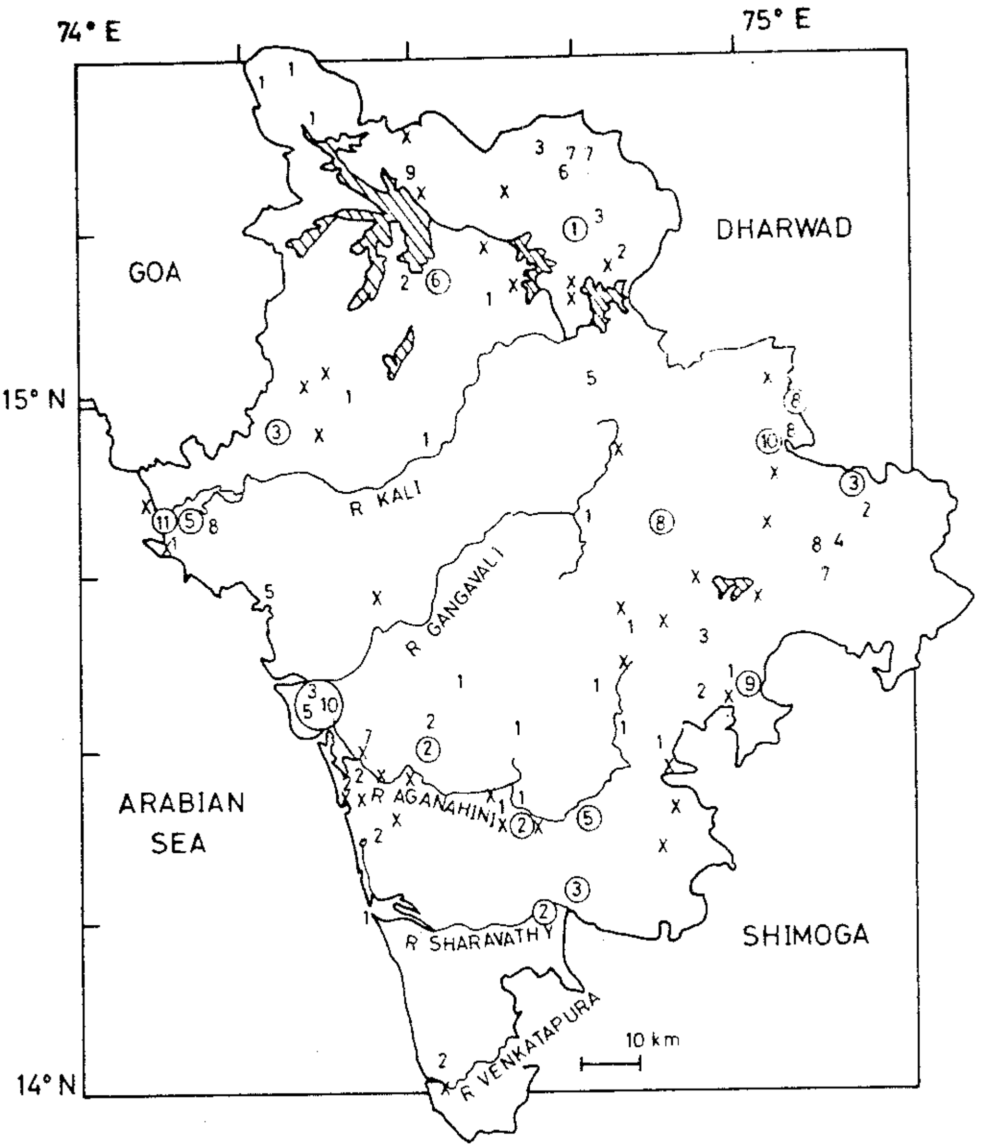

Figure 2. Uttara Kannada district and the adjacent Hangal taluk of Dharwad district showing the 107 localities sampled and the 18 localities of conservation interest. The numbers indicate the number of times a locality was represented in the 12 approaches attempted in this analysis. "X" indicates localities sampled that never occurred within the first 20 in any of the approaches. Circled localities are those recommended for conservation. Hatched areas are major reservoirs.

rarer or more restricted a taxon the more valuable it is and the more taxonomically unique or endangered a taxon the more valuable it is (Nature Conservancy 1983; Dony & Denholm 1985; Miller et al. 1987; Wheeler 1988; May 1990). The measures proposed below ensure that all the values lie in the range 0 to 1.

We have selected for this analysis seven attributes of bird taxa. Four of these relate to the geographic range of the bird taxa; G_1, over the entire world (divided into six zoogeographic regions); G_2, over the oriental region (divided into nine subregions); G_3, over the Indian subregion (divided into eight provinces); and G_4, over the Malabar province (divided into four sections) (Chatterjee 1939; Subramanyam & Nayar 1974; Cox & Moore 1980; Ali & Ripley 1983). The conservation value for a taxon by geographic range is given as

$$G = (N - a)/(N - 1),$$

where N is the number of subdivisions at a given geographic level and a is the number of subdivisions from which the taxon is known. We treat the four levels of geographic distribution as separate dimensions in view of the distinctive patterns of distribution along each level. For instance, a taxon restricted to the Malabar may be widespread within the province. Similarly, a taxon may be found only in the Malabar in India but may be widespread elsewhere in Southeast Asia. The data on geographical distribution used in this analysis are based on Howard and Moore (1980) and Ali & Ripley (1983)

The conservation value of each taxon by habitat preference was computed using the index

$$H = (N - a)(N - 1)$$

where a is the number of habitats in which the taxon is known to occur and N is 24 the total number of habitats for the Malabar province thus birds with more restricted habitat preference are assigned higher values This appears appropriate as birds utilizing more habitats also tend to use the more man-modified ones in the Malabar (Daniels 1989)

The conservation value of a taxon reflecting its taxonomic distinctness was calculated using the index

$$T = 1/(a \times b)$$

where a is the number of species known in the family to which the taxon belongs and b is the number of races under the species to which it belongs based on the information provided by Wallace (1963) and Howard and Moore (1980) The rationale behind such a treatment is that the races or subspecies are the lowest distinct taxonomic units below the level of species and that they indicate the totality of the genes contained in any species (Chambers and Bayless 1983) It would certainly be better to measure taxonomic distinctness on the basis of detailed information contained in the phylogenetic tree of birds with a taxon having fewer existing relatives taking a higher conservation value than another with more relatives (May 1990) Since we do not have access to such complete information we have used a simpler index

The conservation value by degree of endangerment for each taxon was assigned by

$$E = p$$

where p is the proportion of endangered taxa in the family to which the taxon belongs We prefer this to using the available lists of threatened birds because only three bird taxa of Uttara Kannada figure in such a list and our field studies strongly suggest that this choice is arbitrary and does not reflect the true situation The Peafowl (*Pavo cristatus*) the Nilgiri Wood Pigeon (*Columba elphinstonii*) the Lesser Adjutant Stork (*Leptoptilus javanicus*), and the Redfaced Malkoha (*Phaenicophaeus pyrrocephalus*) are the only Malabar birds among those listed as endangered in India (World Conservation Monitoring Centre 1988) The Redfaced Malkoha, however, does not occur in Uttara Kannada The wood pigeon and the stork are locally rather common in appropriate habitats over the Malabar (Daniels, personal observation) and the Peafowl is widely distributed in India with many pockets of local abundance thanks to strict religious protection

In a taxonomic survey of endangered birds Temple (1986) distinguished four types of birds (1) taxa that are endemic to islands (2) taxa that are narrowly confined to scarce habitats (3) taxa that are particularly sought after by human consumers and (4) taxa that depend on easily-disturbed food chains The first category is irrelevant to this analysis but the other three are pertinent Birds of prey and those in families such as Podicipedidae Haematopodidae Gruidae Rallidae Phasianidae and Psittacidae are more threatened than others because they share some common trait (more palatable flesh ground- or hole-nesting poorly developed dispersal abilities) Temple argues that families in which 10% or more of the constituent birds are endangered should be considered especially sensitive Our assignment of conservation values reflects this notion and birds in families with more endangered taxa are assigned a higher conservation value on the basis of the proportion of endangered taxa in a family (Temple 1986)

We thus arrive at a conservation value for each of the 586 bird taxa of the Malabar as a point in a seven-dimensional space (Figs 3 & 4) The set of bird taxa of interest to us is those occurring in one of the provinces, the Malabar Fully 40% of these are restricted to the Oriental region and within the Orient, 29% are restricted to the Indian subregion The distributions of conservation values at global and regional levels are therefore unimodal with the mode occuring at the higher extreme of the conservation value Within the subregion however a much smaller proportion 17% are confined to the Malabar province, many being shared with two other provinces Hence this distribution is bimodal Finally a high proportion of taxa (41%) are distributed over all the four sections of Malabar Hence this distribution is unimodal, but with the mode occuring at the lower extreme of the frequency distribution Taxa restricted to India are necessarily restricted to the Oriental region; many of these are also confined to the Malabar Hence the conservation values along these axes are highly positively correlated

The frequency distributions of values along the other three axes are unimodal; those for taxonomic value and degree of endangerment are confined within a very narrow range at the lower extreme This implies that most bird taxa belong to families with several species or species with several subspecies, the only monotypic family in the Malabar being the Dromadidae represented by *Dromas ardeola* Similarly most taxa of birds in the Malabar belong to families in which only a very small proportion of species are listed as endangered

REDUCING THE DIMENSIONALITY

The conservation value of a bird taxon can thus be represented as a point in the seven-dimensional space Because it is difficult to visualize and inconvenient to han-

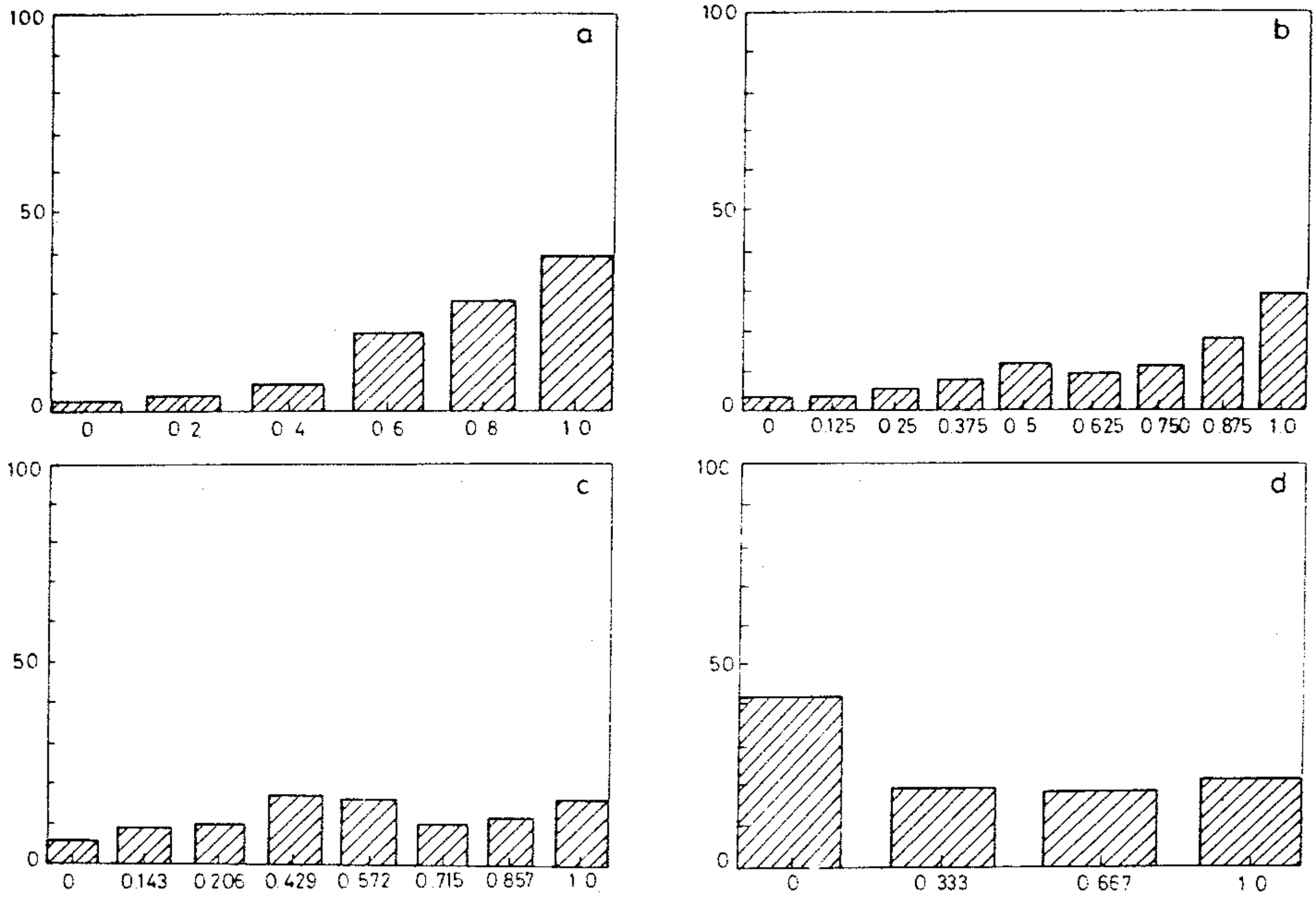

Figure 3. Frequency distribution of conservation values based on geographical distribution for the 586 taxa of Malabar birds. (a) G_1 Global (b) G_2 Regional; (c) G_3 Subregional; and (d) G_4 Provincial.

dle the distribution of points in space of such dimensionality, it would be useful to reduce it. We may do this in two ways. First, if the conservation values in two or more dimensions are highly positively correlated, it would be enough to retain only one of those dimensions. To explore this possibility we have computed the correlation matrix in the 7 × 7 dimensional space for the 586 bird taxa of the Malabar (Table 1). As discussed above, the conservation values in dimensions G_1, G_2, and G_3 are significantly correlated among each other, and it should be sufficient to choose just one of these. The dimension to be so chosen should be minimally positively correlated to the other six. An inspection of the matrix shows that G_1 satisfies this condition. We therefore propose to leave G_2 and G_3 out of further consideration in this presentation. We did, however, look at the implications of continuing to take G_2 and G_3 into account and found that they do not change our subsequent conclusions. We have also considered the use of techniques such as principal components analysis; this does not affect the final conclusions in any way either. It therefore appears justifiable to leave out the dimensions G_2 and G_3 and thereby further simplify analysis.

As a second device for reducing the dimensionality of the problem we looked at the distribution of the conservation values along each individual dimension. It turns out that for the dimensions of taxonomic position and degree of endangerment, most of the values are concentrated in a very narrow range between 0 and 0.05 (Figs. 4b & 4c). This is because the Malabar bird fauna, as discussed above, includes just one taxon belonging to a monospecific family (Dromadidae) and only a few taxa belonging to families such as Phasianidae, Gruidae, etc., that have a high proportion of threatened taxa. We can therefore further reduce the dimensionality of our analysis by leaving out these two attributes. Again we have carried out the full analysis retaining these dimensions and confirmed that the conclusions are not affected in any way.

We therefore suggest that it is useful to reduce the dimensionality of the valuation procedure by using internal correlations and distribution of the values over the total range. We do not, however, imply that the specific dimensions removed in our analysis would turn out to be the dimensions to be neglected in other such analyses. We propose only that all possibilities of reduc-

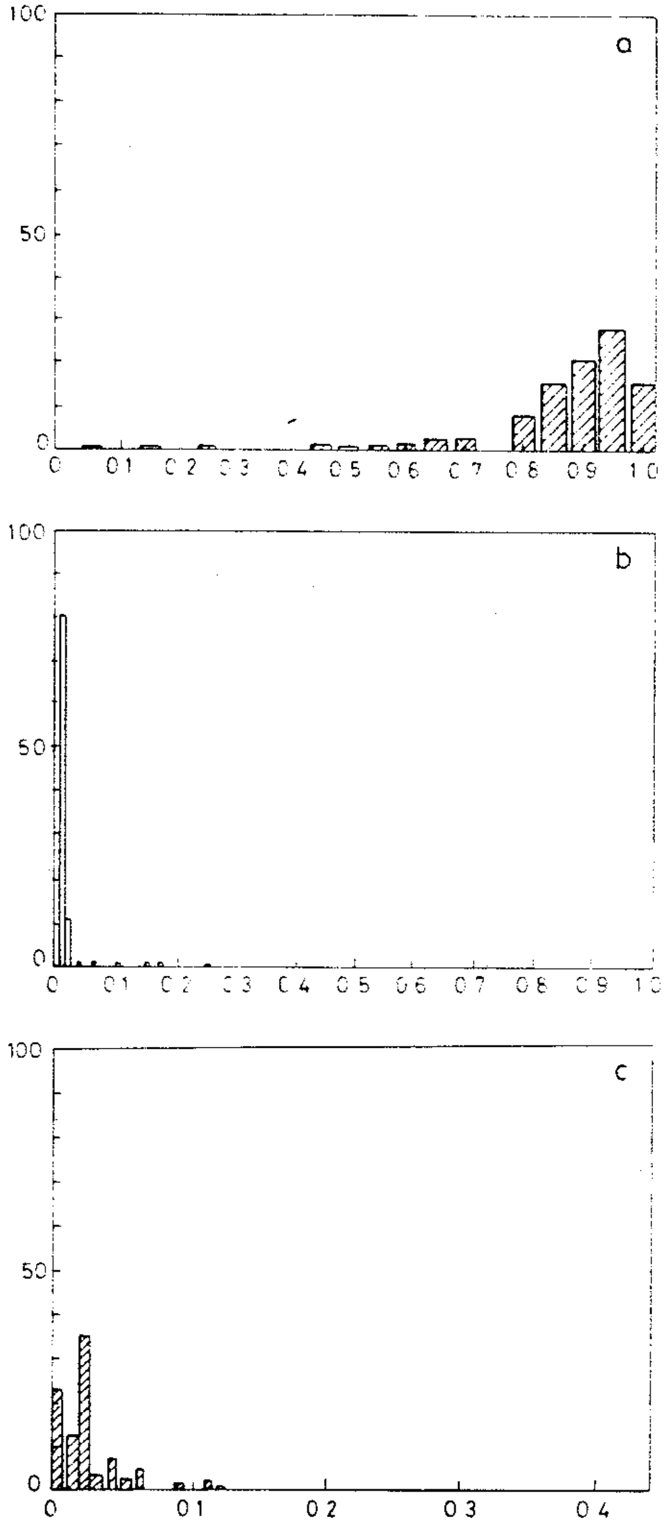

Figure 4 Frequency distribution of conservation values for the 586 taxa of Malabar birds. (a) H: Habitat preference; (b) T: Taxonomic position; and (c) E: Degree of endangerment.

tion of dimensionality should be explored and judged on a case-by-case basis.

Step Two: Geographical Element Level

The second step in the process concerns the occurrence of bird taxa in given localities, habitats, or zones. The criterion for assigning conservation value to such geographical elements could be species richness (number of bird taxa) or a measure of diversity (e.g., the Shannon-Wiener index), the total conservation value summed for all taxa occurring in a given geographical element, or the mean conservation value of a taxon in each geographical element. We carry out this analysis with the conservation value being considered as a point in the reduced three-dimensional space of G_1, G_4, and H. We do not have adequate data on the relative abundance of taxa to compute an index such as the Shannon-Wiener diversity index. This means that any given geographical element could be assigned a conservation value along one of the following seven dimensions: richness of taxa and total as well as mean conservation value along the dimensions of G_1, G_4, and H.

Again it is possible to reduce the dimensionality of the problem. Table 2 presents a 7-×-7 matrix of correlation between the conservation values for the 107 localities. It is evident that the total conservation values along all three dimensions are very highly correlated with richness of taxa. Indeed, similar analyses for habitats and ecological zones show the same trend. We therefore retain just the simplest parameter, number of taxa, for further analysis. As before we have gone through the analysis preserving the full dimensionality of the problem and confirmed that deleting these three dimensions does not change our conclusions. We thus have reduced the problem of valuation of geographical elements to a four-dimensional problem with values being assigned for (1) number of taxa and mean conservation value in terms of (2) global geographical distribution, (3) distribution within the biogeographic province of Malabar, and (4) habitat preference.

Conservation Values

Zones

Table 3 presents the conservation values along these four dimensions for the five ecological zones, the five natural and quasinatural and seven manmade terrestrial habitats, and the three aquatic habitats. Of the five ecological zones none has the highest conservation value along all four dimensions. The coastal zone with its rich aquatic habitats has the highest value for birds with narrow habitat preference and restricted geographical distribution within the Malabar. The northern evergreen forest zone scores highest in the global geographical

Table 1. Spearman's correlation coefficient r between the conservation values under the seven attributes for the 586 taxa of the Malabar birds.

Attributes	G_1	G_2	G_3	G_4	H	T	E
G_1: Global	—	0.31**	0.33**	−.12**	−.19**	−.05	−.07
G_2: Regional		—	0.72**	0.22**	−.08*	−.06	−.04
G_3: Subregional			—	0.22**	−.07	−.03	−.07
G_4: Provincial				—	0.29**	0.08*	0.06
H: Habitat preference					—	0.07	0.11*
T: Taxonomic position						—	−.02
E: Degree of endangerment							—

$^{*}p \leq 0.05$
$^{**}p \leq 0.01$

distribution, harboring a number of taxa restricted to the Oriental region and Indian subregion. The moist deciduous forest zone has the highest number of taxa sheltering a large number of land birds. The dry deciduous forest-scrub zone with freshwater lakes shares the highest conservation value for habitat preference with the coastal zone. It is only the southern evergreen forest zone with its extensive man-modified habitats especially betelnut (*Areca catechu*) orchards, that does not score the highest along any dimension. While human interference has not had an adverse effect on the total diversity of birds within the district, it has affected the "quality" of birds, generalist invaders displacing the birds more specialized to utilize the natural forests (Daniels et al. 1990*a,b*).

Habitats

Among the natural and quasinatural terrestrial habitats, the evergreen forest scores highest on the dimension of global geographical distribution because many forest bird taxa are restricted to the Indian subregion of the Oriental region. The moist deciduous habitat is richest in taxa, the scrub in taxa having narrow habitat preferences, and the scrub and dry deciduous forest in taxa with restricted distribution within the Malabar province. Again it is the degraded evergreen forest that is not among the highest along any of the four dimensions.

Of the manmade habitats, eucalypt plantations score high on richness of taxa and on birds with restricted distribution within Malabar. This is because in this district the plantations are in small patches and share a number of taxa from the surrounding habitats, mostly of dry deciduous forest and scrub (Daniels et al. 1990*b*). The betelnut plantations closely resemble the evergreen forest in their structure and microenvironment and share bird taxa characteristic of the latter, such as the Malabar Whistling Thrush (*Myiophonius horsfieldii*) and the Spiderhunter (*Arachnothera longirostris*). Hence they score high on birds restricted to the Indian subregion and Oriental region. Finally the cultivation does well for taxa with limited habitat preference, resembling the scrub with which it shares a number of taxa. Teak (*Tectona grandis*) follows the betelnut closely with regard to globally restricted taxa of birds. Other exotic plantations such as *Acacia auriculiformis*, coconut groves, and urban settlements do not score the highest along any of the four dimensions (Table 3).

The three aquatic habitats score quite high along three of the four dimensions. Freshwater ponds and lakes have a high richness of taxa, even exceeding that of the moist deciduous forest. Estuaries and beaches have taxa scoring high in terms of habitat preference. As expected, aquatic habitats score very poorly in terms of geographic distribution on a global and regional scale, many migratory taxa having a worldwide distribution.

Localities

This assessment of the conservation values of ecological zones and habitats is useful for developing a regional conservation strategy. Furthermore, our analysis can

Table 2. Spearman's coefficient r for the correlations between the conservation values of birds from the 107 localities.

		Summed values			*Mean values*		
Attributes	R	G_1	G_4	H	$\overline{G}_1$	$\overline{G}_4$	$\overline{H}$
R: Richness of taxa	—	0.90**	0.70**	0.99**	0.00	−.07	0.14
G_1: Global		—	0.54**	0.84**	0.42**	−.18	−.09
G_4: Provincial			—	0.74**	−.20*	0.64**	0.33**
H: Habitat preference				—	−.09	−.02	0.31**
$\overline{G}_1$: Global					—	−.28*	−.46**
$\overline{G}_2$: Provincial						—	0.35**
$\overline{H}$: Habitat preference							—

$^{*}p \leq 0.05$
$^{**}p \leq 0.01$

Table 3. The number of taxa of birds and the mean conservation value of a taxon in the different zones and habitats of Uttara Kannada.

Zones/Habitats	*R*	$\bar{G}_1$	$\bar{G}_4$	$\bar{H}$
Coastal zone	130	0.70	0.18	0.85
Northern evergreen zone	111	0.89	0.12	0.81
Southern evergreen zone	165	0.84	0.13	0.83
Moist deciduous zone	185	0.83	0.14	0.84
Dry deciduous zone	160	0.77	0.17	0.85
Natural and quasinatural terrestrial habitats				
Evergreen forest[a]	33	0.97	0.13	0.76
Degraded evergreen forest	36	0.94	0.09	0.71
Moist deciduous forest	43	0.93	0.13	0.72
Dry deciduous forest	28	0.88	0.14	0.70
Scrub	28	0.74	0.14	0.81
Manmade terrestrial habitats				
Eucalypt plantation	41	0.90	0.13	0.71
Teak plantation	37	0.92	0.11	0.72
Betelnut plantation	36	0.93	0.09	0.70
Other exotic plantation	35	0.83	0.09	0.71
Coastal coconut garden	29	0.80	0.09	0.71
Urban	29	0.74	0.09	0.74
Cultivation	42	0.71	0.12	0.78
Aquatic habitats				
Freshwater ponds or lakes	47	0.76	0.13	0.77
Estuarine	35	0.66	0.15	0.79
Beach	24	0.71	0.15	0.77

[a] Average number of bird taxa per sample has been used for the habitats because 2–20 transects were sampled in each habitat type

help pinpoint localities that merit protection under a nature reserve system on a priority basis. In the specific context of Uttara Kannada, the state Forest Department, which is responsible for nature conservation, has set up a network of nature reserves by constituting a large wildlife sanctuary at Dandeli and protecting several freshwater marshes notable for water birds as bird sanctuaries. The large wildlife sanctuary functions only on paper, being severely disturbed by the construction of several dams and a paper mill inside its boundaries. The official approach thus is of little value (Rodgers & Panwar 1988). The scientific approaches largely focus on identifying localities harboring rare or endangered taxa (Dony & Denholm 1985; Miller et al 1987; Slater et al 1987; Wheeler 1988) or maximizing the number of taxa protected (Hague et al 1986). Both approaches have serious limitations in the present context. First, only three taxa of birds have been considered endangered in Uttara Kannada, and since there is reason to doubt the appropriateness of the choice, this cannot serve as a useful basis. Second, as we will see in more detail below, attempts to maximize the number of bird taxa protected would lead to a focus on secondary habitats and birds with wide ranges and habitat preference. Our attempt therefore is to bring information on a number of attributes to bear on the choice of localities to be protected.

The data base for this analysis is the 273 taxa of birds noted during the 2-hour transects over the 107 localities. This is only a fraction of the taxa actually present in each locality. For the present purpose, however, we want the data to be strictly comparable and hence do not take into account bird taxa sighted at other times in these localities. These 107 localities also include 15 of the 21 broad habitats in the district. The six habitats left out are insignificant because they occur either as small patches (dimensions less than that of a transect) or as mosaics, as in the case of a freshwater marsh-paddyfield complex.

Given the variety of information available, it is possible to devise several alternative methods of valuing the localities and ranking them in terms of conservation priorities. Table 4 lists twelve such alternatives. Each involves choice of an initial starting point and a criterion for adding another locality. The natural choice for a starting point can be a locality scoring highest on any one of the attributes, for example, the total number of bird taxa, total conservation value, or the average conservation value of a taxon in terms of habitat preference. The criterion for adding a locality may refer to some property of the totality of bird taxa represented when that addition is made. Such a property could be total diversity, total conservation value, or average conservation value of bird taxa. A decision also needs to be made as to the total number of localities to be selected. Following Rodgers and Panwar (1988) we may aim at bringing 6% of the total area under the network of protected localities. If this is a highly dispersed network, the minimal size of protected localities may be fixed at 30 km², since reserves of this size are considered appropriate for tropical forest birds including some of the raptors (Leck 1979; Thiollay and Meyburg 1988). This

Table 4. Localities of Conservation Interest in Uttara Kannada.

	Procedure followed			*No. of taxa (out of 273), habitats (out of 15), predominant habitats and zones (out of 5) represented in the first 20 localities chosen*			
S. No.	*Criteria*	*Starting point*	*Criteria for subsequent choices*	*Taxa*	*Habitats*	*Predominant habitat type*	*Zones*
1	Maximizing number of bird taxa	The locality with the highest no. of taxa	Choosing the next locality with the maximum no. of taxa different from those that have already been included	242	6	Marsh, beach and manmade	5
2		The locality taking the highest rank $\overline{G}_1$	As in 1	239	9	Marsh, beach, and manmade	5
3		The locality taking the highest rank $\overline{G}_4$	As in 1	244	8	Marsh, beach and manmade	5
4		The locality taking the highest rank under $\overline{H}$	As in 1	244	8	Marsh, beach, and manmade	5
5		Localities ranking the highest under no. of taxa $\overline{G}_1$, $\overline{G}_4$ and $\overline{H}$	As in 1	238	8	Marsh, beach, and manmade	5
6	Maximizing total conservation value	Locality ranking the highest under $\overline{G}_1$	Next locality chosen such that it maximizes the total conservation value	242	8	Marsh, beach, and manmade	5
7		Locality ranking the highest under $\overline{G}_4$	As in 6	229	9	Marsh, beach and manmade	5
8		Locality ranking the highest under $\overline{H}$	As in 6	243	7	Marsh, beach and manmade	5
9	Maximizing the value per taxon protected	Locality ranking the highest under $\overline{G}_1$	Next locality chosen such that the value per taxon remains at the highest level possible	109	5	Evergreen forest	3
10		Locality ranking the highest under $\overline{G}_4$	As in 9	162	5	Beach and marsh	4
11		Locality ranking the highest under $\overline{H}$	As in 9	165	8	Beach and marsh	3
12	Equal representation of all 4 attributes	Localities ranking the highest under no. of taxa, $\overline{G}_1$, $\overline{G}_4$, and $\overline{H}$	Those ranking the next and thus up to the first five ranks	207	5	Marsh and evergreen forest	5

suggests that we should identify about 20 localities for this purpose.

The first eight alternatives listed in Table 4 all lead to essentially similar results because the total conservation value is highly correlated with the total number of taxa. These procedures all lead to representation of a high proportion of taxa (about 240 out of a possible 273), habitat types (six to nine out of a possible fifteen) and all five ecological zones in the first 20 localities selected. A major drawback of these choices is the emphasis on secondary, manmade habitats and taxa with broader habitat tolerance. Such habitats and taxa do not really need special conservation efforts. Alternatives 9 through 11 attempt to maximize average conservation value. Hence they tend to emphasize taxa with narrow geographical ranges or habitat preference, a relatively small number of total taxa being represented in the top 20 localities. **The last alternative, 12, attempts to bring together the desirable features of both sets of alternatives. It selects the localities with the five highest scores on the four attributes, namely the total number of taxa, average conservation value along two levels of geographic distribution, and average conservation value on habitat preference. Because of some common represen**tation this leads to the selection of only 18 instead of 20 localities. While with this procedure the total number of taxa and habitats represented is somewhat lower than for the first eight procedures, it ensures good representation of primary habitats deserving urgent attention, namely the evergreen forests, beaches, estuaries, freshwater marshes, and dry scrub (Table 5). Figure 2 shows the distribution of all the localities, 66 in all, that were identified as worthy of preservation by any of these 12 procedures and the number of procedures in which each locality was represented. The 18 localities of procedure 12 are specially highlighted as we believe these represent a very good combination of the various attributes that may be employed toward selecting localities for conservation (Table 4).

Discussion

Valuation of localities of high priority for conservation purposes is one of the many significant inputs to a conservation strategy. However, most often it is limited by choosing just one set of organisms such as flowering

Table 5 Attributes of 18 localities identified as possessing the five highest conservation values along the four dimensions of total richness of taxa (R) mean value for geographical distribution on a global scale ($\bar{G}_1$) mean value for geographical distribution on the scale of the Malabar ($\bar{G}_4$), and mean value for habitat preference ($\bar{H}$).

Locality	*Ecological zone*	*Habitat*	*Dimension*
Sunkeri	Coastal	Estuary	$\bar{H}$
Sanikatta	Coastal	Estuary	$\bar{G}_4$
Madnegeri	Coastal	Estuary	$\bar{G}_4$
Thenginagundi	Coastal	Estuary	$\bar{H}$
Karwar	Coastal	Beach	$\bar{G}_4$
Bargadda	N evergreen forest	Evergreen forest[a]	R
Patoli	N evergreen forest	Evergreen forest[a]	R
Anegundi	S evergreen forest	Evergreen forest	$\bar{G}_1$
Doddamaneghat	S evergreen forest	Evergreen forest	$\bar{G}_1$
Unchalli	S evergreen forest	Evergreen forest	$\bar{G}_1$
Mastimane	S evergreen forest	Evergreen forest	$\bar{G}_1$
Malamane	S evergreen forest	Evergreen forest	$\bar{G}_1$
Bharatnalli	Moist deciduous forest	Freshwater lake	R
Madurahalli	Moist deciduous forest	Freshwater lake	R
Sambrani	Dry deciduous forest or scrub	Freshwater lake	R
Salgaum	Dry deciduous forest or scrub	Freshwater lake	$\bar{H}$
Nyasergi	Dry deciduous forest or scrub	Freshwater lake	$\bar{G}_4$
Yelavatti	Dry deciduous forest or scrub	Scrub	$\bar{H}$

[a] With a considerable admixture of trees typical of the moist deciduous forests

plants, or as in this case, birds, for the evaluation It would be ideal if other groups of organisms such as insects, amphibians, and mammals are also included in the analysis For instance, if we go by diversity alone in the evaluation procedure, it can be misleading because bird diversity in Uttara Kannada is negatively correlated with angiosperm diversity (Daniels 1989) and insect species diversity is correlated with neither of these (Gadagkar et al 1989) The analysis discussed above has not, however, emphasized diversity alone, nor does it try to recommend the sole use of birds in a conservation evaluation procedure Birds were chosen primarily because a good deal of data is available on their status and distribution locally, regionally, and even continentally Such data bases are rather incomplete for most other groups of organisms in India A second limitation of this approach is that it leaves out details of the area of each protected locality and the distances separating them Third, it does not specifically look into endangerment due to human pressures, the ecological roles played by birds, and other relevant issues such as social acceptability, cultural and aesthetic appeal, and long-range economic benefits (McNeely et al 1990) We are therefore conscious that a whole range of issues would have to be brought in before a conservation strategy is given proper content (Gadgil, 1991) We have already looked at some of these issues in the context of working out an ecodevelopment strategy for Uttara Kannada (Gadgil et al 1985–86) In a companion paper to this study we have elaborated a first proposal for a broader conservation strategy that takes into account many of the aspects left out here (Daniels et al , in preparation) However, within this overall context we believe that derivation of conservation prescriptions based on an explicitly stated procedure with all assumptions clearly exposed as has been done above is very useful

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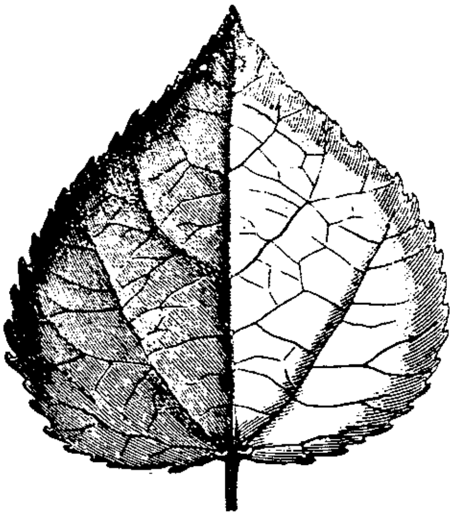

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The elephant populations of India—Strategies for conservation

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Abstract. Between 17 and 22 thousand elephants are found in 4 distinct regions—the northwest (525), northeast (8725–12130), central (2300) and south India (5750–7150). Elephants largely prefer the deciduous forests where both browse and grass are available. Annual home range size usually varies between 100 and 500 km². The major threats to the elephant include loss of habitat due to spread of agriculture, degradation of habitat through human impact, developmental projects such as hydroelectric dams and poaching of males for ivory. Suggestions for conservation of the elephant have been made. These include the maintenance of minimum viable populations, habitat integrity, habitat mosaic and reduction in poaching. Measures to reduce crop depredation by elephants such as the use of high-voltage electric fences are recommended.

Keywords. Asian elephant; *Elephas maximus*; elephant distribution; ivory poaching; minimum viable population.

1. Introduction

Despite the long and spectacular evolutionary history of the Proboscidea, extending back to the Eocene, there are only two living representatives—the African elephant (*Loxodonta africana*) and the Asian elephant (*Elephas maximus*). While an estimated 1.3 million *Loxodonta* range over a vast area of the African continent (Douglas-Hamilton 1980), *Elephas* has been reduced to a number of relatively small populations comprising 36–54 thousand individuals in South and Southeast Asia (Olivier 1978a; Sukumar 1985).

During the past century between 30 and 50 thousand elephants have been captured for domestication in the Indian sub-continent alone. The offtake has been consistently very much higher in the northeast than in south India. The reason for this disparity lies in the method of capture. In the north elephants have been traditionally captured in stockades and thus entire herds are taken at one time. By contrast, in the south elephants were usually captured solitarily in pits. The Kheddah method introduced by Sanderson (1878) was confined only to the Mysore State and less than 2000 elephants were captured between 1874 and 1971.

At present between 17 and 22 thousand elephants are confined to forested, hilly tracts of northwest, northeast, central and south India (figure 1). Only a brief account of elephant status and distribution in these 4 major regions will be given here. More detailed descriptions are available elsewhere (Daniel 1980; Sukumar 1985) based on the surveys carried out by the Asian Elephant Specialists Group (AESG) of the International Union for the Conservation of Nature and Natural Resources (IUCN).

2. Status and distribution of the elephant in India

2.1 *Northwest India*

An isolated population of about 525 elephants inhabits the *terai* belt along the Himalayan foothills in Uttar Pradesh (Singh 1978). The important elephant areas are

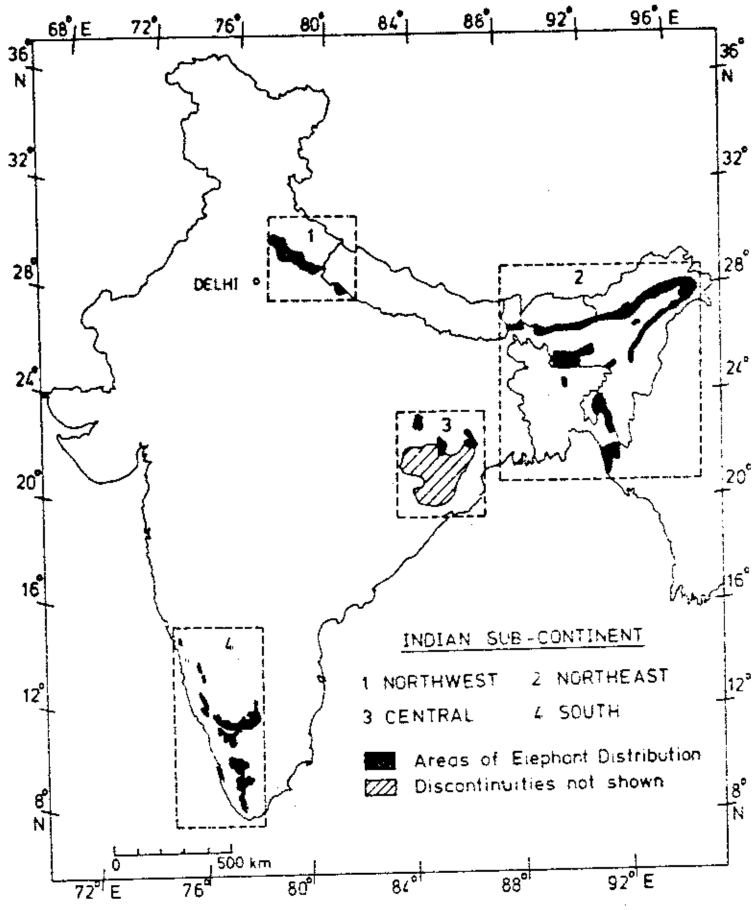

Figure 1. Elephant distribution in the Indian sub-continent

the Corbett National Park and Landsdowne Forest Division Threats to the habitat from the Ramganga reservoir, the Rishikesh-Chilla power channel and a paper mill have been discussed by Singh (1978)

2.2 *Northeast India*

The elephant habitats in this region are being mapped by the Northeast India Task Force of the IUCN/AESG in collaboration with the concerned state forest departments (Choudhury 1980, 1983; Northeast India Task Force 1981).

In the northeastern region only a series of fragmented elephant habitats exist. These extend from the Himalayan foothills of the Bhutan-north West Bengal border eastwards into the states of Assam, Arunachal Pradesh Manipur. Mizoram, Tripura and Meghalaya Some of these populations also extend into Bangladesh and Burma.

In northern West Bengal, out of an estimated 155 elephants about 80 elephants range as a distinct population to the west of the Torsa river, while the rest are found to the east of the Torsa and are continuous with Assam This is part of a larger area which extends in a belt along the sub-Himalayan hills and plains of Arunachal Pradesh and Assam to the north of the Brahmaputra river. In Arunachal Pradesh alone the forest department has estimated 2000–4300 elephants within a 20000 km^2 area of mostly rugged terrain. These elephants also move into the border zones of Assam. In Assam itself the forest department has estimated 1200 elephants for the Manas Tiger Reserve and 400 for the Darrang West and East Divisions.

It is not clear whether the elephants to the north of the Brahmaputra river are linked with those to the south of the river. Some maps in the above mentioned reports show a continuous range in Arunachal Pradesh–Assam which extends in a horseshoe shape through the Tirap district in the southeast into Nagaland. However, Choudhury (1983) indicates that the elephants to the south of the Brahmaputra constitute separate populations. One such population is found in the Dibang-Tirap (estimate included with Arunachal Pradesh) and Dibrugarh region (200 elephants). Another major population of about 1900 elephants inhabits the Kaziranga Wildlife Sanctuary (780), Sibsagar and Nagaland hills. The large population in the Garo hills–Khasi hills of Meghalaya, estimated at 2500–3500 elephants, is certainly isolated from the others in the northeastern region. Smaller populations have been described for the Jainti hills–North Cachar region (150–175), South Cachar (100–150) and Tripura (120–150). The picture in the states of Manipur and Mizoram is not clear but the numbers are certainly low.

Apart from the tremendous human pressure on the habitat for shifting cultivation and the tradition of capturing elephants in large numbers, the prospects for the conservation of the elephant in northeast India are seriously affected by a volatile socio-political situation.

2.3 *Central India*

Information for this region comes mainly from the efforts of the Central India Task Force of the IUCN/AESG (Shahi 1980). The bulk of the elephant population is found in the state of Orissa. An estimated 20000 km^2 of deciduous forest spread over 21 forest divisions including the Simlipal Tiger Reserve, is believed to hold about 2000 elephants. The elephant range also extends into the adjoining states of Bihar and West Bengal. In Bihar the adjacent tracts are Singhbhum (area 2250 km^2, 200 elephants) and Dalbhum (70 elephants). A population of 40 elephants is isolated within the 1000 km^2 Palamau region. Incursion into West Bengal is sporadic.

2.4 *South India*

The elephant populations of South India have been studied and characterized better than those in other parts of the country (Krishnan 1972; Nair and Gadgil 1978; Nair *et al* 1980; Sukumar 1985). The elephant is distributed over forested hilly tracts of the Western Ghats and adjacent Eastern Ghats in the states of Karnataka, Kerala and Tamil Nadu. Along the sharp rainfall gradient from west to east in the Western Ghats, there is a striking transition in vegetation from wet evergreen forest and evergreen shola-grassland through semi-evergreen, moist deciduous and dry deciduous forest to scrub or thorn jungle. Elephants are found in the entire spectrum but attain the highest density in the deciduous belt. Their status and distribution can be conveniently described under sub-regions.

Table 1. Population status of the elephant in India

1 *Northwest India*	
Uttar Pradesh	525
2 *Northeast India*	
West Bengal	155
Arunachal Pradesh	2000–4300
Assam	
Manas Tiger Reserve	1200
Darrang West and East	400
Dibrugarh	200
Kaziranga-Naga hills	1900
Meghalaya	
Garo-Khasi hills	2500–3500
Jainti-Cachar	250–325
Tripura	120–150
Manipur. Mizoram	?
3 *Central India*	
Orissa	2000
Bihar	310
4 *South India*	
North Kanara-Crestline	100
Malnad-Bhadra	100–150
North Wynad-Nagarhole	600–800
Bandipur-Mudumalai-Nilgiris	1200–1500
Nilambur-Palghat hills	300–500
Eastern Ghats (South)	1800–2000
Anamalais-Palani hills	800–1000
Periyar-Varushanad hills	700–900
Agasthyamalai hills	150–200
Total	17310–22115

See text for sources of information

2.4a *North Kanara: Crestline of Karnataka Western Ghats*: The North Kanara district of Karnataka is the northern limit of elephant distribution in South India. There has been considerable incursion into the forests by cultivation, mining and the giant Kalinadi hydroelectric project. To the south, the crestline of the Western Ghats with its high rainfall evergreen forest and grassland extends as a narrow belt down to the Brahmagiri hills. In both these regions only a few scattered herds of elephants occur at a low density (Nair and Gadgil 1978) Perhaps less than 100 elephants are found here

2.4b *Malnad plateau-Bhadra*: This habitat lies to the east of the crestline, separated from it by a wide belt of coffee plantations and cultivation An irrigation project on the Tunga-Bhadra rivers is situated here. Elephants inhabit the Bhadra and Shettihally Wildlife Sanctuaries (area 827 km^2) and number about 100–150 individuals.

2.4c *North Wynad-Nagarhole-Kakankote*: The deciduous forests of the Kerala North Wynad, Nagarhole National Park and Kakankote (total area 1250 km^2)

stretch from south of the Cauvery river to the Kabbini river. Extensive plantations of teak are seen at Nagarhole. This is an important region holding 600–800 elephants.

2.4d *Bandipur-Mudumalai-South Wynad-Nilgiris North and East*: The Kabbini reservoir has left only a 6 km wide corridor between the forests of Kakankote and Bandipur. The deciduous forests extending south from the Kabbini to the slopes of the Nilgiris constitute one of the finest elephant habitats in South India. The perennial Moyar river is an important water source. This region includes the Bandipur Tiger Reserve (874 km^2), Mudumalai Wildlife Sanctuary (321 km^2) and the Kerala South Wynad (251 km^2). In addition, the semi-arid Sigur plateau to the east of Mudumalai and the northern and eastern slopes of the Nilgiris (700 km^2) are contiguous. Between 1200 and 1500 elephants may be present in the entire region.

2.4e *Nilambur-Nilgiris west and south Palghat hills*: To the west and south of the Nilgiris are the well preserved wet evergreen forests, shola-grasslands and semi-evergreen forests of Nilambur, New Amarambalam, Upper Bhavani-Kundah, Silent valley and Attapadi. In the rain shadow southeastern slopes are the dry forests of the Coimbatore Division, through which flows the Bhavani river. South of Attapadi, the forested hills end at the Palghat gap. Between 300 and 500 elephants occur at a low to medium density in this 1700 km^2 area.

2.4f *Eastern Ghats (south)*: This vast hilly region with a forested area of 7000 km^2 is contiguous with the Nilgiris on the southwest. Vegetation is largely dry deciduous and scrub but moist deciduous forest and evergreen shola-grasslands are found on the Biligirirangan hills. The Cauvery which flows through this region is forested on both its banks for a stretch of nearly 100 km. The constituent forest divisions are Bangalore, Mandya, Kollegal and Chamarajanagar (Karnataka), Hosur, Dharmapuri, Erode and Satyamangalam (Tamil Nadu). A detailed study on elephant ecology has recently concluded in the Chamarajanagar and Satyamangalam Divisions (Sukumar 1985). For the entire Eastern Ghats a reasonably accurate estimate is 1800–2000 elephants.

2.4g *Nelliampathis-Anamalais-Palani hills*: South of the Palghat gap, the great hill chain of Nelliampathis, Anamalais and Palanis forms a continuous elephant habitat. This includes the Parambikulam and Anamalai Sanctuaries. An entire spectrum of vegetation types is seen. The habitat has been disturbed by a series of hydroelectric projects and its associated canals. Elephants are absent towards the eastern portion of the Palanis. About 800–1000 elephants may inhabit this region.

2.4h *Periyar-Elamalai-Varushanad hills*: From the High Ranges at the southern end of the Anamalais, the Periyar plateau stretches south till the Shencottah gap. The Periyar Tiger Reserve has been constituted around the reservoir on the Periyar river. On the plateau the vegetation varies from evergreen to moist deciduous, while dry forest is seen on the eastern slopes of the Srivilliputhur range of Madurai district. An estimate of 700–900 elephants has been made for the region.

2.4i *Agasthyamalai-Ashambu hills*: The Shencottah pass maintains a tenuous link between the Periyar plateau and Agasthyamalai, but it is not clear whether elephant move across the railway line and highway in this corridor. This region includes the Neyyar, Mundanthurai and Kalakad Sanctuaries. Elephants are largely confined to the interior evergreen and semi-evergreen forests and grasslands. A tentative estimate of 150–200 elephants has to be taken.

3. Ecological requirements of the elephant

Elephants inhabit an entire spectrum of vegetation types from wet evergreen forests to semi-arid scrub zones. In the Himalaya, elephants are known to ascend upto 4000 metres above mean sea level, and they are also found in the dry thorn forests in coastal southeastern Sri Lanka. But they attain the highest densities in the moist and dry deciduous forests. The carrying capacity of prime deciduous habitats may be upto 3 elephants/km^2 compared to only 0·1/km^2 in the evergreen belt.

Due to its large body size the elephant consumes an enormous quantity of plant fodder, estimated at 1·5% (dry weight) of its body weight every day. Thus, an 'average' elephant weighing 1·8 tons requires 27 kg dry (about 108 kg fresh) matter daily. To achieve this intake the elephant has to be a generalist feeder, sampling a wide variety of plants. Though over a hundred plant species may be consumed in the wild, the bulk of the diet consists of just a few botanical taxa—the order Malvales and the families of Leguminosae, Palmae and Gramineae. In one area over 80% of the elephant's diet consisted of under 25 plant species from the above mentioned taxa (Sukumar 1985). With the aid of its trunk the elephant is able to exploit a wide range of feeding levels from tiny ground herbs to stout overhead tree branches.

The optimal diet is one of a seasonal alternation between a predominance of grass or browse. After the rainy season commences the fresh growth of tall grasses, especially in fire-burnt areas, attracts intensive utilization by elephants. During this period the grasses have a high protein content. Later, when the grasses mature they become silicaceous and unpalatable. Elephants now switch over to browse, which is especially important during the dry season as it retains a higher protein value than grasses.

The seasonal movement pattern of elephants is largely geared to optimizing its diet and also obtaining sufficient water. Elephants are far ranging animals. There is no evidence for territoriality in elephants but different 'clans' (each clan consists of many related elephant families numbering between 50 and 200 individuals) consistently range over particular areas which overlap with adjacent ones. The annual home range may be typically between 100 and 500 km^2 depending on the habitat factors. The relatively large home range requirement has important implications for conservation planning

4. Conservation strategies

4.1 *Minimum viable population size*

Any animal population in the wild undergoes normal fluctuations in response to extrinsic or intrinsic factors. It is well known that a species whose population dips below a certain viable size is prone to extinction due to stochastic events such as a disease epidemic or adverse climate (Shaffer 1981; Soule and Wilcox 1980). This viable size varies from one species to another.

There is also the consideration of the genetic viability of a population. In small populations the gene frequencies change randomly from generation to generation with a fixation or a loss of alleles. This process is known as genetic drift. Ultimately, this leakage of alleles leads to an increase in homozygosity (Frankel and Soule 1981). The central question in conservation genetics is the relationship between genetic variation and the fitness of the species. This can be considered both on a short-term and a long-term scale.

In the short-term the most serious consequence of an increased homozygosity is inbreeding depression (Ralls *et al* 1979; Soule and Wilcox 1980; Frankel and Soule 1981). The immediate effect of intensive inbreeding is a loss of fitness-lowered fertility, higher juvenile mortality, depressed growth, etc. Based on experiences with breeding of domestic mammals, it has been suggested that a minimum of 50 effective breeding individuals is needed to keep inbreeding depression to a negligible level of below 1% inbreeding per generation (Franklin 1980).

The issue of long-term fitness of a population, in terms of evolutionary potential, is still rather speculative. There have been attempts to derive the minimum population size above which the effects of genetic drift can be countered through natural selection or by gain from mutation (Franklin 1980; Frankel and Soule 1981). From both angles a figure of about 500 effective breeding individuals has been derived. Populations maintaining this effective size can be expected to remain viable from an evolutionary viewpoint.

A clarification has to be made here regarding the 'effective population size'. The census figure N for a species constitutes the genetically effective population size N_e only under idealized conditions such as an equal sex ratio of breeding individuals, an equal number of progeny per mating pair per generation and no fluctuation in population size. Of these the most important issue for elephants is the sex ratio. Due to a higher mortality of male elephants (compared to females) due to natural causes and poaching, the sex ratio of adults is usually unequal. At best it may be 1 male:2 females; at worst it may go upto 1:20 or even more disparate as in parts of south India. The more unequal the sex ratio, the greater will be the amount of genetic drift. The formula for calculating the effective population size N_e is given by

$$N_e = \frac{4N_m N_f}{N_m + N_f},$$

where N_m and N_f are the number of breeding males and females, respectively. The more skewed the sex ratio, the lower will be the value of N_e.

What are the implications of conservation genetics theory for the elephant populations in India? In south India the largest population inhabiting the Nagarhole-Nilgiris-Eastern Ghats belt consists of 3600–4300 elephants. Of these 7% are adult males and 35% are adult females (Sukumar 1985). Thus, there are atleast 252 males and 1260 females capable of breeding. Using the formula given above this translates into an effective population size of 840 breeding individuals—a comfortable level to counter the loss of genetic variation through drift. Unfortunately, the same is not true of other elephant populations in south India. Large populations do exist in the Anamalais and the Periyar plateau, but rampant poaching especially in the latter area has drastically reduced the number of male elephants resulting in a highly disparate sex ratio.

In northeast India the 3 large populations are those in the Arunachal Pradesh-north Assam region, the Kaziranga-Naga hills, and the Garo hills-Khasi hills of Meghalaya. Since 50% of the male elephants are *makhnas* (tuskless males) the sex ratio is not likely to be as highly skewed as in south India due to pressure from poaching, though the frequency of *makhnas* could increase in the population.

4.2 *Minimum viable area and habitat integrity*

This leads to the related concept of the minimum viable habitat area necessary for the long-term survival of a species. The principles of 'island biogeography' as enunciated in the classical work of MacArthur and Wilson (1967) have been extended to the design of terrestrial nature reserves (Wilcox 1980). The fundamental principle is that in a smaller 'island' area the rate of extinction of species will be higher than in a large area. In an insular habitat the species most vulnerable to extinction are usually the *K*-selected ones with low reproductive rates and those at the summit of trophic levels (Terborgh 1976). The question of new colonization of habitat patches, while possible for taxa such as birds, does not usually arise in the case of elephants. It is a matter of either having one large elephant population ranging freely over a large area, or allow it to break up into a series of smaller populations in fragmented patches. Clearly for the elephant a single large area is desirable.

What would be the minimum viable area for the conservation of the elephant? This is related to the minimum viable population size and to the carrying capacity of the habitat. Assume that the minimum size needed is 500 breeding individuals and with the prevailing sex ratio (1 adult male : 5 adult females) this translates into a total population size of 2200 elephants. Further assume that the crude carrying capacity of a given area is 0.5 elephant/km^2 and the population is close to this level. A minimum area of 4400 km^2 would be needed for its long-term conservation. This area would vary with different values of the parameters; the above typical situation is merely to give an idea of the scale at which one should think when planning reserves for elephant conservation.

For a species with a large home range and a need for seasonal movement from one habitat type to another, further human encroachment reducing and fragmenting the habitat would affect the conservation prospects. Habitat reduction also intensifies the incidence of crop raiding by elephants (Sukumar 1985). In the Bannerghatta-Anekal-Kanakapura ranges of Karnataka, the habitat has been reduced to a long, narrow strip only 2–3 km broad in places. If elephants move through this belt the chances that they would come into contact with cultivation are very high. Forays by elephants into cultivation are very common here; in January 1985 a herd of 9 elephants strayed into the suburbs of Bangalore City, a distance of 15 km from their habitat.

Agents of habitat fracture in south India are mainly agriculture and dams. In the Eastern Ghats the numerous enclaves of cultivation have made large dents on habitat integrity. All over the Western Ghats tea and coffee plantations have made considerable inroads into the natural habitat. These are mainly responsible for the discontinuity in elephant distribution in south India. In recent years a portion of the elephant habitat on the southwest of the Nilgiris (Nilambur-Attapadi) has been virtually cut off from the larger Nilgiri-Eastern Ghats region by tea plantations in the Gudalur Division. The practice of slash and burn—shifting cultivation is a major threat to the habitat in the northeastern states (Choudhury 1980).

Hydroelectric and irrigation dams are common all over the Western Ghats These have submerged river valleys which are prime habitats for elephants. Many such projects, as in the Anamalai hills of Tamilnadu-Kerala, have also disrupted the traditional movement pattern of elephants and served to localize herds to smaller areas Not all dams have led to habitat disruption. The century-old reservoir on the Periyar river in Kerala forms the nucleus of an important wildlife sanctuary with a perennial source of water for animals

It has been suggested that a disease epidemic is likely to cause the extinction of an entire animal population in a large area. If distributed over numerous smaller habitats the species as a whole would still survive even if one population becomes extinct. This point is valid. But it is not a justification for fragmenting a large area if the option to retain it intact is available. The Asian elephant today exists over a broad area of the Indian sub-continent in a number of discrete populations It is in that sense buffered against extinction through an epidemic in one region Thus an effort should be made to keep intact as many large areas as possible along with a number of smaller viable ones. Then one would not run the risk of 'keeping all the eggs in one basket'.

4.3 *Maintenance of habitat quality*

The habitat has to provide the basic resources of food and water for elephants. In most areas elephants have to share these resources with people Sites of human settlement are usually prime habitats such as valleys with the best water sources, fertile soil and a high potential plant productivity There is intense competition between elephants and people for water in many regions (e g. Eastern Ghats). By a proper landuse planning the elephant's access to important water sources has to be ensured.

Human manipulation of the habitat has altered the vegetation structure from primary or climax stage to secondary or early seral stages. What are the consequences of this change for elephants? It is well known that the highest herbivore densities are often found in habitats manipulated by man. For instance, in the Serengeti region man's impact through burning of the grassland and grazing of domestic livestock is ancient. The highest animal densities are found in such areas of past and present pastoral activity (Bell 1971) Conversion of a climax vegetation such as the evergreen rain forests to secondary forms causes a corresponding increase in elephant density (Olivier 1978b). In a climax rain forest the bulk of the plant biomass is trapped in the upper canopy and unavailable for animals In secondary vegetation, pioneer and light demanding *r*-selected plants such as grasses, bamboos and *Kydia calycina* provide abundant food for elephants.

A model depicting the changes in carrying capacity and elephant density along two gradients in vegetation is shown in figure 2.

4 3a *Across forest types*: Elephant density increases from evergreen forest through

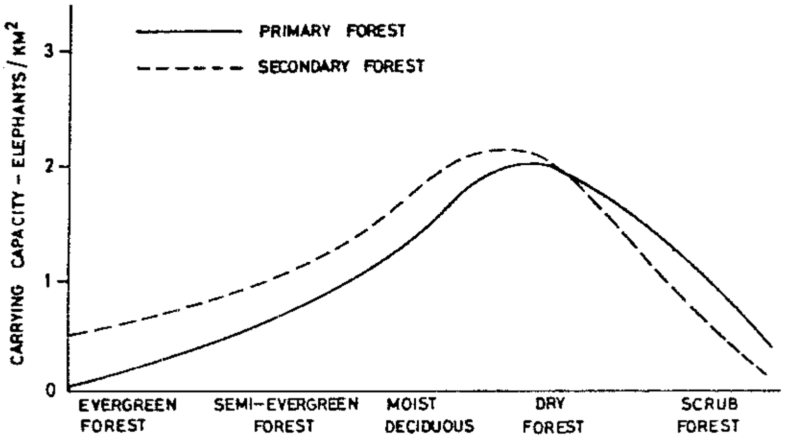

Figure 2. Carrying capacity of primary versus secondary forest

the semi-evergreen type only until the deciduous forest. Beyond this there is a decline as the vegetation progressively changes into poor scrub.

4.3b *Within forest types*: The process of change from climax to early seral stage does not elicit the same response in the different vegetation types. The highest relative increase in carrying capacity may occur in the evergreen forest, but beyond the deciduous forest it is unlikely that this trend would continue. Xerophytic vegetation is characteristically short-statured and ensures a high proportional browse availability for elephants. Further exploitation of the dry zone scrub would reduce the carrying capacity. This model, of course, does not take into consideration other factors such as water availability. A scrub habitat along a perennial river may support a higher density than a dry deciduous forest with scarcity of water.

Undoubtedly, the optimum environment for elephants is one with a diversity of habitat types. This would include the moist and dry deciduous forest, scrub (which provide abundant leguminous browse shrubs such as *Acacia* spp.), riverain or gallery forest and patches of swampy grasslands. Alluvial floodplains of large rivers are also favoured when associated with a habitat mosaic. This diversity in habitat types enables the elephant to optimize its diet depending on seasonal changes in plant phenology.

It is often inevitable that elephant and man have to share the habitat and resources. Human land-use need not always be incompatible with the elephant's need. It is not possible to generalize for all areas; each situation has to be considered separately.

(i) Selective logging in forest habitats is not detrimental to the elephant. In certain moist vegetation types this may actually create a more favourable niche.

(ii) Elephants may adapt themselves to certain monoculture plantations such as teak, provided the understorey vegetation has sufficient food plants. The Nagarhole National Park has a high elephant density even in the teak plantations. However, this should not be taken as a justification for raising plantations on a large scale. In many instances other disturbances associated with plantations depress herbivore densities.

(iii) Invasion by noxious weeds such as *Lantana* and *Eupatorium* is a consequence of disturbance to the natural vegetation, especially clear-felling an area or even just clearing the understorey vegetation. This is undesirable as both these species are not consumed by herbivores and further suppress the growth of indigenous plants. With the intensive exploitation of bamboos in many areas, it is possible that *Lantana* may now be occupying this niche.

(iv) The role of fire in altering the plant community needs further study. Burning of grassland in the African savannas helps in maintaining a high diversity and density of grazing ungulates. In the deciduous forests of south India, too, elephants prefer to feed on freshly growing grass in burnt areas after the rains commence. However, the effect of fire on the woody vegetation has to be also considered. In particular, the deflection of the woody plant succession towards a 'fire climax' may be undesirable if unpalatable trees such as *Anogeissus latifolia* become dominant because of their resistance to fire.

(v) Should wildlife managers purposely manipulate the habitat so as to maintain a high carrying capacity for elephants? I personally consider human attempts at 'management' of natural habitats and animal populations unnecessary except under certain pressing circumstances. As argued earlier, habitat manipulation is likely to increase carrying capacity only in evergreen-moist deciduous vegetation. Tropical evergreen forests represent a relatively stable climax with their own unique assemblage of plants and animals. It is unwise to disturb this community for the sake of increasing elephant numbers. In the dry deciduous and xerophytic vegetation any conversion to secondary forms will not benefit the elephant.

Where the elephants range over a sufficiently large area, it is not necessary to manipulate the habitat even if this means that they will exist at only a low density. An artificial build up of the elephant population will result in increased crop raiding, damage to trees and crash in numbers during drought. If elephants are confined within a smaller area, then some management may be justified in order to maintain a viable population size.

4.4 *Reduction of poaching*

The levels of poaching in south India seem to have reached unacceptable levels during the past few years. In the states of Karnataka, Kerala and Tamil Nadu about 100–150 male tuskers were shot annually during 1980–83 (Sukumar 1985). With a mean tusk weight of 9·5 kg, even taking the lower figure of 100 elephants and 190 tusks (assuming some were one-tusked), this supplied 1800 kg of ivory valued at Rs. 2,700,000 to the illegal trade.

It may be impossible to completely eliminate poaching; it would be unrealistic to expect to do so with the limited manpower available. If one has to live with a certain amount of poaching, then what would be a 'safe level' of male mortality at which the adult sex ratio would not become very disparate? The sex ratio, of course, depends not just on the male mortality but also on the differential mortality between the sexes and, thus, the female mortality must also be considered. Female mortality, however, usually varies within a small range (2–5% per annum) over most of its sub-adult and adult life span (5–50 years).

Computer simulations, using the age-structured Leslie matrix model, have shown that at current levels of poaching in parts of south India the adult sex ratio could reach 1 male : 10–20 females. The implications of this disparity have been discussed earlier. If the male mortality rate due to both natural causes and poaching is kept below 8% per annum, the adult sex ratio may be pegged at 1 male : 5 females (Sukumar 1985). This calls for a regular monitoring of the elephant population numbers, mortality and sex ratio.

4.5 *Reduction of crop damage by elephants*

Raiding of agriculture crops by elephants is common over most of its range. Further, people guarding their fields may be sometimes killed by elephants. These have served to label the elephant as a pest to human interests. Conservation of the elephant will never gain acceptance among the vulnerable villagers as long as this state of affairs is not rectified.

This is easier said than done. The main problem is to find an economically feasible solution to keep elephants away from fields. Simple methods like bursting of fire crackers are useless against these intelligent mammals which have learnt to recognize such bluffs. Trenches are expensive and, moreover, have a high risk of failure since elephants often learn to fill the trench by digging the soil with the forefeet and then crossing over.

The high-voltage electric fence (of a non-fatal type) seems to have the best potential. This consists of one or more strands of galvanized steel wires strung at appropriate heights (1–2 m for elephants) above the ground by hardwood posts. The posts are protected by vertical wires and insulators may be provided at places where the wires come into contact with the posts. The heart of the fence is the 'energiser' which passes every second an electric pulse of 5000 volts at a duration of 3/10000 second. Due to the high voltage but short duration of the electric pulse, any animal coming into contact with the wire receives a severe jolt but is no danger of dying or even any serious injury. The energiser may be powered by a 12 V car battery, from the 230 V mains or even by solar cells.

Numerous experiments with electric fencing in Africa (Piesse R L, unpublished results) and Malaysia (Blair 1980) have shown that it is generally effective against elephants. During a period of 32 days in 1982, a total of 259 elephants made 184 contacts with an electric fence in Namibia-Etosha, but not a single elephant got through. In Malaysia a few thousand kilometres of fencing have been erected around oil palm and rubber plantations. One trick that an elephant may try is use its tusks (non-conductor) to break the wire. It must be emphasized that the electric fence is not strictly a physical barrier but more of a 'psychological bluff'.

The elephant is an integral part and a grand symbol of Indian culture. Any plan which focuses on elephant conservation need not be incompatible with the conservation of biological diversity. Elephants still range over a number of biogeographic regions in the Indian sub-continent. The protection of representative areas in each of these regions would contribute significantly to the conservation of the overall biological diversity.

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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

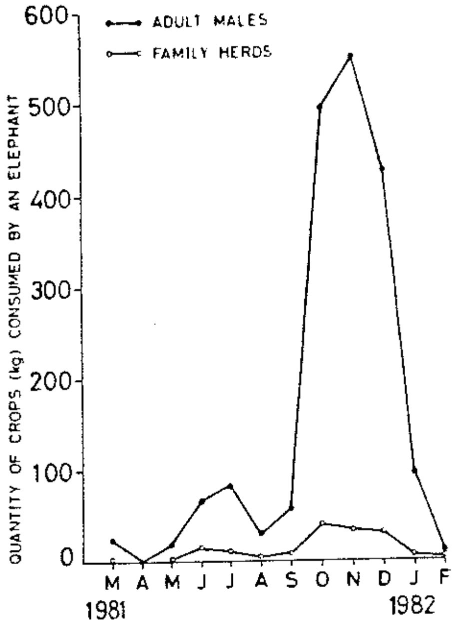

Fig 1. Quantity of crops in kg (dry weight) consumed by an average adult male elephant or an average individual in a family herd during different months

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 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).

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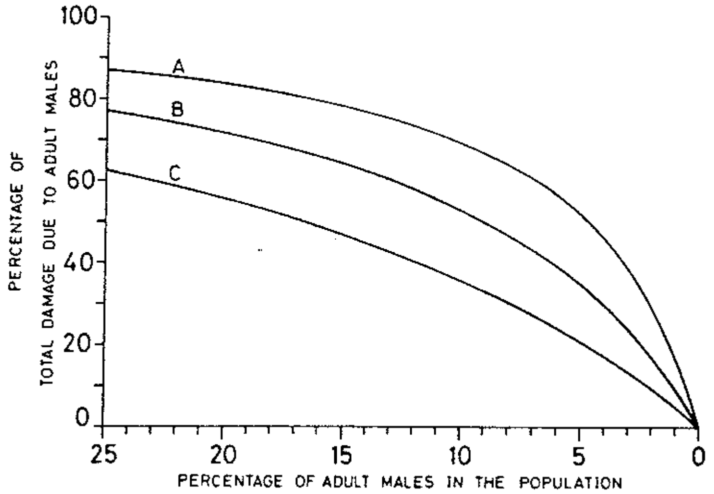

Fig 2. Percentage of total economic loss to crops caused by adult male elephants as a function of differing percentages of males in the total population assuming (A) 20-, (B) 10- and (C) 5-fold difference in *per capita* damage by an adult male compared to an individual in a family herd

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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ECOLOGY AND MANAGEMENT OF THE TIGER IN TROPICAL ASIA

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Key words: tiger, tropical Asia, distribution, habitat, spacing, social organization, dispersal, feeding ecology, mortality, reserves, hunting

INTRODUCTION

The tiger is the top predator in a wide range of complex and diverse biological communities throughout its geographical range in tropical Asia. Being large carnivores with extensive range needs, tigers come into conflict with human interests easily, rendering them especially vulnerable to extinction. However, this is a valid reason for using the tiger as an "umbrella" for conserving overall regional bio-diversity. Primarily owing to the tigers' influence on human imagination as a flagship species, conservation efforts have succeeded in south Asia (Panwar 1982).

I have reviewed the biology of the tiger here, based on past studies and some preliminary insights from our (Ullas Karanth and Mel Sunquist) current work in Nagarahole Park, India. Because Conservation Biologists often over-emphasize the need for expensive, cutting-edge technologies to field problems of tiger conservation (Foose 1987; Seal et al. 1987), I have highlighted the need for basic biological data and the primacy of tackling immediate management problems. I am indebted to Mel Sunquist and Fiona Sunquist for useful discussions which contributed greatly to this paper. I also acknowledge the financial support from the organizers of INTECOL 1990 and The Wildlife Conservation International of the New York Zoological Society, which enabled my participation.

ECOLOGY AND BEHAVIOR OF THE TIGER

Though many anecdotal publications on tigers are available, scientific studies have been scarce. Schaller (1967) and the Chitwan Tiger Ecology Project (Seidensticker 1976; Sunquist 1981; Tamang 1982; Smith 1984) have produced important quantitative studies. Valuable long term observations at specific localities, albeit anecdotal, have also been published by McDougal (1977), Singh (1984) and Thapar (1986).

Distribution and Habitat Needs

Past and present distribution of the tiger has been recently summarized (Hemmer 1987; Seal et al. 1987). Using field assessments by managers, biologists have tried to generate population estimates of wild tigers (Seal et al 1987). For Bhutan, Laos, Kampuchea, Thailand, and Vietnam, there are no estimates. The tiger numbers for Bangladesh (300 – 430), Burma (750), Malaysia (600 – 650) and Indonesia (650) seem to be merely guesses of varying quality. In India, seemingly exact numbers (4005) are derived using demonstrably unreliable techniques (Karanth 1987, 1988a). Tigers are reported to occur in several insular populations whose boundaries are undetermined. However, the size and distribution of tiger populations in Nepal (230) alone have been derived using density estimations from radio-tracking, and their extrapolations based on abundance of prey and tiger sign, and habitat quality assessment (Smith 1984). Tigers of tropical Asia inhabit forest formations termed as dry-deciduous, moist-deciduous, semi-evergreen, wet evergreen, riverine, swamp and mangrove, showing remarkable tolerance to variations in altitude, temperature and rainfall regimes. Availability of surface water and shade seem to be important factors for thermo-regulation.

Feeding Ecology and Prey Requirements

Assuming a carcass utilization of 70%, Sunquist (1981) estimated that an average tiger has to annually kill 45 - 50 prey animals weighing 50+ kg at roughly 8 day intervals. In case of females with young the need is higher at 60 - 70 kills/year. The actual requirement may be higher than above where tigers are disturbed and their kills appropriated by people. Thapar (1986) found a high degree of carcass utilization at Ranthambhore, India. At Nagarahole, where prey densities are perhaps higher (Karanth 1988b), I have often observed a lower degree of utilization, particularly in large prey species such as gaur (*Bos gaurus*) and sambar (*Cervus unicolor*). This suggests kill rates may not necessarily be higher at higher prey densities.

Though tigers do take small prey, based on several food habit studies (Schaller 1967; McDougal 1977; Sunquist 1981; Johnsingh 1983; observations in Nagarahole), it appears that tigers cannot survive if their principal prey, mammals in the 30 - 1000 kg body size class, are not readily available. Prey biomass estimates are not necessarily correlate to the tigers' densities (Table 1).

Tigers are solitary, cryptic, often nocturnal, stalk-and-ambush hunters (Sunquist 1981). Vulnerability of their prey may be relatively dependent on vegetation structure, and consequently, tiger densities may correlate to vegetation in addition to prey density.

Social Organization and Spatial Needs

Long term studies in Chitwan (Sunquist 1981; Smith 1984; Smith et al. 1987) show that a tiger population consists of the following segments: (i) Resident adults (3+ years) which defend their home ranges against other adults of the same sex (ii) Pre-dispersal young, aged 17 - 28 months that stay with their mother or within her range. (iii) Transients, which include post dispersal young adults or residents who have lost their ranges.

In Chitwan, male ranges overlapped several female ranges. Transients were generally excluded from residents, ranges and lived in marginal habitats in the edge of the ecological unit (Sunquist 1981, Smith 1984). During 1980, Smith (1984) estimated that the density of residents was 2.5 tigers/100 km², with a male:female ratio of 1:2, and that there were 2.6 - 4.0 young and/or transients for every breeding female. Using these figures, the overall density of tigers works out to 8.78 animals/100 km² in the Chitwan region (Table 1). Sub-adults dispersed from their natal ranges at around 18 - 28 months of age. Males dispersed about 3 times farther than females. Some dispersers ultimately took over resident ranges by evicting incumbents. Some females gradually "inherited" their natal ranges. These land tenure and dispersal patterns created neighborhoods of closely related tigers (Smith 1984).

Table 1 Prey biomass and tiger densities

Study Site	Area km²	Prey Biomass kg/km²	Tiger Density nos./100 km²
Kanha	318	4066	6.92
Chitwan	1024	1946	8.78
Ranthambhore	400	2765	10.00
Nagarahole	103	7658	11.65

* The above figures are derived from estimates made by reliable observers familiar with the area, but using different methods. Sources are: Schaller (1967) for Kanha; Tamang (1982) for Chitwan; Thapar (1986) for Ranthambhore and from our ongoing study for Nagarahole. The prey biomass for Kanha includes livestock.

Tigers communicated through scent marking, vocalization and visual markers such as fecal deposits and scrapes. Intra-species aggression of Chitwan tiger population was less observed at lower density (Sunquist 1982) than at higher density (Smith 1984).

Population Dynamics and Mortality Factors

Females first breed at about 3 years, after establishing ranges. They may maintain resident status for the next 8 - 10 years producing 4 - 5 litters (12 - 18 young), of which only 50% may reach dispersal age. Juvenile mortalities result from fires, floods, human action, parental neglect and infanticide by males (Schaller 1967; Sunquist 1981; Thapar 1986; personal observations). Because females breed early, have a short gestation (104 days), and come into estrous rapidly following loss or dispersal of young, the reproductive potential is high. Initial response to improved habitat conditions may be increased numbers of breeding females. Thereafter, resident numbers may remain stable, numbers of transients may increase and competition for space, kills and mates may intensify in both sexes. This may result in a high degree of intra-specific aggression between residents, between residents and transients, and through infanticide following changes in male ranges and shorter resident tenures (Smith 1984; Thapar 1986; my observations in Nagarahole) Injuries and resultant starvation may be important mortality factors in such situations.

All over tropical Asia, tigers also perish from human persecution such as deliberate and accidental forest fires, trapping or snaring, poisoning and shooting (McDougal 1977; Khan 1987; Santiapillai 1987). The above review of population dynamics, and the huge takes reported (Schaller 1978) from tiger hunts from several regions in the past, suggest that under moderate hunting pressures a "complete compensation model" may apply to high density tiger populations

FUTURE MANAGEMENT OF WILD TIGERS

The future management of wild tigers in tropical Asia needs to be based on thoughtful application of our knowledge of their biology to the social context in which wildlife management takes place. Though excellent reserves exist in Nepal and India, tigers, their prey and habitat are under serious threat from hunting, poaching and human encroachment all over the region. These problems are rooted in rising populations, extreme poverty, developmental activities and cultural influences (Panwar 1982; Mishra et al. 1987; Santiapillai 1987; Khan 1987). Though addressing these causes is not the domain of the wildlife manager, he has to face their consequences. Local wildlife managers have sometimes empirically come up with intelligent solutions to problems, as exemplified by the grass cutting schemes in Chitwan (Mishra et al. 1987) and mitigating man-killing by tigers in Sundarbans (Sanyal 1987).

With the partial exception of Nepal, management is hamstrung by lack of basic biological data on tiger populations such as; their boundaries, size, social organization, dynamics, genetics, prey density, and habitat quality over most of the region Even basic protection is inadequately funded. A majority of reserve managers are untrained in wildlife biology and hence incapable of even basic monitoring (Karanth 1988a) There is urgent need for research, and for its integration with training to upgrade management skills.

The present range of the tiger covers an extensive area of poor quality habitat used for forestry, live-stock grazing, and several forms of intensive biomass extraction for subsistence Densities of wild prey and tigers are low. Such habitats are in blocks of 100 – 3,000 km² size, and surrounded by landscapes incompatible with tigers Within this matrix, there are "hot spots" of high quality habitat, where breeding populations of tigers are producing local surpluses. Where such "hot spots" interface with human settlements, the incidence of problem tigers has increased alarmingly (McDougal 1987; Singh 1984; Sanyal 1987) and conservation has suffered through public antipathy. Though quick removal of such problem tigers (mostly transients) is recommended, identifying them for elimination has been an unsolved practical difficulty. Behaviors such as intra-specific aggression, and lack of fear of humans, are both likely to find expression in protected, high density tiger populations and give rise to such problem tigers (McDougal 1987). Some degree of tiger hunting in peripheral areas may alleviate both these behaviors. However, implementation of hunting schemes is difficult, given the lack of biological data, paucity of management skills, and probability of abuse

Observations in Nagarahole show that in humid forests, habitat manipulations such as creation of a mosaic of diverse habitat types, maintenance of secondary growth and grassy areas through cutting back/burning, and facilitating perennial water resources can result in high densities of prey (Karanth 1988b) Such manipulations can be integrated with forest management cost effectively to "pack" more tigers into existing habitat.

Tiger populations in tropical Asia are small (25 – 250 animals) and insular. Based on our present knowledge of their social organization, and of recent population bottlenecks, it is likely that animals in each disjunct population are highly related. In response, conservation biologists often see potential for genetic management of wild tigers, through sophisticated technologies such as captive-breeding/reintroduction, artificial insemination, and embryo transplants (Foose 1987). However, for these conservation techniques to work on a meaningful scale, the minimum requirements are: huge investments that tropical Asian countries cannot afford, basic population and genetic data on wild tigers which are unavailable (Smith 1984), and deployment of skilled personnel who do not exist.

Therefore, for the next couple of decades at least, these approaches to tiger conservation may not be very relevant. I suggest that actively moving individuals between populations or enhancing potential for natural gene-flow by improving habitat connectivity may be the only options open The former scenario may still have very poor probability of success (Wemmer et al 1987) Tigers move through almost any sort of dense cover Enhancing habitat connectivity by incorporating fiscal incentives for plantation forestry on agricultural land adjacent to tiger habitats (Panwar 1987) may be the most realistic strategy

In conclusion, I would argue in favor of deploying scarce funds and skills to realizable goals of tiger conservation outlined here, even if this implies a philosophical acceptance of small and insular tiger populations by conservation biologists well into the next century

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Diversity: Cultural and Biological

Madhav Gadgil

Early human populations utilized a wide range of biological resources in a tremendous diversity of environments. As a result they possessed high levels of cultural diversity dependent on and supportive of high levels of biological diversity. This pattern changed drastically with technological innovations enabling certain human groups to break down territorial barriers and to usurp resources of other groups. The dominant groups have gone on to exhaust a whole range of resources, depleting both biological and cultural diversity. Traditions of resource conservation can, however, re-emerge when the dominant cultures spread over the entire area and the innovations diffuse to other human groups. This could change once again as genetically engineered organisms become an economically viable proposition with the accruing advantages concentrated in the hands of a few human groups: a further drastic reduction in biological and cultural diversity may ensue.

The diversity of life on earth is currently under serious threat; so is the diversity of human cultures. Since the now dominant technological culture is often perceived as a major cause of loss of biological diversity, there is serious interest in understanding how the diversity of human cultures relates to the conservation of biological diversity, and whether the attempts to conserve biological and cultural diversity could go hand in hand[1].

Biological diversity has increased through evolutionary time, presumably because much of it arises through diversity of adaptations to environmental heterogeneity, which itself has been continually enhanced by the activities of living organisms[2,3]. Part of the adaptation of organisms is behavioural, with behaviour becoming increasingly flexible in higher animals. Thus birds and mammals take to new food sources by imitating other members of their social group[4]. Biologists define culture as such acquisition of behavioural traits from conspecifics through social learning; and man's close relatives, such as chimpanzees, have progressed further by introducing deliberate teaching[5]. The capacity for tool use and symbolic communication has, however, enabled the

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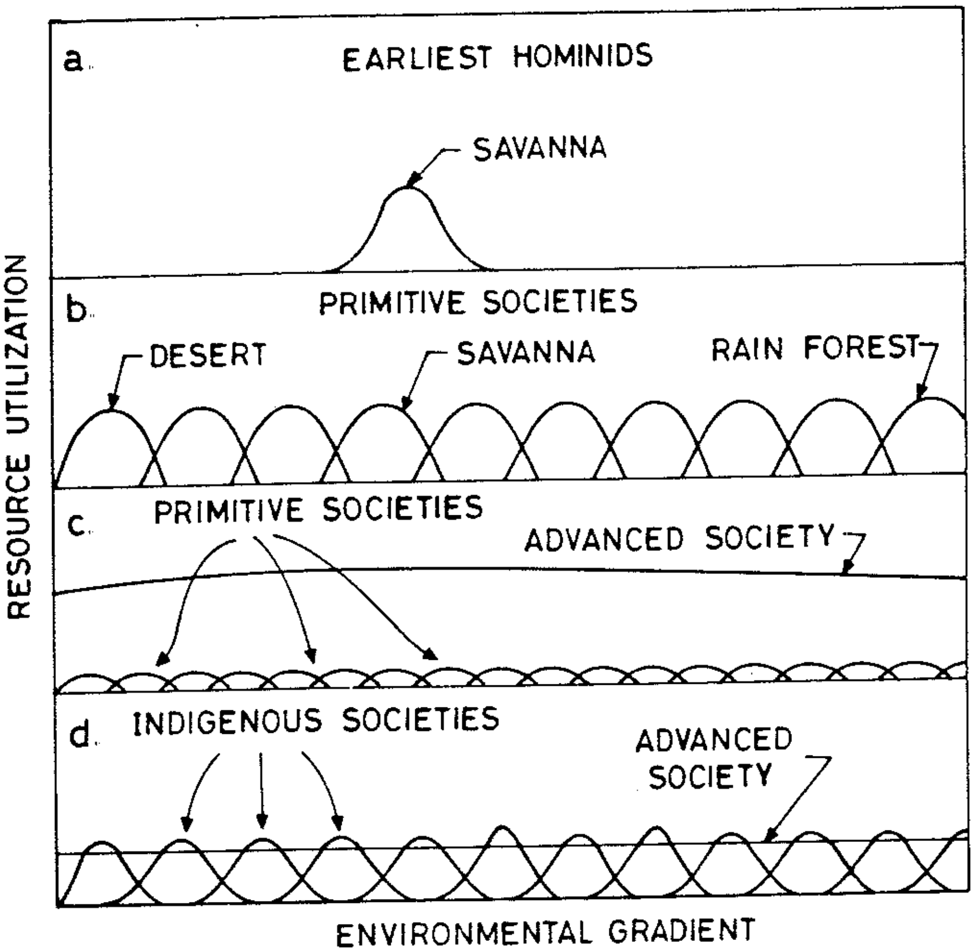

Fig. 1. Historical changes in patterns of resource utilization by human societies (a) The earliest hominids were genetically and culturally adapted to utilize the biological resources of tropical savannas (b) Cultural adaptation then enabled hunter–gatherer societies to occupy a wide range of environments with each local society fine-tuned to utilize the biological resources of its own environment (c) Technological advances enabled a few societies to usurp the bulk of resources from the more primitive and culturally more diversified societies. Technologically advanced societies initially maintained rather high levels of resource utilization while the availability of resources to more primitive societies was markedly depressed (d) With diffusion of technologies and depletion of the resource base the advantage enjoyed by the technologically advanced societies is reduced so that the less advanced indigenous societies can begin to reassert some control over resources

human species far to outstrip all others in the complexity of its culturally transmitted behaviour This has rendered possible a tremendous variety of cultural behaviours in the different human populations across the world[6]

Human cultural behaviour encompasses a great range of traits, but we are concerned here only with those pertaining to the biological environment: information regarding and patterns of behaviour relating to other living species and artifacts fabricated from or meant to deal with them. Any given human group may possess a wealth of culturally transmitted behaviour in this context; and just as we talk of α-species diversity or ecological species packing, such within-group diversity of elements of cultural behaviour patterns may be termed α-cultural diversity. These cultural patterns also differ from one human group to another, and this may be termed β-cultural diversity in analogy with β-species diversity or ecological species turnover[3]

Human niches

When populations of *Homo erectus* learned to make and use tools two million years ago, they greatly expanded the range of food items accessible to them They could then not only consume small animals and berries, but also dig for roots and tubers, and cut through tough hides of animal carcasses[7]. Techniques of making tools from stone, wood and bone, and information on what to eat and what to avoid eating, would have become a vital component of the culture of these hominid groups. For instance, a 1.5 million year old fossil of *H. erectus* from Koobi Fora in Kenya shows signs of suffering from a poisonous overdose of vitamin A, probably caused by consumption of large quantities of raw liver.

As Leakey[6] remarks such consequences would be expected when meat eating was a novel pursuit and could have been avoided only when a lore was built up of what was good to eat and what was to be avoided Since African savannas are exceptionally rich in biological resources and the early hominids occupied a particularly varied environment comprising a mosaic of grassland, woodland and gallery forest[7], these groups must have possessed high levels of α-diversity of elements of cultural behaviour patterns relating to biological diversity

When control over fire and effective group hunting were added to tool-using abilities, hominid groups could colonize all but the most arid zones. Survival in such a wide range of environments by populations equipped with relatively simple technologies depends on a tremendously detailed knowledge of the local environment and of appropriate ways of dealing with it (Fig 1). Biological resources would have been significant to such populations not only as food and raw materials for tools, but also as bait, drugs and so on This importance of a diversity of biological resources is reflected in the wealth of folk systematics of present-day primitive societies which often discriminate up to 800 different kinds of living organism[9] The different human groups in early days must have diverged culturally in their adaptations to the use of biological resources, exhibiting high levels of β-diversity For instance two different groups of Neanderthals living in close proximity in France are believed to have maintained specific cultural identities with one group specializing in preying on reindeer and the other in hunting horses[8]

Ecological prudence

At what rate would humans have used the variety of biological resources that they depended on? The resources could have been foraged for at rates that would maximize immediate energy or nutrient returns, and this might have caused extinction of some biological populations, at least locally Of course, even while foraging optimally the human predators may not have exploited the prey populations to extinction switching to other patches or other species when lowered prey population levels reduced the returns below a threshold It would often be quite difficult to distinguish such behaviour from behaviour designed to conserve the various prey populations on a long-term basis[10]

There are however certain patterns of human utilization of biological resources that cannot be interpreted as part of an optimal foraging strategy For instance many biological communities receive total protection (e g sacred groves or ponds) and function as refugia Keystone species such as *Ficus* trees may receive total protection over a wide area and may serve to support a whole range of insects birds primates and other organisms These practices suggest that human populations may indeed have developed traditions that specifically serve to conserve a diversity of biological resources of value to them

It is possible to think of scenarios favouring the cultural evolution of such deliberate conservation measures Many hunter–gatherer societies as well as shifting cultivator or horticultural societies significantly dependent on foraging are known to have been highly territorial, with each endogamous group constantly struggling with neighbouring groups[11] Being a *K*-selected species with a long generation time humans cannot quickly convert resources into increased population size The well-being of a human group therefore requires the availability of resources and possibly a wide diversity of resources at a minimal level over periods of several years For territorial groups this implies the need to sustain resource levels on a long-term basis within their own territory Any group that failed to achieve this would find itself weakened and subject to the territorial aggression of neighbouring endogamous groups, and become culturally, even if not genetically, exterminated Cultural group selection, which may be quite effective under these special conditions, might then favour behavioural traits that would ensure sustainable use of the biological resources of the territory[6] In addition, within-group cooperative behaviour promoting prudent resource use is also expected to prevail in endogamous groups where a relatively small number of individuals repeatedly interact with each other over long periods (Ref 12; F Berkes and A Kence, unpublished) Such practices may be particularly common in groups inhabiting stable productive habitats where territoriality is likely to be strong

It is then not surprising that some of the best documented examples of conservative use and protection of a wide spectrum of biological diversity come from human groups of small Pacific islands and of New Guinea rain forests[1,13–17] Such groups possess a variety of practices apparently leading to sustainable use of a wide range of biological resources and conservation of biological diversity as a whole. These include total protection of certain biological communities or species; protection of certain life history stages, or during certain seasons; restrictions on methods and amounts of harvest, and on certain social, age or sex groups from harvesting certain species; and restriction of access to certain localities to certain groups or individuals

Of course some of these practices may be a consequence of optimal foragers reducing the rate of exploitation in response to local depletion of a given prey population[10] We may so interpret the moratoria on hunting of certain birds imposed by New Guinea chiefs when their populations appear to have declined or the ban on certain methods of fishing by Pacific islanders following the decline of fish populations[14,16] However these decisions do appear to be taken and enforced by the group as a whole suggesting that what is being ensured is long-term group interest in resource conservation, which may be against the short-term interest of individual foragers

Sequential exploitation

Cultural traditions of conservation would confer no advantage on human groups under a variety of conditions:

(a) When the resource level fluctuates independently of the extent to which the resources are harvested, for instance with populations of migratory prey species This might also be the case in highly seasonal or unpredictable environments, such as deserts where the human user group is also likely to be nomadic

(b) When a conquering human group is able to move into new areas displacing the former occupants As the resources of any locality are exhausted, the group may derive no advantage from conservative use if the option of moving into a new locality is open to it. At the same time, subordinated groups would also fail to derive any advantage from practices of conservation

(c) When humans have developed the technological abilities to deploy newer and newer resources to meet their various requirements, they may find little advantage to conservative use of any particular resource

(d) When a human group is unable to ensure the cooperative behaviour of its members

Technological innovations must have played a vital role in affecting the patterns of resource use by human populations Some, such as the use of the horse or gunpowder, significantly affect the relative coercive abilities of different human groups Others, like the iron axe or snowmobile, increase the rate of resource harvest and thereby enhance the possibilities of resource exhaustion unless there is persistent motivation for conservative resource use Yet others, for instance the ability to convert any kind of woody matter into a variety of paper and polyfibre products, eliminate the motivation for the conservation of a diversity of species Finally, technology can dramatically increase the sizes of human groups having access to the particular resources, thereby rendering difficult the enforcement of cooperative behaviour on the part of all group members so necessary to ensure conservative resource use

By and large, technological innovations would thus tend to favour non-conservative use of biological resources In particular, whenever a technologically superior group moves into a region occupied by groups at more primitive

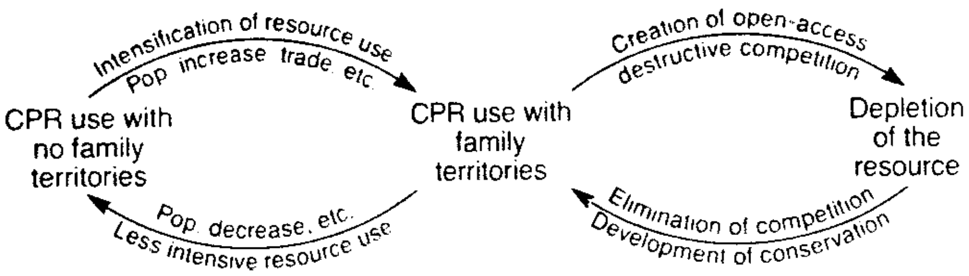

Fig 2 The cycle of utilization of a potentially common property resource (CPR) the beaver in Eastern subarctic Canada occupied by Cree Amerindian people At relatively low levels of use the resource is owned and used communally With increasing levels of exploitation the resource is still used communally but under a system of family-controlled territories White trappers broke down this system in 1920–30 resulting in resource depletion Under conservation laws introduced after 1930 outsiders were banned from trapping in this area and Cree communal and family territories were legally recognized, resulting in productive harvests after 1950 *Redrawn from Ref 12*

levels of technology the dominant group would have the option of moving on to fresh pastures as resources of any locality are exhausted and would derive no advantage from traditions of sustainable conservative use. At the same time groups now subordinated would lose any advantage from traditions of conservative use that might have been favoured in times when they could exclude other groups from their territory (Fig. 1). The result would be a relatively rapid use of resources, with the wave of resource exhaustion spreading outward from localities first affected by the dominant group.

Such a pattern of resource use has been termed the *fishing-up sequence* in the context of fisheries and *sequential exploitation* in a broader context[18]. This process would tend to deplete biological diversity. It would also diminish cultural diversity, for two reasons. First, a significant component of cultural diversity relating to fine-tuning of cultural behaviour to the local biological environment would lose its functionality. Secondly, subordinated groups may begin to imitate the culture of one or few dominant groups, thereby losing part of their cultural diversity. Indeed, there is abundant historical evidence of such a process accompanying the two major technological revolutions in human history. Thus, the colonization of the Gangetic plains by the dominant agricultural–pastoral people of the so-called Aryan culture from about 1200 to 600 BC was accompanied by systematic destruction of natural biological communities and breakdown of cultures of indigenous populations as they were subjugated[19]. Similarly, a wave of overfishing and overhunting swept over North America along with the depletion of cultures of indigenous people at the time of the colonization of that continent by European populations[18]

Reassertion of the conservation ethic

This process may cease, however when dominant groups no longer have 'virgin' territories to take over and when the technological innovations of the dominant group have been absorbed by other human groups. It is then likely that local populations of subordinated, as well as dominant groups may assert restricted access to certain localities and/or resources (Fig 1). Practices of sustainable resource use may then again confer advantage on the local group involved and may become reestablished[12,18]

With groups tuning in to the use of local resources, cultural diversity relating to biological diversity may partially reappear. This seems to have been the case with the caste society that emerged at the conclusion of the wave of agricultural colonization of the Indian subcontinent around AD 500. This society was made up of tens of thousands of endogamous groups each with its own, often highly specialized mode of subsistence. Its sympatric endogamous groups had so partitioned the use of specialized biological resources that a particular resource tended to be monopolized by a particular endogamous group in a given region[20]. For example, three major groups of nomads indulging in extensive hunting in semi-arid tracts of Maharashtra had so elaborated their hunting techniques that one of them had virtual monopoly over antelopes and deer, another over small carnivores and a third over small herbivores and wild pig[21]. In addition, resources more commonly in demand such as fuel wood and bamboos were controlled by multicaste village communities on village common lands. The result was the persistence of cultural practices of sustainable resource use and conservation of diversity on the Indian subcontinent right down to the present day. Thus the turtle *Trionyx nigricans* survives today only because it is protected in a single pond sacred to a moslem saint in Bangladesh; and a new species of a leguminous climber *Kunstleria keralensis* was described a few years ago from a sacred grove on the otherwise thickly settled west coast of India[19,22,23]

World conservation strategy

The colonization of the world by the dominant technological culture pouring out of Europe is now nearing completion, and with this traditions of sustainable use of biological resources and conservation of diversity are reappearing. They have re-emerged most readily in regions where the technological revolution was first completed. Thus the Japanese have successfully established highly sustainable use of their inshore fisheries basing it on earlier communal controls by artisanal fishermen (although Japanese fishermen practice exploitative fishing in the open access ocean areas)[24]. Even outside of these regions the control over local resources is reverting to local people as resources are reduced to levels too low for profitable exploitation by those employing more sophisticated and hence more expensive technologies (Fig 1). Thus in the Canadian North the Amerindians are reasserting territoriality in areas once depleted of fur-bearing mammals (Fig. 2), in the Torres Straits of the Pacific the indigenous islanders are reestablishing control over islands now depleted of pearl-bearing oysters, and in the Garhwal Himalayas the local peasants are claiming rights over once-forested hill slopes now rendered largely barren through over-exploitation by the urban–industrial sector[12,17,25].

The intriguing question is this: apart from establishing rights over resources, will the local communities bring back some of their earlier cultural traditions of conservation of biological diversity? There are some signs of this happening: for instance with the Valley of Flowers in Garhwal Himalayas and sacred groves on the Western Ghats of India. In fact in the Uttara Kannada district of the Western Ghats tract local farmers have taken the lead in establishing new sacred groves[25–27]. The same forces appear to be partly responsible for the newly emerging concepts and practices of conservation of biological diversity such as the World Conservation Strategy and the Biosphere Reserve Programme.

These are complemented however by an entirely new awareness in technologically advanced cultures of the value of biological diversity. This awareness seems to be related to new developments in biology, especially the ability to create organisms of novel genetic constitutions. These possibilities suggest that genetic material in all sorts of apparently insignificant organisms may turn out to be of great utility. Conservation of biological diversity has therefore become a new interest of technologically advanced cultures as well.

Prospects

Creation of genetically engineered organisms could revolutionize the world's stock of biological diversity. These technological developments may motivate profit-making enterprises wishing to establish monopoly over genetic diversity to promote destruction of natural populations once the genetic material of interest to them has been added to the gene banks under their own control. The new engineered organisms could also convert all lands and waters however unproductive they may appear today into highly profitable bases of resource production. This would tremendously increase the pressure for converting all habitats into sites for man-made production – perhaps in the end wiping out all natural biological communities and thereby a great deal of biological diversity. As the technological advances provide a competitive edge to the technologically sophisticated societies, there is likely to be further erosion of cultural diversity too[28].

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ENVIRONMENT UPDATE

Conserving India's biodiversity: the societal context

by Madhav Gadgil*

India is one of the world's top 12 megadiversity countries This reflects its position at the junction of Ethiopean, Palaearctic and Oriental realms of biogeography, and its rich variety of biological community types that includes coral reefs and alpine meadows, rain forests and desert scrub (McNeely *et al*, 1990) India's cultural diversity is equally remarkable; with modes of subsistence ranging from hunting and gathering, nomadic herding and subsistence cultivation to intensive agriculture and modern industry Given this heterogeneity of cultures, the pressures of large human and livestock populations and the substantial resource demands of the modern sector, conserving India's heritage of biodiversity is a daunting task This paper analyses the challenge from the perspective of human ecology and suggests possible approaches to tackling it effectively

Indian society

People of India belong to three major ecological categories The majority live in villages, hamlets and nomadic camps much as their ancestors did, and depend on living resources gathered from their surroundings to meet many of their basic needs To this category belong tribals and nomadic herders, peasants and agricultural labourers Following Dasmann (1988) we may call them *ecosystem people* A significant proportion of these have been alienated from their traditional resource base, for example by submersion of their lands under dams or have been deprived of it by compulsions of population growth They have proceeded either to encroach on forests (as on Western Ghats slopes or Andaman islands) or, more often, have ended up in city slums We may term these uprooted people with limited resource access *ecological refugees*

A minority of India's people, around one-sixth, are larger landowners in tracts of intensive agriculture or work in organized industries and services Together they hold all the power; economic, political, administrative and employ it to draw resources, often with high levels of state subsidies from a wide catchment to satisfy their much larger resource demands (Fig 1) Unlike ecosystem people, they suffer little from resource exhaustion in any particular locality If the river Ganga is polluted, they can eat fish grown in ponds of Orissa; if the timber of the Western Ghats is exhausted, they can get it from Andamans Devouring all manners of resources brought from everywhere, this component may appropriately be termed *omnivores*

Of prudence and profligacy

The motivation of any segment of Indian society for sustainable or exhaustive resource use is governed by its relation to the resource base People rooted in a locality dependent on resources drawn from a limited area that they are personally familiar with, are much more likely to identify their own interests with the health of their resource base Their motivation to utilize the resources sustainably also depends on how firmly they are in control of the resource base and on whether they can exclude outsiders and regulate the behaviour of group members. This is because only such authority can ensure that they reap long-term benefits of prudent resource use Furthermore, people are only likely to practice prudence if they perceive the resource base as finite and limited If, on the other hand, they have open to them possibilities of access to resources of newer and newer localities or of newer and newer kinds, they are apt to use them in a profligate fashion (Fig 2)

This suggests that the social group most likely to practice prudence is the ecosystem people in control of resources of their immediate vicinity But in India, such a situation is presently an exception By the large, the country's resources are under firm control of an alliance of industry – bureaucracy – landlords – politicians, the core of omnivores Given the large catchment and perception of an ever-expanding resource base thanks to technological innovations, the omnivores have little reason to care for its sustainable use Exhaustive patterns of resource use are also the rule with the bulk of ecosystem people lacking control over their resource base, including the uprooted ecological refugees No segment of the Indian society is then presently motivated to use biological resources in a prudent fashion This is the dilemma that underlies India's biodiversity crisis

Current focus

The current Indian approach to biodiversity conservation is naturally moulded by the interests of those in power;

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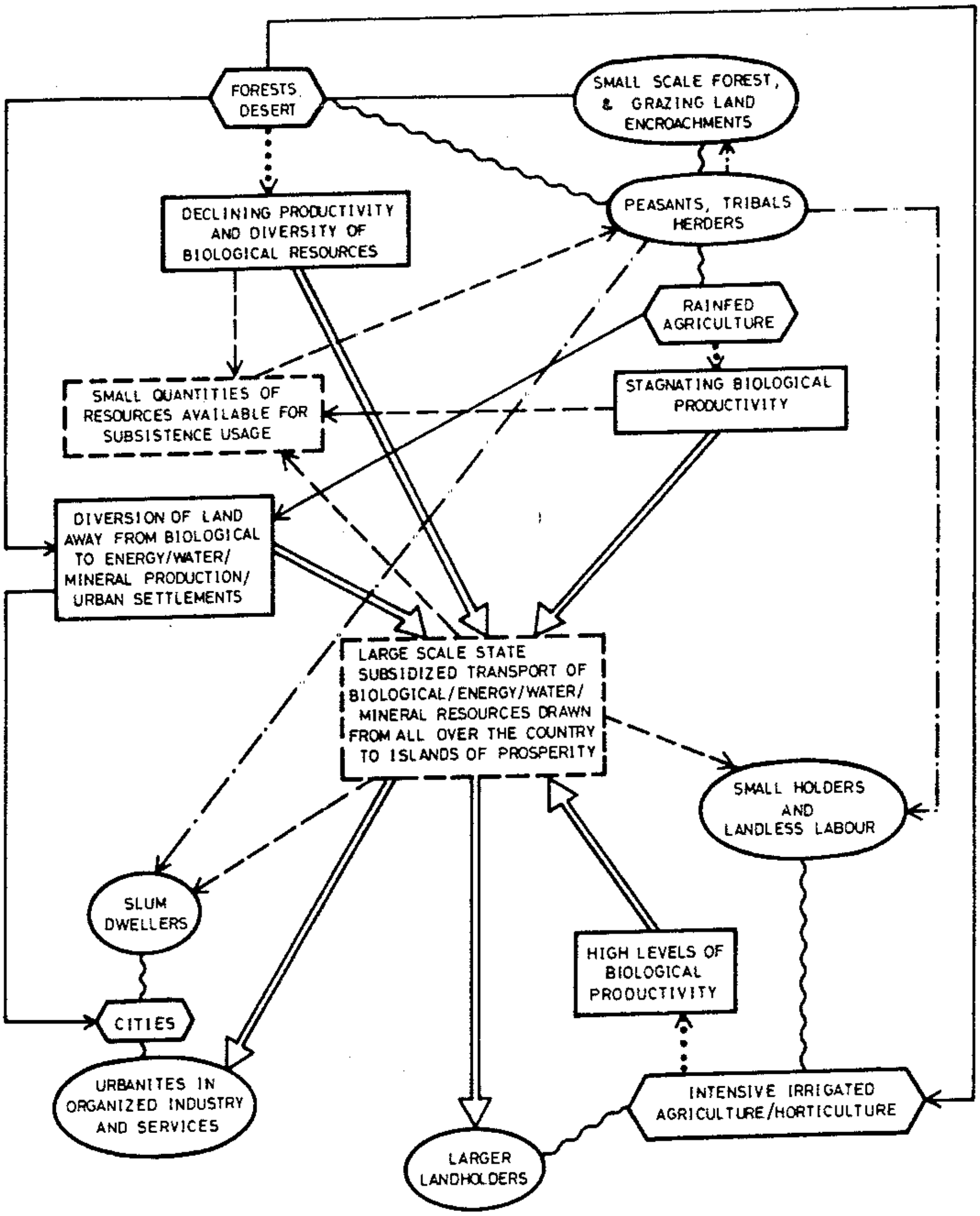

Fig. 1. Organization of Indian society in terms of resource use The figure leaves out fluxes of marine and freshwater resources and fluxes into and outside the country ⬡, land category; ⬭, components of population; □, resource production; ⬚, resource pools; →, land transformation; ⇨, intense resource flows; →, weak resource flows; ⇢, flows of people; →, land—resource production links; ∿, land—people links.

the omnivores. The official policy therefore focuses narrowly on establishment of a few, large nature reserves that serve as centres of outdoor recreation. The omnivores prefer to gloss over the significance of the ever-escalating resource demands of the urban–industrial–intensive agriculture sector, and instead attribute all environmental ills of the country solely to the population pressure of the ecosystem people and the ecological refugees (Gadgil 1991, in press) The cardinal principle for the management of nature reserves therefore becomes the exclusion of all subsistence demands. Such blind prejudice can lead to tragedies such as that at the Keoladeo Ghana bird sanctuary in Rajasthan. This prime water bird habitat of India is a man-made wetland that had traditionally supported large herds of village buffaloes. Without any scientific evidence, this grazing was halted in the early

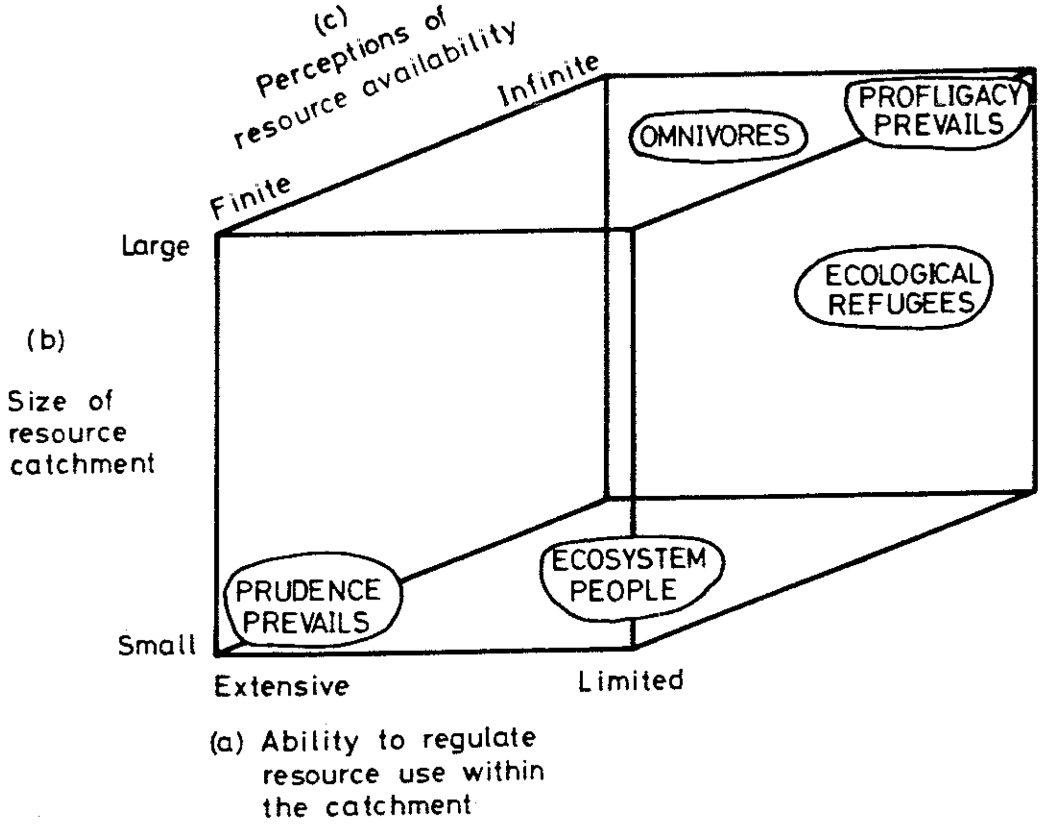

Fig. 2. Motivation for ecologically prudent or profligate behaviour by a human social group is related to (a) its ability to effectively regulate the use of the resource base on which it is dependent. (b) the size of the resource catchment from which it derives resources, and (c) its perception as to how finite the resource base is. The position of the three major components of Indian society; the ecosystem people. the ecological refugees and the omnivores in this space has also been indicated

'80s The result has been rank growth of a grass *Papsalum*, that has rendered the habitat far less suitable for the birds The administration is now trying to remove the grass at great expense using bulldozers This. however, is proving ineffectual (Vijayan, 1987).

India's biodiversity is by no means confined to nature reserves Many areas outside the nature reserve system are rich in diversity, for example, some of the Andaman–Nicobar islands now threatened by pressures of tourism and forest-based industry. Furthermore, subsistence usage can often be compatible with conservation, as had been the case in Keoladeo Ghana bird sanctuary India's conservation strategy therefore needs to broaden its focus to recognize the value of natural and semi-natural areas outside the nature reserve system as well as those inside them

Traditions of conservation

India has rich folk traditions of conservation of biodiversity as well as sustainable use of natural biota to which its ecosystem people still adhere to varying degrees (Gadgil and Vartak, 1976; Gadgil, 1987; 1989) The most widespread of these traditions is that of protecting trees belonging to genus *Ficus* that dot the countryside and are often the only large trees in the midst of towns and cities Notably enough. *Ficus* is now considered a keystone resource genus in the tropical forests (Terborgh, 1986). Apart from individual species, whole communities may be protected as sacred ponds and groves (Fig 3). The last population of the turtle *Trionyx nigricans* now survives in a sacred pond in Bangladesh (Reza Khan, 1980), and new species are being discovered in sacred groves of the densely-settled plains of Kerala (Mohanan and Nair, 1981).

The system of sacred groves is largely intact in parts of the tribal hill state of Mizoram These often adjoin or are surrounded by village woodlots subject to regulated use Interestingly enough, locals refer to the sacred grove and the woodlot as the safety forest and the supply forest (Malhotra, 1990).

The state apparatus has been hostile to such traditions and forest departments have opened up, even clearfelled many sacred groves, as well as liquidated many village woodlots (Gadgil and Iyer, 1989). Indeed, a senior

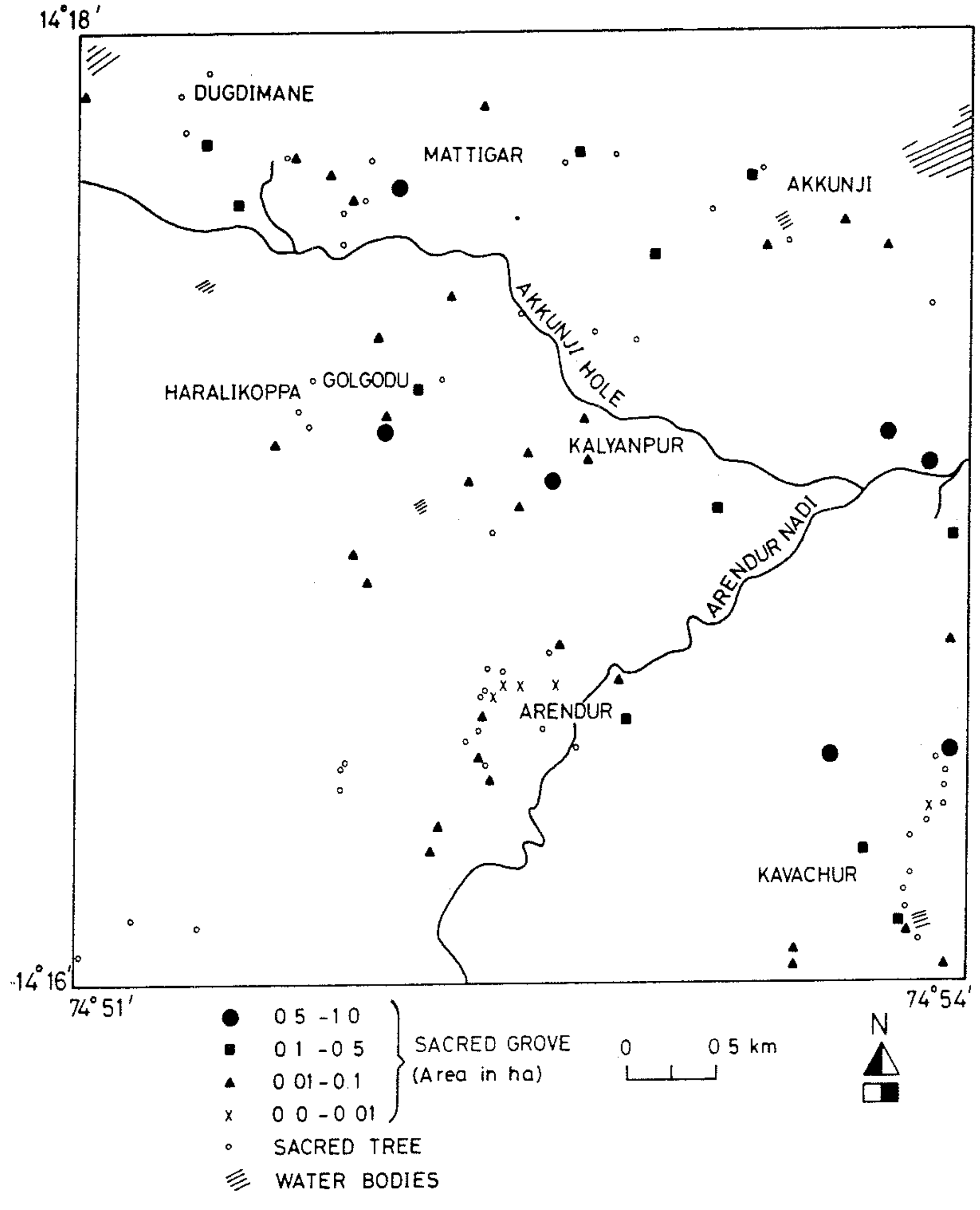

Fig. 3. Remnant network of sacred trees and sacred groves presently existing in an area of 25 km^2 on the Western Ghats of Karnataka state in south India It is estimated that 6% of the land area was originally under sacred groves This has now been reduced to 0 31% under 54 groves in addition to 45 sacred trees These groves cover all the topographic elements from hill top to stream bank and harbour a large number of wet, evergreen forest species that have otherwise disappeared from the neighbouring forest areas

forester once explained to me the wisdom of releasing the locked-up capital of overmature timber in the sacred groves.

A new approach

It is then essential to improve on the current approach to conservation of India's biodiversity in more ways than

Table 1. Proposed changes in patterns of biological resource use that would simultaneously promote conservation of biodiversity, greater sustainability, enhance environmental services and benefit the weaker segments of India's tribal and rural population

Land category	(a) Hill slopes/arid lands under cultivation	(b) Non-cultivated lands adjoining human settlements	(c) Non-cultivated lands away from human settlements
Current ownership status	Privately owned or illegally encroached government land	State owned, often with user privileges but no rights of regulation assigned to local people; occasionally owned privately	State owned with few or no user privileges and no rights assigned to local people
Current dominant usage pattern	Subsistence agriculture responsible for continuing degradation of land, vegetation resources and biodiversity	Unregulated biomass harvests by local people and their livestock, encroachment for cultivation, leading to degradation of land, vegetation and biodiversity	Non-sustainable harvests to fulfil urban-industrial demands at highly subsidized rates not only from outside, but sometimes within nature reserves; all out attempts to exclude local people
Proposed management pattern	Privately managed with links to urban-industrial consumers; special incentives for conserving biodiversity	Well organized, community-based management with land ownership vested in the state, special incentives for conserving biodiversity	State managed with active involvement of local communities in sustainable use of non-wood-forest produce and in conservation of biodiversity
Expected vegetation cover	Mono- or poly-cultures of trees or pastures in small pieces forming a rich mosaic; good population of protected trees like *Ficus* and small sacred groves	Good standing crops of indigenous multiple use trees, shrubs and grasses with nuclei of protected forests on the model of safety and supply forests of Mizoram	Good standing crop of indigenous tree species enriched with a variety of species yielding non-wood-forest produce; larger, strictly protected nature reserves
Expected economic services	Supply of wood to urban-industrial consumers at prices fair to tree growers	Fulfillment of biomass needs of tribal/rural population; surplus (if any) for urban-industrial sector	Non-wood-forest produce for industrial needs; support to tribal/rural economy
Expected benefits for biodiversity conservation	Sacred trees like *Ficus*; many small sacred groves ponds	Protected, species diverse nuclei of community woodlots; sacred trees and small sacred groves and ponds	Larger nature reserves protected well with local co-operation and removal of commercial pressures; much more diverse composition of forests generating non-wood-forest produce
Other environmental services	Maintenance of tree cover on hilly, arid lands; better watershed protection; higher levels of carbon sequestration	Maintenance of tree cover on non-cultivated lands near human settlements; better watershed protection; higher levels of carbon sequestration	Maintenance of natural vegetation with good cover on all land away from human settlements; better watershed protection; higher levels of carbon sequestration

merely ensuring better coverage under the protected areas system (Gadgil and Meher-Homji, 1986; MacKinnon and MacKinnon, 1986; Rodgers and Panwar, 1988). This is because even areas already under the system are subject to a variety of threats. Kanha National Park, one of the best tiger reserves in Central India, is adversely affected by setting of fires and poaching by tribals who have been displaced from the reserve. Dandeli, the largest wildlife sanctuary on the Western Ghats, now remains only on paper with the setting up of a paper mill and a series of dams in its midst (Rodgers and Panwar, 1988).

What is therefore now vital is to mould the societal forces to promote ecologically prudent behaviour on a broad front. Such an approach should focus on protected elements on all scales (from individual *Ficus* trees and small sacred groves and ponds to the larger nature reserves) as well as areas subject to different levels of human usage outside the nature reserve system (Table 1 a,b and c). Although none of the segments of the Indian society practice prudence today, the ecosystem people are most likely to become motivated to do so. For their personal well-being is closely tied to the health of the local resource base, and they are the custodians of conservation traditions and folk knowledge of local ecology. They should therefore be empowered to set up effective community-based management systems to take care of their own biomass requirements, to handle non-wood forest produce as well as to protect biodiversity. Such measures would also help reduce the rate at which ecosystem people are becoming ecological refugees. Of these, those subsisting as encroachers on forests should be stabilized economically through involvement in tree farming and non-wood forest production.

Most importantly, the power of omnivores who today preside over a process of economic development that is both liquidating the capital stock of natural resources and lowering the quality of life of the bulk of the population should be drastically curtailed. This should be done by cutting out state subsidies favouring the rich and by genuine decentralization of power down to the level of the village assemblies. It is only such a restructuring of the power balance within the society that could steer the country on to a course of socially and environmentally sustainable development and promote conservation of its heritage of biodiversity on a long-term basis.

Acknowledgements

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Article Madhav Gadgil

Conserving Biodiversity as if People Matter: A Case Study from India

India has rich traditions of nature conservation as well as a vigorous official program of protection of nature reserves developed over the last 40 years. However, the official program suffers from total reliance on authoritarian management arrangements in which decisions are made centrally and coercion is used to implement them. At the same time, the state apparatus organises subsidized resource flows to the urban-industrial-intensive agricultural complex which promote inefficient, non-sustainable resource-use patterns that are inimical to conservation of biodiversity. These processes are illustrated within the concrete setting of the district of Uttara Kannada in southern India. It is suggested that the interests of conservation would be served far better by an approach that withdraws the subsidies to the elite so that a much more efficient, sustainable and equitable pattern of resource use, compatible with conservation of biodiversity, can be instituted. In conjunction with this, the larger society should involve local people in working out detailed plans for conservation of biodiversity and offer them adequate authority as well as appropriate financial incentives to implement these plans. The paper goes on to illustrate how such an approach may be implemented in the case of Uttara Kannada

INTRODUCTION

With extensive tracts of humid tropical forests and great heterogeneity of environmental regimes. India is one of the top twelve megadiversity countries of the world. Given the large biomass needs of its tribal and rural populations and the exploding resource demands of its growing urban-industrial-intensive agriculture complex. conserving this heritage of biodiversity is a formidable challenge. India has rich traditions of nature conservation; following independence it has also developed an extensive network of nature reserves

The Project Tiger with 17 reserves spanning the country has saved this magnificent animal from the brink of extinction. There are however signs that all is not well with the country's programs of conservation. India's cultural traditions have preserved an enormous network of trees of the genus *Ficus*, an important keystone resource- throughout the countryside. These trees are now being increasingly felled to bake bricks and to make crates. At the same time, key reserves in the network of Project Tiger such as Kanha and Manas are threatened by discontented local tribal people. The important questions that must now be tackled, relate not only to identifying the deficiencies in the coverage of the national network of nature reserves, but to how decisions are made on what elements of biodiversity are to be conserved and how this is to be accomplished (1, 2).

It is important to look critically at the processes affecting overall patterns of natural-resource utilization and not just at those impinging on nature reserves. Very broadly the ongoing processes may be summarized as follows:

a. Intensification of resource fluxes in favor of industry-organized services-intensive agricultural complex involving large-scale state subsidies.

b. Increasing biomass demands of a growing rural population forced to meet its requirements from open-access public lands

Together these two kinds of pressures promote nonsustainable, inefficient use of natural-resources, resulting in decimation of biodiversity. This is coupled to

c. Attempts at conservation of biodiversity in a network of officially constituted nature reserves, relying on policing by the state apparatus, while the traditional practices of conservation are given short shrift

How do these processes affect biodiversity? What specific elements are responsible for negative impacts? How might these problems be overcome and what would come in the way of overcoming these problems?

UTTARA KANNADA

The two richest humid tropical forest tracts of India fall in the biogeographic provinces of Eastern Himalayas and Malabar, the latter comprising the west coast and the hill range of Western Ghats (3, 4). The district of Uttara Kannada (13° 52' to 15° 30' N and 74° 05' to 75° 5'E) with an area of 10 200 km² lies at the center of Malabar (Fig. 1). It is a region of gentle undulating hills, rising rather steeply from a narrow coastal strip bordering the Arabian Sea to a plateau at an altitude of 500 m with occasional hills rising above 600 to 860 m. The annual precipitation largely confined to the monsoon months of June to September ranges between 3500 mm on the coast. rising to 5000 mm on the crestline and declining to 1000 mm on the eastern plateau. An interpretation of the Landsat imagery suggests that around 6900 km² of the district is under forest cover, around 2000 km² is under paddy and millet cultivation, 130 km² under coconut and betelnut orchards, 200 km² under rocky outcrops and the balance under habitation and reservoirs (5). This tract of 6900 km² of forest land is the largest single contiguous tract of humid tropical forest in Peninsular India. Today, it harbors 1741 species of flowering plants and 403 species of birds. Notable wildlife includes the tiger, elephant, gaur or Indian bison, liontailed macaque, Wynaad laughing thrush, Travancore tortoise, several species of legless amphibians and dipterocarp trees (6)

Colonial Period

Uttara Kannada has been well known historically for its forests and wildlife. In the 17th century both the British and Dutch had established trade stations on its coast. These dealt extensively in wild pepper and cardamom, sandal and teak wood and poon (*Calophyllum elatum*) for ship masts. Accounts of Europeans who worked at these stations mention the rich wildlife with an abundance of tiger, panther, elephant, bison and several species of deer. The district came into British hands in 1799. Buchanan, a naturalist in the employ of the East India Company travelled extensively through the district in 1800–1802. His very detailed accounts confirm that apart from the southern parts of the coastal tract, the district was thickly forested and abounded in wildlife. He also mentions, the cultural traditions of local people that focused on nature conservation such as sacred groves. However, he interprets the almost-total protection offered to these groves as a "contrivance" to prevent British rulers from laying a claim to what was now its rightful property (7).

The history of the British period can be summarized as a series of attempts by the colonial power to appropriate the rich forest resources of the district as cheaply as possible. To this end, the community-based systems of restrained use and conservation had to be scuttled. This was accomplished through refusal to recognize the legitimacy of all customary and community ownership rights. The British recognized only two forms of ownership, state ownership of all non-cultivated lands and private ownership of all cultivated lands. The bulk of state-owned lands were converted into reserve-forest lands. A fraction, about 25% was set aside as minor or leaf-manure forest lands for meeting the subsistence biomass needs of local people. These are substantial since agriculture in this hilly district with its laterized nutrient deficient soils depends heavily on organic manure inputs. But the minor/leaf-manure forest lands came to be treated as open-access resources and have consequently been subject to escalating degradation as envisaged in the tragedy of the commons scenario. The reserve forests were dedicated to supply cheap raw material, primarily, teak to serve colonial interests of shipbuilding, railways and other constructions. As a result, they were almost totally depleted of natural teak between the years 1800–1850; followed by depletion of other hardwoods, especially *Terminalia* and *Lagerstroemia* species, and conversion to single species plantations of teak. The evergreen tree species were of little commercial value until the 1940s, and up to that time forest working focussed on their replacement by the more valued timber species. Although a succession of management plans initiated in early 1900s professed sustainable harvests as their aim, in fact there was only further depletion. All management plans were set aside during the two world wars, permitting totally unregulated harvesting from reserve forests (8–10).

Since Independence

The British forest-management regime in Uttara Kannada was dedicated to export of teak and other timber as cheaply as possible. World War II brought about an important change, however, when the British decided to encourage plywood manufacture in India. With its rich evergreen forests providing abundant raw material, one of India's first plywood factories was set up in the Uttara Kannada district. This was followed by a paper factory and a polyfiber industry, both of which were established soon after independence.

The policy of dedicating state-owned forest lands to furnish a cheap supply of industrial raw materials was carried to further extremes after independence. Thus, in 1958, bamboo, earlier prescribed to be eradicated as it constituted a weed in teak plantations, in spite of its manifold rural uses, was sold to the paper industry. The price was as low as Rs. 1.50 (USD 0.30 at the then prevalent exchange rates) per tonne, i.e. over a thousand times less than the market value. Giant wild mango trees that regularly yielded much valued fruit worth more than Rs. 100 per year, were also made over to plywood industry for as little as Rs. 150 for a whole tree. The result has been rapid decimation of a whole range of species in the more humid tracts, especially on the steeper western hill slopes. Other natural-resources have also been made available at highly subsidized rates to the urban, industrial, intensive agriculture complex. For example, there have been a series of state sponsored hydroelectric projects within the district. The electricity so generated has been supplied to industrial consumers and urban households as well as used in water lifting for irrigated agriculture at greatly subsidized rates. At the same time the cultivators whose lands were submerged under the reservoirs have been poorly compensated and often forced to encroach on forest land to eke out a living. This whole system of subsidized resource use has ensured that neither resource managers nor resource users are concerned with resource-use efficiency.

While the commercial pressures have mounted, so have the subsistence demands of the rural population that has grown rapidly as a result of the eradication of malaria after World War II. These subsistence demands continue to be met from open-access public lands, with further erosion of traditional practices of disciplined harvests from common lands. Consequently, highly inefficient and wasteful patterns of natural-resource use have prevailed (11).

Traditions of Conservation

In common with the rest of the Indian society, people of Uttara Kannada have inherited a rich variety of traditions of nature conservation (12, 13). These include:

- Protection of individual plants and animals considered to be sacred, e.g., trees of the genus *Ficus* or monkeys such as the hanuman langur and bonnet macaque.
- Protection of specific life history stages, such as birds breeding at heronaries.
- Protection of entire biological communities in the sacred groves and sacred ponds.
- Protection of animals from overhunting through devices, such as a ban on hunting of fruit bats at the roosting sites but not outside the sites.

The British colonialists and, following independence, Indian resource managers have both consistently attacked these traditions in many ways. For example, the plywood industry has harvested *Ficus nervosa* as a preferred species and many sacred groves have been clearcut to supply timber. Fisheries managers have poisoned sacred ponds removing indigenous fish and restocked them with exotic carps for sale to outside agencies.

State Initiated Conservation Efforts

The main focus of regulation of hunting during the British period was on the traditional subsistence/ritual hunting by local people, which aimed to ensure supply of game to the European hunters. These hunters began to hunt many species, such as elephant, that had previously been immune from hunting by local people. They also vigorously pursued extermination of species perceived as vermin such as the Indian wild dog. Indeed, there was a rapid decline in wild-animal populations during the British regime. The pace of this decline increased further after independence with the introduction of the jeep and widespread availability of firearms (14).

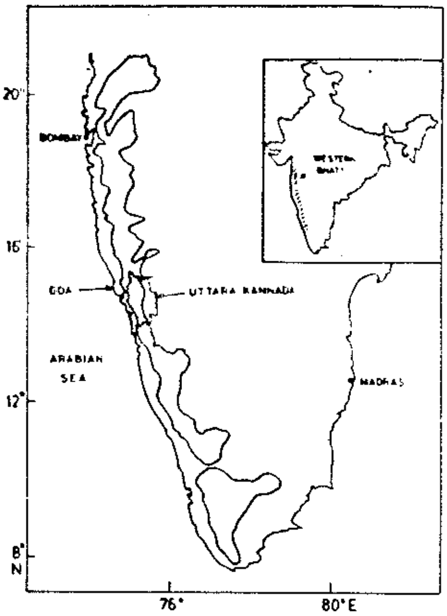

Figure 1. A map of peninsular India indicating the location of the hill range of Western Ghats. The district of Uttara Kannada stretches from the coast, across the hills to the peninsular Indian plateau

This ever accelerating depletion of wildlife led to the beginning of conservation measures in the 1950s with the establishment of an Indian Board for Wildlife and of Wildlife Wings in Forest Departments. The main tool of conservation that was adopted was a ban on hunting of endangered species everywhere together with the establishment of Wildlife Sanctuaries and National Parks.

A major Wildlife Sanctuary, Dandeli W. L. S., of over 5730 km^2, was established in 1953 in the northern parts of Uttara Kannada. However, little protection to natural vegetation and wildlife was provided since a large paper mill was established in the very heart of this sanctuary in 1958 and a series of dams of the giant Kali hydel project covered the rest of the sanctuary in the 1970s (15). The ban on hunting has not been very effectively implemented since it is operated in a centralized, rigid fashion without allowance for local conditions. For example, farmers claim that there are now too many wild pigs in the district with the newly arriving weeds, *Lantana* and *Eupatorium* providing excellent shelter, and depletion of panther and tiger populations, cutting down predation. These pigs cause severe crop damage and farmers hunt them relentlessly. Nevertheless, hunting wild pig remains an offence in law. So does the annual ritual hunting by local communities such as the *Halakki Vakkals* who engage in such a hunt as a religious observance. At the same time official managers continue to

The coastal landscape of Uttara Kannada. There is little left of natural vegetation. However the coastal stretch is covered by coconut plantations mixed with a tremendous diversity of cultivars of mango (*Mangifera indica*) and jackfruit (*Artocarpus integrifolia*) along with a number of fruit yielding tree species belonging to genera *Myristica, Spondias* and *Garcinia*. All of these also occur in the wild. Photo: M.D. Subash Chandran

The mosaic of disturbed natural forest and anthropogenic grasslands near the crestline of Western Ghats in Uttara Kannada district. Such vegetation supports the greatest diversity of bird species within this district. Photo: R.J. Ranjit Daniels.

An irrigation pond in the eastern part of Uttara Kannada district. These ponds support a wide diversity of resident and migratory waterfowl. Photo: R.J. Ranjit Daniels

violate traditions of conservation of the local people

Social Conflicts

This whole system of resource management initiated under the British rule and further elaborated after independence is based on alienating local people from control of and access to resources. Its primary objective has been to make natural resources available as cheaply as possible to the elite, be it the British ruling classes or the industry-organized services-intensive agriculture complex of the Indian society. The elite that benefits from resource mobilization is shielded from the ill-effects of the degradation of the resource base, since it can shift to the use of other resources or resources from other regions as the occasion demands.

The pattern of natural-resource use promoted by centralized authority has been non-sustainable when viewed from local areas such as the Uttara Kannada district. It has also led to severe conflicts with the local populations attempting to maintain their customary rights over and access to resources (5, 11). In the process, the local traditions of resource conservation have been increasingly disrupted or have broken down altogether.

Nevertheless, the effectiveness of traditional conservation can be clearly seen in the landscape of Uttara Kannada, where a large number of monkeys still survive and thousands of *Ficus* trees dot the countryside due to their religious significance. The only remaining natural stand of the genus *Dipterocarpus* persists in a sacred grove, as does the last large patch of a *Myristica* swamp.

RE-ORIENTING CONSERVATION

Evidently, there is a case for working out a new approach to conservation of biodiversity in Uttara Kannada. It is clear that conservation cannot be considered in isolation from local people, and broader patterns of natural-resource use and development, but must be complemented by policies promoting sustainable and equitable development of the natural-resource base as a whole. To be effective, any approach must give a larger role to the local people. This would entail restoring to them much of the authority they have lost over the past two centuries along with appropriate financial incentives. Local people must be involved because their well being is still intimately linked to the health of the natural-resource base of their own localities, hence they have a real stake in its sustainable use. Thus, in Uttara Kannada people depend on natural vegetation to meet almost all the needs of domestic cooking and water heating, 90% of fodder needs for livestock, and 80–90% of nutrient-supply needs for cultivated lands. Local people are also dependent on natural vegetation for making ropes, baskets, agricultural and fishing implements and for thatching their huts and cattle sheds (5). They still collect many wild fruits, hunt birds and wild pigs and fish the rivers to provide a significant fraction of their nutrition (16). For them degradation of natural-resources is a genuine hardship, and of all the people and groups who compose the Indian society they are the most likely to be motivated to take good care of the landscape and ecosystems on which they depend. The many traditions of nature conservation that are still practiced could form a basis for a viable strategy of biodiversity conservation (2).

Involving local people in conservation, however, does not imply as some Gandhian environmentalists have stated that India must abandon all efforts at industrialization and return all authority to village communities in an effort to recreate an agricultural society in balance with nature (17). Such a scenario is simply not feasible for a variety of reasons, including the pressures of the international economic and political system. The practical option is to continue the processes of industrialization and intensification of agriculture, but with an emphasis on efficient, sustainable and equitable resource use.

The central argument so far has been that inefficient, non-sustainable and inequitable resource use is promoted by the large-scale state intervention through subsidies to the industrial-organized services-intensive agriculture complex that is shielded from the costs of environmental degradation. These costs are passed on, for instance to the peasants and artisans of Uttara Kannada district who have been deprived of all authority over the local natural-resource base. The proper response would then be to withdraw the subsidies that presently flow to the elite. Instead, the elite should be made to

BOX

Existing Apparatus for Planning and Implementing Biodiversity Conservation in India.

CENTRAL GOVERNMENT

Ministry of Environment and Forests

Primarily advisory, and as disburser of funds for special projects such as Project Tiger *since Land Use, Forestry and Law and Order are responsibilities of State Governments. Advisory Boards provide minimal inputs to the Central Ministry*

STATE GOVERNMENTS

Forest Departments: Territorial and Wildlife Wings

These two wings have joint jurisdiction throughout a state. Wildlife Wings *are manned by Forestry Personnel on temporary secondment. All the decision-making power of these as well as all other State Government agencies is concentrated in the hands of Ministers, Secretaries and and Departmental Heads operating from the state capitals. At the state level a Wildlife Advisory Board provides minimal inputs: there are no inputs from a more local level*

Assessing conservation priorities for Uttara Kannada (6)

Sl No.*	Attribute	Criterion	Prescriptions for UK	The only or best representative localities of conservation interest
1.	Species richness of constituent biological communities	Greater value attached to communities with larger number of species	Evergreen forests harbor largest number of species of flowering plants and amphibians, and moist deciduous forest zone that of birds	Bharatnalli Madurahalli, Gunjavati Range, Bargadda-Patoli Hulidevargodlu-Unchalli, Aganashini estuary, Kulgi-Virnoli
2	Geographical range of constituent biological communities	Greater value attached to communities with more restricted range	*Myristica* swamps harbor communities with a restricted range	Kathlekan
3	Spatial occurrence of constituent biological communities within their range	Greater value attached to communities with more restricted spatial occurrence	Communities of spray zones of waterfalls are of very restricted occurrence; Limestone outcrops	Unchalli waterfalls Yan
4	Identity of species making up consitutent biological communities	The more distinctive the component of species, the greater the value	Mangrove vegetation and beaches harbor a highly distinct set of sepcies	Sunkeri, Thenginagundi Aganashini estuaries Karwar-Kamat Bay
5	Endangerment due to human pressures	The more endangered communities are of greater value	Riverine forests are greatly endangered by human pressures	Hulidevaragodlu-Unchalli waterfalls
6	Attributes of component species			
(a)	Restricted geographical range	Greater value attached to species with more restricted range	Evergreen forests harbor birds with more restricted range	Suremane Hulidevaragodlu
(b)	Narrow habitat preference	Greater value attached to species with narrow habitat preferences	Freshwater ponds and estuaries harbor birds with narrow habitat preferences	Madurahalli, Nyasergi, Salgaum, Sanikatta, Masur
(c)	Taxonomic uniqueness	Greater value attached to species with fewer related species	Gnetum, a gymnospermous climber of evergreen forests is the only member of its order in UK	Hulidevaragodlu
(d)	Endangerment due to human pressures	Greater value attached to species subject to greater pressures	Wintering waterfowl in marshes are hunted extensively	Aganashini estuary and Nyasergi
(e)	Ecological role	Species serving as keystone resources would be attached greater value	Ficus species are keystone resources of tropical forests throughout the district	Ficus trees protected on religious grounds are scattered
7	Interaction with adjacent communities	Greater value attached to communities serving as links in maintaining higher diversity	Betelnut plantations serve as links between patches of evergreen forests	

* Sl = Specific locality

compensate the rural poor for the decline in their quality of life, consequent on degradation of the natural-resource base. At the same time the local people should be increasingly involved in controlling and managing the natural-resource base of their localities. This ought to promote a far more efficient, sustainable and equitable process of intensification of natural-resource use, a process that would be compatible with conservation of biodiversity.

Outside Control

The natural-resource development approach advocated here, would of course have to be complemented by an effort more specifically focused on biodiversity. The current approach treats conservation as a matter of keeping local people out of a few large nature reserves and preventing them from killing most larger species of wild reptiles, birds and mammals anywhere within the district. All the decisions pertaining to such regulations are made centrally, partly in the national capital of Delhi and largely in the state capital of Bangalore by the Forestry Service personnel (Box). Substantial amounts of funds are then placed at the disposal of the Forest Departments to discharge their regulatory function. The state apparatus has at its disposal little detailed locality-specific knowledge of either the distribution of biodiversity or the various pressures impinging on it. Its functionaries have no real personal stake in conservation of biodiversity, nor are they in a position to effectively discharge their regulatory function. It is then no wonder that these efforts have not been very fruitful.

Involving the Local People

A far more effective conservation effort would focus on the whole landscape instead of a few reserves, on the whole diversity of species and ecosystems instead of only on larger vertebrates and emphasize positive rewards for promoting conservation in place of regulation by the state apparatus. Above all, it would place the major responsibility for the task squarely in the hands of the local people, rather than with an impersonal centralized bureaucracy or technocracy.

The local people would not however be

in a position to operate entirely on their own and the conservation effort would have to be one of co-planning and co-management. Local people do possess very detailed information on local biodiversity, its history and the forces impinging on it. But they lack a broader, global perspective. Outside experts collaborating with local scientists, when these are available, could provide such a perspective (6)

The starting point of this exercise was to note that we might wish to conserve biodiversity, defined as the entire spectrum of variety and variability among living organisms and the ecological complexes in which they occur, for a variety of reasons. These reasons may include subsistence use value, e.g. herbal medicines used locally; commodity use value, e.g. cane or wild honey; non-consumptive use value, e.g. watershed services; option value, e.g. wild relatives of cultivated plants that may provide useful genetic material for future breeding programs; transformative value, provision of experience of unspoilt nature; and existence value, for its own sake. This rationale suggests certain conservation priorities. These priorities must be related to attributes of any locality to assess the locality's significance for conservation. In general, a locality will be valued more if it contains elements that are distinctive, threatened, rare or of restricted occurrence; and if it harbors many such elements (see Table).

The local people must be intimately involved to take this broad prioratization further and to decide on specific action points. For example, the evergreen forests of Uttara Kannada district are rich in wild relatives of cultivated fruit trees, as well as many cultivars of fruit trees. Quite a few farmers have developed large collections of such species, especially of genera *Mangifera*, *Artocarpus*, *Myristica*, *Garcinia* and *Spondias* on their own lands, out of personal interest. Many local people also know of individual wild mango trees that bear fruit of special flavor or have exceptionally high yields. Their inputs would obviously be of value in deciding on the focus of a program to conserve wild relatives of cultivated plants. Similarly some habitat types are now conserved only in sacred groves, e.g. *Myristica* swamps in Kathlekan. Local people know of such patches in forest interior; they also appreciate their religious significance.

Conservation priorities must also take account of the whole set of human demands on a given locality. For example, articificial freshwater irrigation ponds constructed in preBritish times in the eastern parts of the district are important habitats of migratory waterfowl. These ponds are now being encroached by paddy cultivators. The local people are fully aware of who is encroaching and what their economic motivations are. Today, the state apparatus tries to regulate such encroachment through coercion. This often fails. Instead, the resources devoted to enforcement could be offered to local communities so as to motivate them to continue to conserve the freshwater ponds in their own villages. The different villages concerned could submit bids based on the annual level of financial incentive they would need to accept the conservation option. If the state that speaks for the broader public interest finds these bids acceptable, it could decide to implement conservation programs in partnership with some or all of the villages involved. Conversely, it could decide to write off some of the freshwater ponds of the Uttara Kannada district to extend paddy cultivation. Local communities should of course receive payment only if they succeed in conserving the freshwater ponds involved.

Undoubtedly, more research and practical experience is required to design and implement an alternative to the centralized and authoritarian approach to conservation. An important obstacle is likely to be the resistance of the central authority because a large bureaucratic apparatus to implement programs locally would simply be unnecessary. Rather a much smaller, technically more sophisticated apparatus would be required, one which would have a capability to assess broader priorities, to help local authorities work out detailed plans and monitor to determine whether the local authorities are in fact implementing the conservation measures as agreed. The local authorities would have to be strengthened and better organized and capable of taking further programs of decentralization of political and administrative responsibilities. This would entail rendering local governments much more accountable to people than is presently the case. The central authority would also have to transfer a great deal of its jurisdicial and policing powers to the more locally-oriented institutions.

Such a local involvement management strategy is very much in the spirit of the proposal to involve local communities that is an important element of the *Global Biodiversity Strategy* being developed by WRI, IUCN and UNEP (18). It is also consistent with the microlevel planning initiative of the National Wastelands Development Board of the Government of India (19). Such international and national support is critical to the success of an alternative approach, for it is apt to run into serious opposition on the part of the political-economic-bureaucratic vested interests that benefit from the present-day pattern of nonsustainable resource use and of a rigid policing approach to conservation. Fortunately, the global trends are today exceptionally favorable for a decentralized, peopleoriented approach. As a result, more and more attempts like that exemplified by the Marine Conservation and Development Program on the Visayas islands, Philippines, are likely to be initiated in the coming years (18). Their success would be greatly enhanced if they are backed by a locality specific analysis of the situation in its concrete historical setting. Involvement of local people is absolutely essential for implementing the conservation measures on the ground.

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Minimum Population Sizes for Species Conservation

Mark L. Shaffer

Many species cannot survive in man-dominated habitats. Reserves of essentially undisturbed habitat are necessary if such species are to survive in the wild. Aside from increased efforts to accelerate habitat acquisition for such species, the most pressing need facing conservationists is development of a predictive understanding of the relationship between a population's size and its chances of extinction.

Biologists have long known that the smaller the population, the more susceptible it is to extinction from various causes. During the current era of heightened competition for use of the world's remaining wildlands, this qualitative understanding is of limited utility to conservation and natural resource planners. The old adage that "the bigger the reserve, the better" must be replaced with more precise prescriptions for how much land is enough to achieve conservation objectives. Efforts at making such determinations have been clouded by inconsistencies in the focus on the unit to be preserved (population, species, community, ecosystem) and lack of an explicit definition of what constitutes successful preservation (persistence for 10, 100, 1000 years, etc.).

The intricate interdependencies of living things dictate that conservation efforts be focused on the community and ecosystem level. Unfortunately, the very magnitude of complexity of these systems makes such efforts difficult. Moreover, certain species are more sensitive than others to changing conditions and begin to decline prior to any noticeable degradation of the community to which they belong. Consequently, conservation efforts have been and, in many cases, will continue to be at the single-species level. Many species currently in jeopardy are large-bodied and/or specialized, two characteristics that usually lead to low population densities. If we are successful in providing sufficient room for their survival, then other, less space-demanding members of their communities should also survive.

In this paper, I propose tentative criteria for successful preservation at the population level, discuss the various methods available for determining the population sizes and their area requirements to meet these criteria, and relate both to overall conservation strategy.

THE MINIMUM VIABLE POPULATION CONCEPT

Levins (1970) has estimated that, since the beginning of the Cambrian, species have been going extinct at the rate of about one per year (though not uniformly). Extinction thus appears to be a relatively common event. The factors leading to extinction, though varied, can be lumped into two categories: systematic pressures and stochastic perturbations. A necessary first step in the preservation of any species is to identify and, if possible, compensate for any systematic pressures threatening that species. This is not the type of problem of interest here. Rather, the focus is on those stochastic perturbations that may extinguish populations of a species even in an environment that, on average, is favorable for their growth and persistence.

In general there are four sources of uncertainty to which a population may be subject:

- *demographic stochasticity* which arises from chance events in the survival and reproductive success of a finite number of individuals (May 1973, Roughgarden 1975);
- *environmental stochasticity* due to temporal variation of habitat parameters and the populations of competitors, predators, parasites, and diseases (May 1973, Roughgarden 1975);
- *natural catastrophes*, such as floods, fires, droughts, etc., which may occur at random intervals through time; and
- *genetic stochasticity* resulting from changes in gene frequencies due to founder effect, random fixation, or inbreeding (Berry 1971, Soulé 1980).

Little is known about the role of any of these factors in any specific case of extinction. Because all of them increase in importance with decreasing population size, assessing the relative importance of each will always prove difficult.

The extinction of the heath hen (*Tympanuchus cupido cupido*) provides an example of the situation (Simon and Géroudet 1970). Once fairly common from New England to Virginia, the species steadily declined as European settlement progressed. By 1876 the species remained only on Martha's Vineyard, and by 1900 there were fewer than 100 survivors. In 1907 a portion of the island was set aside as a refuge for the birds, and a program of predator control was instituted. The population responded to these measures, and by 1916 had reached a size of more than 800 birds. But in that year a fire (natural catastrophe) destroyed most of the remaining nests and habitat, and during the following winter the birds suffered unusually heavy predation (environmental stochasticity) from a high concentration of goshawks (*Accipiter gentilis*). The combined effects of these events reduced the population to 100-150 individuals. In 1920, after the population had increased to about 200, disease (environmental stochasticity) took its toll, and the population was again reduced below 100. Though the species endured awhile longer, by 1932 the last survivor was gone. In the final stages of the population's decline, the birds appeared to become increasingly sterile, and the proportion of males increased (demographic, environmental, or genetic stochasticity). Which of these events, or what combination, was the critical determinant in the species disappearance is unknown.

The net effect of all these types of perturbations on a population's prospects for survival depends to a great extent on

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the population's relationship to other populations of that species—what might be termed its biogeographic context. Any factor depressing the size or growth of a population may be mitigated by immigration of individuals from other populations.

Clearly then, a minimum viable population is not one that can simply maintain itself under average conditions, but one that is of sufficient size to endure the calamities of various perturbations and do so within its particular biogeographic context. Furthermore, survival (and hence, preservation) must be measured relative to some time frame and some set of conditions. Hooper (1971) has already pointed out this fact, but it does not seem to be widely recognized within the conservation field and certainly not in the minds of the general public. The problem of determining minimum viable population sizes and their area requirements is analagous to designing reservoirs to hold flood waters. A reservoir capable of holding the once-in-50-year flood may be grossly inadequate for the once-in-1000-year flood. What time frame to use and the levels of variation and catastrophe to anticipate in determining minimum viable population sizes are very much open questions, but it is critical to view the problem in this way.

Because the dedication of lands to the preservation of biotic diversity increasingly has to compete with investments of that land for the production of other goods and services, reserves should be evaluated on the basis of their utility for meeting the conservation goals set for them over some reasonable time frame. On the other hand, the uncertain nature of the factors that threaten small populations argues against too precise a set of criteria. Given this dilemma, I tentatively and arbitrarily propose the following definition of minimum viable population size: *A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.*

I must stress the tentative nature of this definition. The critical level for survival probabilities might be set at 95%, or 100%, or any other level. Similarly, the time frame of 1000 years might be lengthened to 10,000 or shortened to 100. Such criteria urgently need discussion among conservationists, planners, and natural resource managers. The important point is that such a definition is an explicit set of performance criteria for a conservation unit under an explicit set of conditions.

DETERMINING MINIMUM POPULATION SIZES

There are five possible approaches to determining minimum viable population sizes and their area requirements: experiments, biogeographic patterns, theoretical models, simulation models, or genetic considerations. None of these is very sophisticated, and certainly none can be considered failsafe. Nevertheless, most can contribute to a better understanding of population size and survival and to more realistic estimates of the land area required to preserve populations of a particular species.

Experiments

The most straightforward approach to the problem of assessing minimum viable population sizes is simply to create isolated populations and monitor their persistence. This approach is intractable for two reasons: First, we cannot experimentally measure persistence in terms of decades and centuries; institutional abilities or willingness to support research projects are usually limited to a decade or less. Second, in most cases irreversible decisions on land use will be made in the very near term (10 to 20 years). Unless conservationists can provide useful estimates of the location, number, and size of reserves in this time period, the opportunity to do so may be permanently foreclosed. Development interests will not (in some cases, cannot) await the results of research that may take a century to complete. This should not be construed as an argument against long-term population-monitoring studies. Such studies are of great potential value in many areas of biology and ecology, but their utility for solving this particular problem is limited.

Biogeographic Patterns

Examination of the distributional patterns of species that occur in insular or patchy patterns can provide a first approximation of minimum area requirements and, provided some estimate of densities, minimum viable population sizes. This approach requires that species communities occupying such habitat patches are in equilibrium and the approximate length of their isolation is known. If these conditions are met, such surveys can reveal both the smallest island or patch inhabited by a species and also the percent of islands or patches of a certain class supporting that species, measured either in area or species diversity.

Robbins' (1979) work on the habitat size relationships of the migrant neotropical avifauna of the eastern deciduous forest employs this approach. Although this is probably the most tractable and reliable approach to the problem, it does have its limitations. The most critical is that there is apparently no clear relationship, either theoretical or empirical, between the percent of occupied patches of a certain size and the potential longevity of the populations they support. This is a key research need.

For example, a particular species might be a breeding resident of 95% of islands or patches 50–100 km² in area. Unfortunately, knowing this fact alone reveals nothing about the frequency with which populations on such patches go extinct or recolonize. Suppose populations of this hypothetical species on patches of the given dimensions go extinct, on average, every 20 years. Relying on a single reserve of this size to maintain the species without alternate reserves to provide sources for recolonization will prove ineffective in the long term. To make this approach workable, there must be good information on both the frequency with which species occur on islands or habitat patches of different sizes and species-specific extinction/colonization rates typical of these units. Some information of this type is available for certain avian species (for an overview see Wilcox 1980 or Terborgh and Winter 1980), but much remains to be done.

An additional complication with this approach is that population characteristics (e.g., density, mortality and fecundity rates) of many species show wide variation from one part of their range to another depending on habitat quality or community structure. Two habitat patches of the same size may not support equally large or enduring populations. Such habitat differences are critical to wise conservation planning, and any research efforts employing this approach must recognize and deal with this fact.

Obviously, this approach cannot be used for those species that have contiguous distributions and do not occur either on islands or patchily distributed habitats.

Despite these drawbacks, analysis of biogeographic patterns, when coupled with studies of species-specific turnover rates, is one of the major means of determining minimum viable population sizes and their area requirements. The most valuable research directions to fully utilize this approach are to extend its application to nonavian species, refine analyses to reflect differences in habitat quality as well as quantity, and determine if there is any relationship between the percent occurrence of a species and its characteristic extinction colonization rates.

Theoretical Models

There are several theoretical models for predicting the probability that a small population will go extinct and the time this will take. There are also numerous models of population growth under stochastic conditions (demographic, environmental, or both). But these models either embody unrealistic assumptions or lead to currently unresolved mathematical problems.

For example, the models of MacArthur and Wilson (1967) and Richter-Dyn and Goel (1972) assume a constant carrying capacity and birth and death rates that change only in response to density. Thus, they deal only with the probability of extinction due to demographic stochasticity. The branching process theory employed by Keiding (1975), though capable of dealing with both demographic and environmental stochasticity, is restricted to exponential growth. Diffusion theory, as employed by various workers (for a review see Shaffer 1978), applies only to a totally unpredictable environment. Moreover, there has been some doubt about the appropriate method of analysis to be applied to diffusion theory equations. Turelli (1977), after a thorough review of analysis methods, emphasized that the diffusion theory models are most appropriately viewed as approximations to more realistic models that are analytically intractable.

The idiosyncratic nature of many species and the great variability inherent in nature probably preclude direct application of any single theoretical model to many real-world situations. Nevertheless, this is an important area of research and deserves increased attention. From a practical standpoint, the most fruitful approach would be the development of a small number of models to fit various scenarios of population growth and regulation and use these to determine both the relationship of population size to extinction probabilities and the sensitivity of the results to assumptions inherent in the models and key population characteristics. For example, in the classic model of logistic population growth, do survival probabilities depend primarily on mortality or fecundity rates, or carrying capacity? Is the mean or variance of these parameters more important in assessing survival? To what extent is survival affected by introduction of time lags in the density-dependent process of mortality and reproduction? Such models should also facilitate development of effective management strategies for reserves that are too small to assure persistence if left alone.

Simulation Models

Because they are not subject to the various constraints of analytical models, computer simulations employing numerical methods may provide a tractable approach to determining minimum viable population sizes and their area requirements. Aside from their greater realism, such models also provide a flexible tool for assessing the effects of changes in various parameter values (e.g., mortality and fecundity rates, etc.) and or relationships (density-dependent versus density-independent mortality rates, etc.)

The principle drawbacks of this approach are a lack of generality (i.e., the simulations have to be altered for different species) and demand for extensive data. At a minimum, such models (for vertebrates) require knowledge of the mean and variance of age and sex-specific mortality and fecundity rates, age structure, sex ratios, dispersal, and the relationship of these various parameters to density. Such information should be gathered over a sufficiently long period to assure that it is representative of the full range of conditions the population is subject to, including cyclic behavior. (For some species this may require very long data bases.)

Based on the extensive data of Craighead et al. (1974) for the grizzly bear (*Ursus arctos* L.) in Yellowstone National Park, I (Shaffer 1978) used the simulation approach to assess minimum viable population sizes and area requirements for this species. The simulations could evaluate the effects of either or both demographic and environmental stochasticity. Natural catastrophes appear to be unimportant for the grizzly, and lack of adequate genetic information precluded testing the effects of genetic stochasticity. The results of this analysis showed that populations of less than 30-70 bears (depending on population characteristics) occupying less than 2500-7400 km^2 (depending on habitat quality) have less than a 95% chance of surviving for even 100 years. Survival probabilities were most affected by changes in the mean mortality rate, cub sex ratio, and age at first reproduction of females.

This type of approach should be expanded to other species when sufficient data exist. Where possible, future field population studies should be designed to gather the types of information necessary to develop simulation models. Such simulations provide the most tractable and realistic alternative to the analysis of biogeographical patterns and species-specific turnover rates.

Genetic Considerations

Several workers have based minimum population recommendations on genetic and evolutionary arguments. Franklin (1980) has suggested that, simply to maintain short-term fitness (i.e., prevent serious in-breeding and its deleterious effects), the minimum effective population size (in the genetic sense) should be around 50. He further recommended that, to maintain sufficient genetic variability for adaptation to changing environmental conditions, the minimum effective population size should be around 500. Soulé (1980) has pointed out that above and beyond preserving short-term fitness and genetic adaptability, long-term evolutionary potential (at the species level) may well require a number of substantially larger populations.

These recommendations were based on very general applications of basic genetic principles and, consequently, are somewhat oversimplified. A more detailed approach would involve gathering information on the degree of genetic variability and the breeding structure of the species to be preserved. Given this information, it should then be possible to determine what size population would provide (at some probability level) a representative sample of the genetic diversity typical of the species and what size would be necessary to assure (at some probability level) that none of this variability would be lost due to inbreeding and genetic drift over some specified period of time. Lacking this sort of detailed work, the above recommendations should be viewed as very

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rough guidelines rather than specific prescriptions

SUMMARY

Nature reserves represent the investment of land for the production of a public good—the persistence of populations of various species and the communities they form The fact that population persistence depends, to a great extent, on population size immediately raises the issue of how persistent society wishes remnant wild populations to be.

This is not a question that can be answered solely on biological grounds In an expanding human world, competition for use of a finite land base can only intensify Conservationists will increasingly be pressed on the need to preserve many species and on the efficiency (in terms of land) with which such preservation can be accomplished In this atmosphere, scientists must develop some consensus on the standards to be applied in determining what constitutes a minimum viable population for successful preservation. I have offered one tentative definition in this paper, but it is not to be taken literally It is intended as an example for consideration, not a standard for application

Given some consensus on the standards to be applied, several of the methods outlined here may be used to begin determining minimum viable population sizes and land area requirements for species in jeopardy The most promising approaches are the extension and refinement of analyses of biogeographic distribution patterns and species-specific turnover rates and the use of available population data in computer simulations designed to test extinction probabilities Theoretical mathematical models may be useful in revealing which population characteristics or processes are likely to be most important in affecting survival probabilities Genetic determinants of minimum viable population sizes are still unclear: their resolution hinges primarily on a better knowledge of the breeding structure and genetic variability of particular species and, most importantly, the role of genetic variability in population growth and regulation

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MINIMUM VIABLE POPULATIONS FOR ELEPHANT CONSERVATION

by R. Sukumar

Introduction and Definitions

It is well known that the smaller the size of a species population the higher the risk of it becoming extinct. This extinction need not be caused merely by deterministic ecological processes such as habitat destruction or hunting but also by chance factors operating on birth and death processes. Thus in a small population all the mature females may fail to reproduce in a given year or all the individuals may die within a short time span due to chance alone.

For small populations it is thus meaningless to talk of average birth, death or population growth rates. Deterministic models of population dynamics provide a reasonably robust approximation of average long-term demographic trends in large populations. These models are, however, quite inadequate for small populations in which not only demographic stochasticity but also environmental and genetic stochasticity or catastrophes may drive the population to extinction, even though life table analysis may indicate that the population has on average a positive growth rate.

Small population biology is especially relevant to the conservation of Asian elephants. Loss and fragmentation of habitat, a process that still continues, has given rise to numerous small, isolated elephant populations in most Asian countries (Sukumar 1989, Santiapillai and Jackson 1990).

The crucial question is what is the minimum population size of elephants that should be maintained to prevent its extinction. Population viability analysis (PVA) could provide useful inputs to management decisions for these populations (see Soule' 1987 for a review). At the outset we must understand that even for a single species the minimum viable population is not a magic number but varies according to various demographic traits and ecological pressures.

The continued survival of a population can be expressed only in probabilistic terms (Schaffer 1981). No population has a 100% probability of surviving for any given period of time. Thus, the minimum viable population (MVP) is usually expressed as that which has a 95% (or 99%) chance of surviving to 200 (or 1000) years.

The MVP thus varies from one species to another and from one population to another, depending on their peculiar demographic, environmental and genetic factors, and most important, on one's personal definition of MVP in probabilistic terms. A population ecologist may define MVP as one that has a 99% chance of surviving for 1000 years (cf. Shaffer 1981); a reserve manager may deem it fit to continue in situ conservation measures for a population that has a 90% chance of surviving for 100 years.

Population viability analysis is thus a process that can yield different values of minimum viable population (Boyce 1992). The results I report in this talk are based on a preliminary analysis and provides a first approximation of the MVP in Asian elephants. For this I used programme VORTEX developed by Robert Lacy (Chicago Zoological Society) who in turn used algorithms provided by James Greir (North Dakota State University).

Stochastic Modelling

Most of the population parameters used in the modelling are based on data obtained from a study of the Nilgiri-Eastern Ghats elephant population in southern India (Sukumar 1989).

Population processes are modelled as discrete, sequential events, with probabilistic outcomes determined by Monte Carlo simulation. Demographic stochasticity is modelled by taking birth and death probabilities as corresponding to observed average annual rates obtained from field data. In the first round of modelling, birth probability was taken as 0.20 to 0.22/mature female/year, while annual age-specific death probabilities were varied (see Sukumar 1989 for mortality values). The parameters were adjusted so as to yield a desired growth rate and sex ratio under a deterministic life table analysis.

Environmental stochasticity is modelled as variation in annual birth and death probabilities by sampling binomial distributions, with the standard deviation (SD) specifying the annual fluctuations. Two populations were simulated, one with a SD equal to 20% and another equal to 40% of the average probabilities of death. SD in fertility was taken to be 5.0 and 10.0 for the two populations respectively, the latter reflecting the variance observed in the study population (also see Douglas-Hamilton 1972).

Two types of catastrophes were modelled, the first (such as a severe drought) with a 2% probability of reducing reproduction to 60% and survivorship to 80% (see Corfield 1973 for drought-related mortality at Tsavo) of the normal values, and the second (such as a disease epidemic) with a 0.5% probability of reducing survivorship to 75% of the normal value.

The carrying capacity (K) was set at 150 (SD=30); this was much higher than the initial sizes of simulated populations

Age and sex-structure of the initial population were adjusted to begin with the stable age distribution. Adult sex ratios at stable age distribution under the first scenario were in the range of 1 adult male for every 3-4 adult female, representative of a natural population not under any serious threat from ivory poaching. All simulations were run 1000 times for 100 years.

Fig. 1 shows the probability of survival for 100 years as a function of population size for populations with different intrinsic growth rates (r) from 0 to 0.02 as calculated from life table analysis of the female segment of the population. To ensure a 99% probability of survival for 100 years, the minimum population sizes required are about 25-30 for one growing at r=0.02 (2% per year) and 65-80 for those growing slowly at r=0.005 (0.5% per year) or remaining stable. When the probabilities of the two types of catastrophes are doubled for the population with potential r=0.02, a population of 45 animals has a 99% of surviving for 100 years

The survival probabilities for the two populations with low and moderate levels of environmental variance were hardly distinguishable. This implies that a long-lived K-selected mammal such as the elephant is relatively well buffered against environmental stochasticity.

For the population potentially increasing at r=0.02, the male mortality rates were increased so as to result in more skewed adult sex ratios (adult male : female ratio going from 1:4 to 1:16) at stable age distribution. This would reflect the trends seen in many Asian (Sukumar 1989) and African elephant populations (Poole & Thomsen 1989) suffering from ivory poaching. The result is a significant reduction in probability of survival (Fig 2). For instance, the population size needed to ensure a 99 % probability of survival increases from 25-30 (at 1:4 sex ratio) to about 55 at 1:8 ratio. With a 1:16 sex ratio a starting population of 150 (at K=150) has only a 92% probability of surviving for 100 years. It is only when K is increased to 250 that a population of 120 elephants has a 99% probability of surviving for 100 years.

In the absence of specific data for elephants I did not model the deleterious effects of inbreeding on the population. The genetically effective population size (EPS) of 50 suggested as the minimum number needed to keep inbreeding below a tolerable 1% per generation can be taken as a useful guide for management. This would, of course, translate into a higher total population size depending on the adult sex ratio and the proportion of pre-reproductives in the population. The EPS as a percentage of the total population varies from about 8% in Periyar, southern India (where ivory poaching has been a problem) to 50% in southeastern Sri Lanka (where poaching is not a threat).

In summary, a total population of 100-200 elephants, depending on demography, sex ratio and ecological pressures, would not only have a high (99 %) probability of survival for the next 100 years in the face of demographic and environmental stochasticity, but also be safe in the short term from genetic erosion. The goal of managers could thus be to maintain these minimum sizes in isolated elephant populations until other options emerge in the future. Let me emphasize that the figures given above are the minimum sizes recommended for short-term conservation of populations that are not under any serious danger of losing their habitat. Such populations may still be unable to maintain their long-term evolutionary potential. For this much larger population sizes would be required.

Population viability analysis could also be usefully combined with other types of ecological analyses in deciding on management options as, for instance, in dealing with elephant populations in conflict with people (Sukumar 1991).

Acknowledgements

I thank Dr. Robert Lacy for providing me with the programme VORTEX, and Dr. N.V. Joshi for useful discussions. A more detailed version of this talk will appear in the second edition of my book on Asian elephants published by Cambridge University Press.

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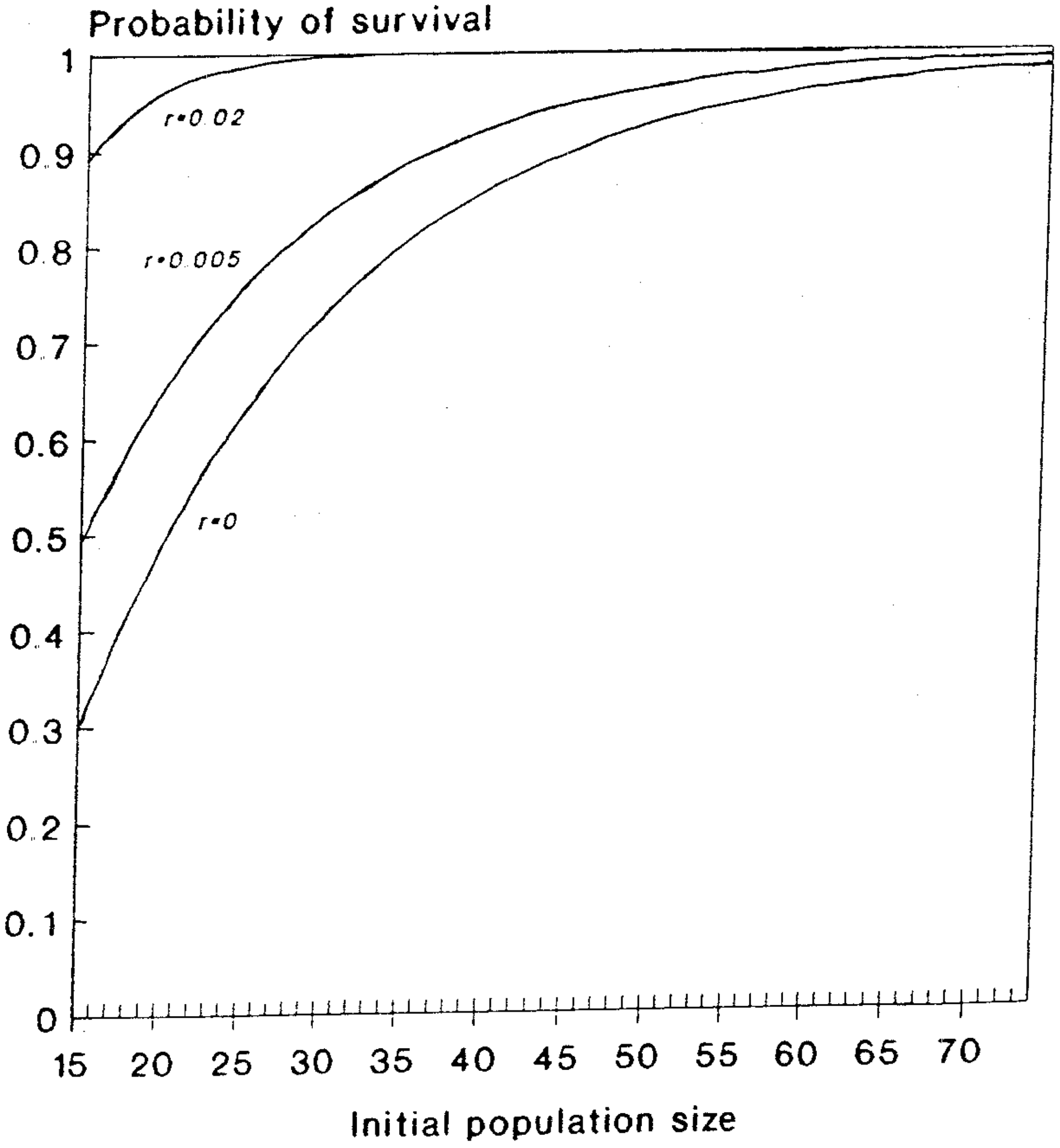
Fig 1


Probability of survival
1
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0.8
0.7
0.6
0.5
0.4
0.3
0.2
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r=0.005
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25
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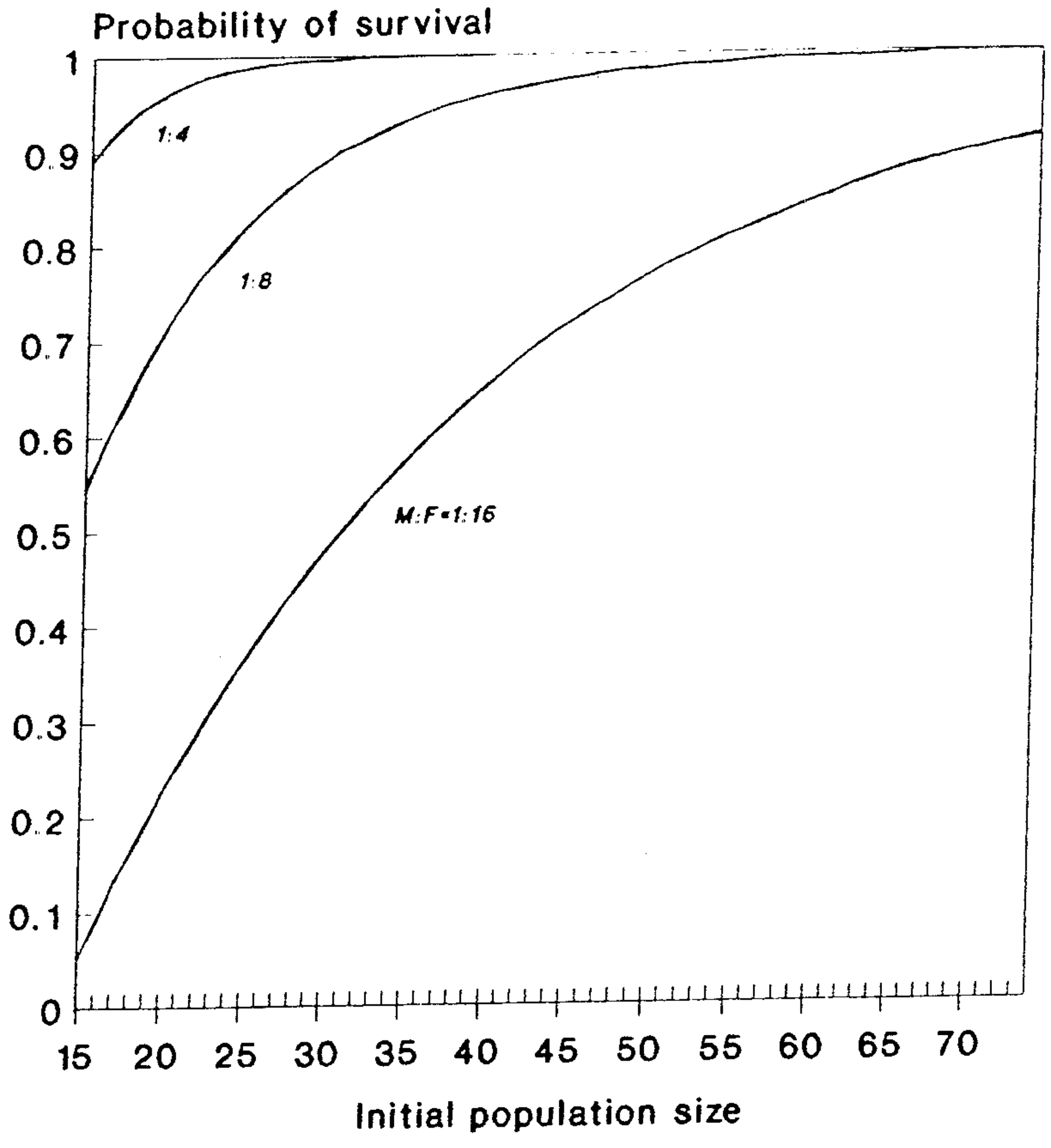
55
60
65
70
Initial population size

Fig. 2.


Probability of survival
1
0.9
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Initial population size

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CHAPTER 6

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INSULAR ECOLOGY AND CONSERVATION

Bruce A. Wilcox

One of the most profound developments in the application of ecology to biological conservation has been the recognition that virtually all natural habitats or reserves are destined to resemble islands, in that they will eventually become small isolated fragments of formerly much larger continuous natural habitat. Hence, beginning with the seminal monographs by Preston (1962) and MacArthur and Wilson (1967), many ecologists and biogeographers have come to recognize the potential importance of studies of islands and other ecological isolates to conservation.

Typically, the term "isolate" has been used to connote any discrete ecological unit which is insulated from other similar units. In addition to a true island, an isolate can be a stand of trees or other distinct vegetation type, or even a pond or lake On a smaller scale, an individual tree, shrub or portion thereof can be an "island" from the perspective of very small organisms. For these reasons, "isolate" as it is used here is an ecological community with more or less distinct boundaries. The study of isolate ecosystems, most commonly called "island biogeography," also implies a narrower scope than is actually encompassed. Because of its generality, the term "insular ecology" is preferred here to "island biogeography."

The attractiveness of insular ecology is due, in large part, to the quantitative manageability of discrete ecological entities which have definable physical and biological properties. In particular, because they have definite boundaries, isolates can be described by the amount of area encompassed, proximity to other habitats, as well as taxonomic composition, which is known to be largely related to the former two properties. These properties are those of primary interest to the conservation biologist

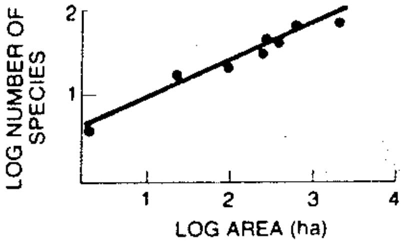

FIGURE 2. **The species-area relation in Figure 1 plotted on logarithmic axes.**

ure 2). This manipulation of the data allows the values of C and z to be readily calculated by applying linear regression analysis where $\log S = z \log A + \text{constant}$; note that z is now the slope of the line.

The power function can adequately describe many, but not all species-area relations (May, 1975; Diamond and Mayr, 1976; Schoener, 1976). When the power function is appropriate, that is when the log-log transformation produces an approximately linear relation, the resulting z-values (slopes) vary depending on whether the observations are isolates or samples—terms used to describe the nature of the entities being sampled (Preston, 1962). Isolate in this sense is analogous to "universe" in that it refers to the total collection of individuals comprising an ecological community. A sample, on the other hand, is some fraction of such a community. Thus a random transect or quadrat is a sample and successively larger samples together eventually become an isolate (a continent could be considered the largest possible isolate). Aside from the form of the species-area curve, a basic empirical rule is that z-values for samples are lower than those for isolates. Samples range between approximately 0.12 and 0.17 while isolates tend to vary between approximately 0.18 and 0.35 (Preston, 1962; MacArthur and Wilson, 1967), although some values may actually be more extreme than this (Diamond and May, 1976). To understand the reasons for this dichotomy it is important to consider the theoretical basis of the species-area relation as it has been recently clarified by May (1975).

The species-area relation and the apparently narrow range of observed z-values are the result of two underlying quantitative properties of ecological communities. The first is the approximately linear relationship between the number of individuals and area. The second is the relationship between the total number of individuals and the number of species, or the distribution of species abundance as it is often called. The form of this distribution is approximately lognormal for intact communities. As emphasized by May, the lognormal distribution is merely a statistical phenomenon of large, heterogeneous communities and probably has no other underlying biological significance. Also, the apparently narrow range encompassing observed z-values results from mathematical properties of the lognormal distribution.

The divergence of z-values for samples from those for isolates can be explained as a result of the failure of samples to represent a complete lognormal ensemble of species (Preston, 1962). That is, relative to an intact community, a sample is characterized by fewer total species and a higher species-individual ratio. In addition, some species are represented by only one to several individuals. The reason for this can be understood as follows. The smallest possible sample consists of one species represented by one individual. At first, successively larger samples will only contain individuals representing new species. This is because even the most abundant species has far fewer individuals than the rest of the species combined. However, as species accumulate, new species will be recorded less frequently and individuals will be added more frequently. As the size of the sample approaches that which encompasses the entire community, only the least abundant species in the community remain unrecorded. The higher species-individuals ratio of smaller samples inflates the species count. This does not occur in smaller isolates since the species-individual ratio should be more equitable regardless of size.

The key feature that differentiates a sample from an isolate is that the latter is a self-contained ecosystem insulated by barriers that tend to restrict normal movement or dispersal of organisms in or out. All of the immediate ecological requirements of a population are contained within an isolate. However, since vagility varies greatly among species, a habitat which produces isolates for some species may act as samples for others.

Isolates Which Behave As Samples

Depending on the degree of habitat insularity or the vagility of organisms, a system may behave either as a sample or an isolate. As an example, in their studies of bird faunas on the Solomon Archipelago, Diamond and Mayr (1976) calculated a z-value of 0.025 for the "highly vagile" species, conforming to that of extreme samples. However, the species with "low vagility" on the very same islands produced a z-value of 0.28, conforming to that of isolates. The same effect can be seen in another example as a result of distance to an archipelago from the source of colonizers. By assigning the archipelagos to "near" and "far" groups (Figure 3) it is seen that the "near" group behaves like samples and the "far" group like isolates. If z-values are calculated for individual archipelagos (within rather than among archipelagos), however, the opposite trend results: more distant archipelagos have lower z-values. This apparent anomaly is actually consistent with the above since distant archipelagos tend to be inhabited by a proportionately greater number of highly vagile species

(Diamond and Mayr, 1976) or have a larger "effective" species pool (Schoener, 1976).

In summary, the loss and fragmentation of natural habitat will have different consequences depending on the vagility of organisms and the proximity of isolated fragments. Before discussing these consequences in more detail, let us first consider the most far-reaching theory in insular ecology.

THE EQUILIBRIUM THEORY

In addition to the foregoing explanation of the species-area relation, the autonomous nature of island ecosystems led Preston (1962) and MacArthur and Wilson (1963), independently, to postulate another. First,

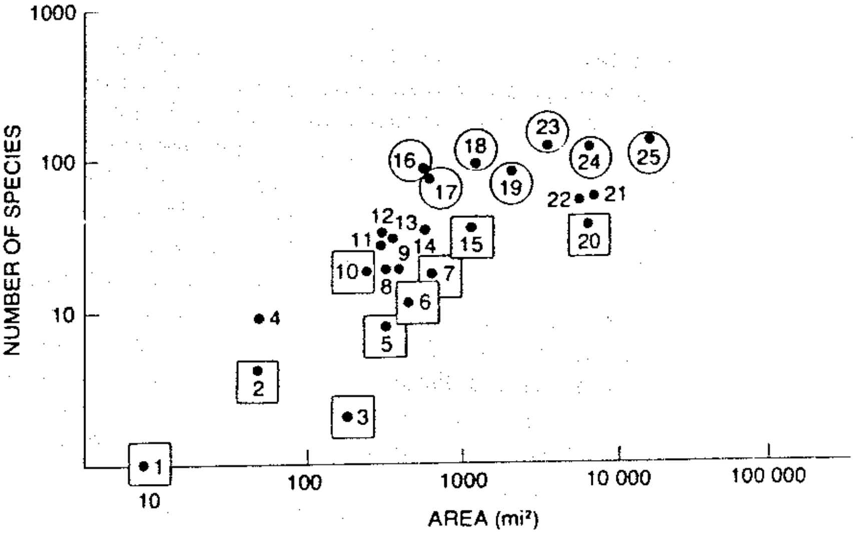

FIGURE 3. The number of land and freshwater bird species on various islands and archipelagos in the Pacific Ocean. "Near" islands (open circles) are those less than 500 miles from a colonization source (New Guinea). "Far" islands (squares) are those greater than 2,000 miles from a colonization source. Dots without circles or squares are islands of intermediate distance. (1) Wake, (2) Henderson, (3) Line, (4) Kusaie, (5) Tua Motu, (6) Marquesas, (7) Society, (8) Ponape, (9) Marianas, (10) Tonga, (11) Carolines, (12) Palau, (13) Santa Cruz, (14) Renell, (15) Samoa, (16) Kei, (17) Louisiade, (18) D'Entrecasteaux, (19) Tanimbar, (20) Hawaii, (21) Fiji, (22) New Hebrides, (23) Buru, (24) Ceram, (25) Solomons. (From MacArthur and Wilson, 1963)

consider that area sets an upper limit on the number of individuals. Second, that the probability of a species becoming extinct will increase with smaller population sizes. This is because small populations are more subject to demographic instability (Chapter 10), inbreeding depression (Chapters 8, 9 and 12) and inclement environmental conditions. Hence, it follows that area acts through extinction to limit the number of species, despite propagules from other islands or the mainland which provide a constant source of new species. This loss of species through extinction can be viewed as being balanced by the gain from colonization.* Thus, the outcome can be expressed as an equilibrium between colonization and extinction.

The equilibrium theory can explain the effects on species number due to variation in area and insularization independently of any assumptions about underlying species abundance distributions. This is demonstrated by the graphical analysis in Figure 4. The curves represent the rates of colonization and extinction for isolates differing in both their distance from a source of colonists and in size, as a function of the number of species present. The curves show that the rate of colonization is highest on "near" isolates and when there are fewer species. This is because the likelihood that a propagule will successfully reach an isolate is greater for shorter distances, and the likelihood that any such propagule will represent a species not yet present is greater when few species exist in an isolate. In a similar manner, the rate of extinction is highest in "small" isolates and when there are more species. This is because extinction probability is greater with less area (smaller population size) and when there are more species to go extinct. At the point of intersection of a colonization and extinction curve, the rates of both processes are equal and the equilibrium number of species, $\hat{s}$, is defined. Figure 4 shows how $\hat{s}$ varies with isolate size and distance; for example, "far" and "small" isolates equilibrate with the least number of species. It also shows (although the curves are purposely drawn in this manner) that the species-area relation can be affected by distance (colonization rates), since the disparity in $\hat{s}$ is greater between the two hypothetical "far" isolates than between the two "near" islands, which would result in a lower z-value for the latter. Figure 3 also illustrates the "distance" effect.

Species Turnover

The most striking feature of the equilibrium theory is its dynamic view of isolates. It proposes that species are constantly being lost and gained, one species being exchanged for another, such that turnover in

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*MacArthur and Wilson (1963, 1967) use "immigration" rather than "colonization" as the addition of new species. Both are to be distinguished from the arrival of new individuals representing species already present.

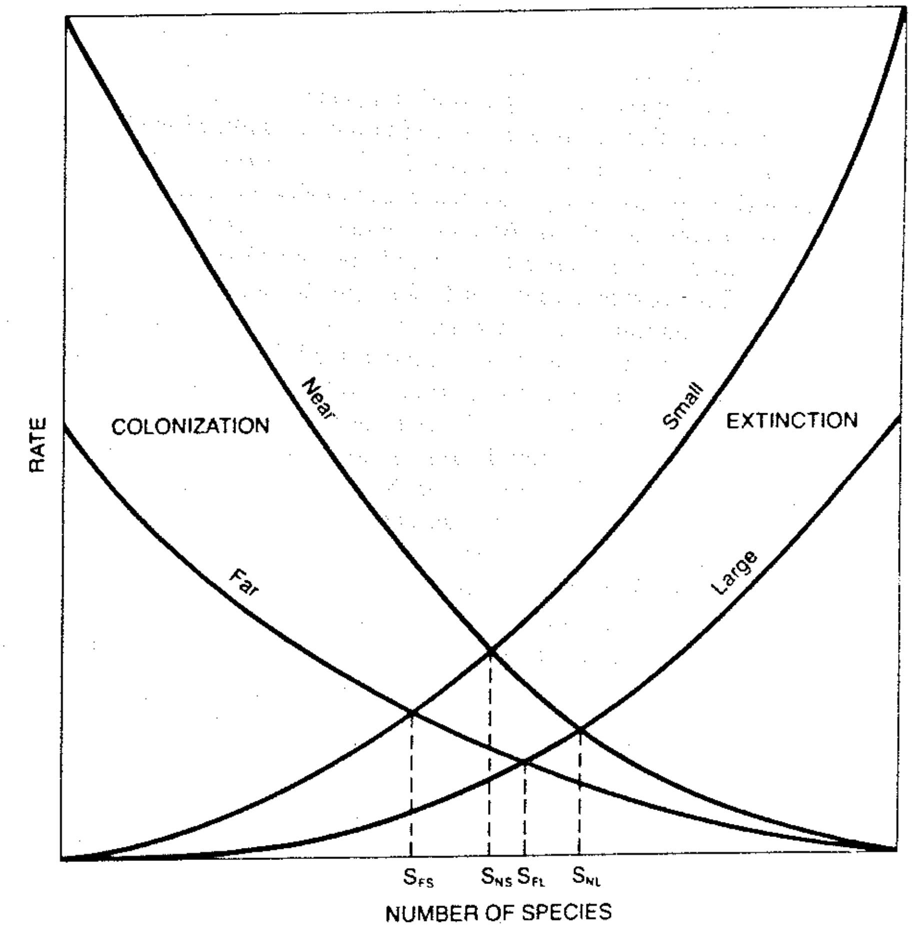

FIGURE 4. Graphic model of the equilibrium theory of island biogeography demonstates the effect of isolation and area on the number of species maintained at equilibrium. The colonization curves represent the rate of addition of new species to an isolate as a function of the number of species already present. This rate should be highest for "near" isolates since proximity to a source of colonists will increase the probability of receiving propagules. The extinction curves represent the rate of extinction as a function of the number of species on an isolate. This rate should be highest on small islands since population sizes are smallest. Concavity of the curves is predicted from heterogeneity in species colonization ability and negative species interactions with increasing species number. For any combination of colonization and extinction curves an equilibrium number of species, $\hat{S}$, is defined at their intersection. (For example, $\hat{S}_{FS}$ is the equilibrium number for an island that is both "far" and "small.")

species composition occurs. Until recently, evidence for turnover, though suggestive, was minimal and based primarily on island bird faunas where census intervals were too infrequent for accurate measurement (Diamond, 1969; 1971; Terborgh and Faaborg, 1973). These early estimates of average annual turnover rates ranged from 0.2 percent to 1.7 percent of the total bird fauna, although total compositional change over a 50 year period was as high as 44.0 percent (Diamond, 1969). Since longer census intervals tend to mask repetitive short-term turnover events, most of these estimates are being modified dramatically as data from short-term censuses become available. Average annual turnover rates for bird faunas are now ranging between 0.9 percent (Jones and Diamond, 1976) and 13.0 percent (Diamond and May, 1976) for islands. Estimates for bird species turnover in mainland habitats are showing similar values. Annual turnover rates of 13.6 percent were calculated for Illinois woods (Whitcomb et al., 1976) and 10.0 percent for a Finnish valley (Järvinen, in press). Where there are a sufficient number of estimates to make comparisons, the turnover rates for smaller islands are highest (Jones and Diamond, 1976). This accords with the prediction of the equilibrium theory for higher per species extinction rates on smaller islands.

These relative turnover rates should be distinguished from absolute turnover rates. According to theory, both vary inversely with area. Distance, however, may not detectably effect relative turnover because the absolute rate and number of species vary in the same direction (Williamson, 1978). Further, absolute turnover may not vary with distance as predicted by the equilibrium theory because of the rescue effect (Brown and Kodric-Brown, 1977).

So far, significant species turnover within the time span of modern biological exploration has not been recorded for vertebrates other than birds. This is not for a lack of data, however, since in theory the time scale of turnover for other groups should be much longer. For birds, at least, the evidence does suggest an important role for colonization-extinction equilibria, particularly in smaller isolates.

NATURE RESERVES

The Sample Effect

Let us now consider insular ecology in terms of nature reserves. Most nature reserves, at the time they are designated as such, are effectively samples in that they represent only a portion of a much larger community. Thus, Serengeti National Park or Manu in the Amazon are samples of African savanna and Amazon rain forest, respectively. They contain fewer species, fewer individuals within each species and more species represented by only several individuals than would similar but larger reserves. A single reserve would have to include virtually the entire Amazon to contain all of its species (albeit a vast system of numerous small reserves could initially accomplish this). On the average though, extrapolating from observed z-values for samples, a reserve will initially exclude roughly 30 percent of the species of a community for each 10-fold decrement in area. For example, a reserve of 10 km^2 will be missing three out of every 10 species found in 100 km^2 of surrounding habitat. We will refer to this initial exclusion as the *sample effect*.

Short-term Insularization Effects

Typically then, a single area designated to preserve any community that does not take in the entire area of the community, will fail to include some of its species. This will occur because of a lack of appropriate habitat or due to species that are rare (Chapter 7) or patchily distributed in spite of habitat (Chapter 4). On the other hand, some species will be included even though their habitat requirements are not met. Under many circumstances, the boundaries of a reserve will not coincide with those of ecological systems, and the requirements for each species cannot be met within its confines. The migration of herds of wildebeest and elephant across the boundaries of large African national parks attest to this fact most dramatically. On any scale, however, the boundaries of a reserve will sever the resources of some species. As long as adjacent habitat remains, these species will be counted among those "protected" within the reserve. However, as the neighboring habitat is removed for agriculture and other forms of land use even more devastating, they will disappear unless intensively managed.

The above implies that dispersal across reserve boundaries as well as the availability of exogenous resources are required for the survival of some species in reserves. Two other conditions can be distinguished where dispersal is responsible for the occurrence of a species. Neighboring habitat may contribute species as non-breeding transients, which are nonetheless recorded as resident species (Simberloff, 1976). Alternatively, neighboring habitat may contribute recruits for minimally stable populations in suboptimal habitats. Since this amounts to preventing extinction in established but marginal populations, it has been dubbed the "rescue effect" (Brown and Kodric-Brown, 1977). The loss of species sustained directly by exogenous resources or dispersal will immediately follow the disappearance of adjacent habitat. These can be considered *short-term insularization effects*.

Long-term Insularization Effects

Colonization-extinction equilibria must, no doubt, play a role in the maintenance of species diversity in samples as well as isolates, although it is much less generally appreciated in habitats without well prescribed boundaries. Here we are simply extending the above notion that individuals dispersing from adjacent or contiguous habitat can shore up a faltering population. It is equally plausible that dispersing individuals may represent new colonists replacing populations which have failed altogether.

As a natural area becomes increasingly insular and colonization sources become increasingly fewer and more distant, colonization rates will, of course, diminish. Since, over the long-term, extinction events are inevitable in even the largest reserves, the reduced colonization rate will result in a net loss of species over time which will continue until the colonization and extinction rates are once again balanced. Of paramount interest, then, is the magnitude and time scale of this putative collapse to a new equilibrium.

Fortunately we need not depend entirely on theoretical conjecture to anticipate *long-term insularization effects*. For example, the frequently cited case of Barro Colorado Island provides a striking illustration (Chapters 2, 3, 4 and 7). Formed around 1914 with the flooding of the Panama Canal, Barro Colorado was designated a reserve soon thereafter. Since that time, however, many of its original species have become extinct, including 48 of its 208 breeding birds. About one-third of the extinctions appear to be the result of a colonization-extinction disequilibrium (Willis, 1974). Similar consequences of habitat fragmentation are documented in Chapter 7.

There is another matter of concern regarding the long-term effects of habitat insularization, particularly in nonflying taxa. These are the shifting climatic zones associated with glacial-interglacial cycles. The Pleistocene Epoch was marked by global temperature oscillations during which fairly extensive latitudinal (and altitudinal) shifts in climatic zones occurred. Normally, as climatic zones shift, so do the associated biotas. Insular regions, however, typically do not span a sufficient latitude to provide refugia for species ill-adapted to a novel climatic regime—and extinction results.

As an example, many species presently adapted to arid southwestern North America probably had the limits of their northernmost ranges pushed several hundred kilometers southward at the peak of the last glacial period. The adjacent islands apparently bear witness to this. Those of higher latitude have fewer nonflying vertebrate species than expected given the present mainland distributions of species. Notably, the arid-adapted reptile species are disproportionately under-represented on the more northern California islands, even on those with apparently suitable habitat (Wilcox, in press).

Barring catastrophic global temperate modification caused by man, the temperature oscillations of the past will be repeated. Therefore, unless long-term climatic shifts are taken into account, another factor can be added to the long-term effects of insularization.

FAUNAL COLLAPSE

Pleistocene Land-Bridge Islands

The combined short- and long-term insularization effects discussed above (even omitting climatic shifts) can potentially result in the eventual loss of most of the vertebrate species in even the largest reserves. This faunal collapse is documented by studies of land-bridge islands, whose mainland connections were severed by the rising sea level around the close of the Pleistocene (Diamond, 1972*b*, 1973; Terborgh, 1974; Chapter 7). The last episode of rising sea level began around 18,000 years ago and ended some 6,500 years ago (Bloom, 1971). During this time the sea rose over 100 meters, inundating lowlands and leaving isolated fragments of such formerly vast continental regions as the Sunda Shelf in southern Asia (Figure 5). In this example, based on the present ocean depths of this region and the rate of sea level rise (Wilcox, 1978), the islands of Borneo, Sumatra and Java, and their fringing archipelagos were probably completely isolated by 10,000 years ago.

By estimating the number of species lost on these and other islands with a similar history, we can gain at least some idea of the fate of our reserves which are presently undergoing the insularization process. As shown in the following example, this is typically done by assuming that each island, before falling to its current level, originally had the same number of species that a mainland sample of the same size has at present.

The faunal composition and distribution of species on the Sunda Shelf prior to inundation cannot be known with certainty, though present faunal resemblance and fossil evidence strongly argues for its similarity to the Malay Peninsula. For example, the islands of Borneo, Sumatra and Java combined have virtually a complete Malaysian mainland mammal fauna though each is deficient in a number of species (Darlington, 1957; Terborgh, 1975). That is, a species missing on one island is often present on another (see Table I in Chapter 4). Evidence that these islands supported larger faunas at the close of the Pleistocene is also provided by fossil remains (Terborgh, 1975). Figure 6 shows the current level of diver-

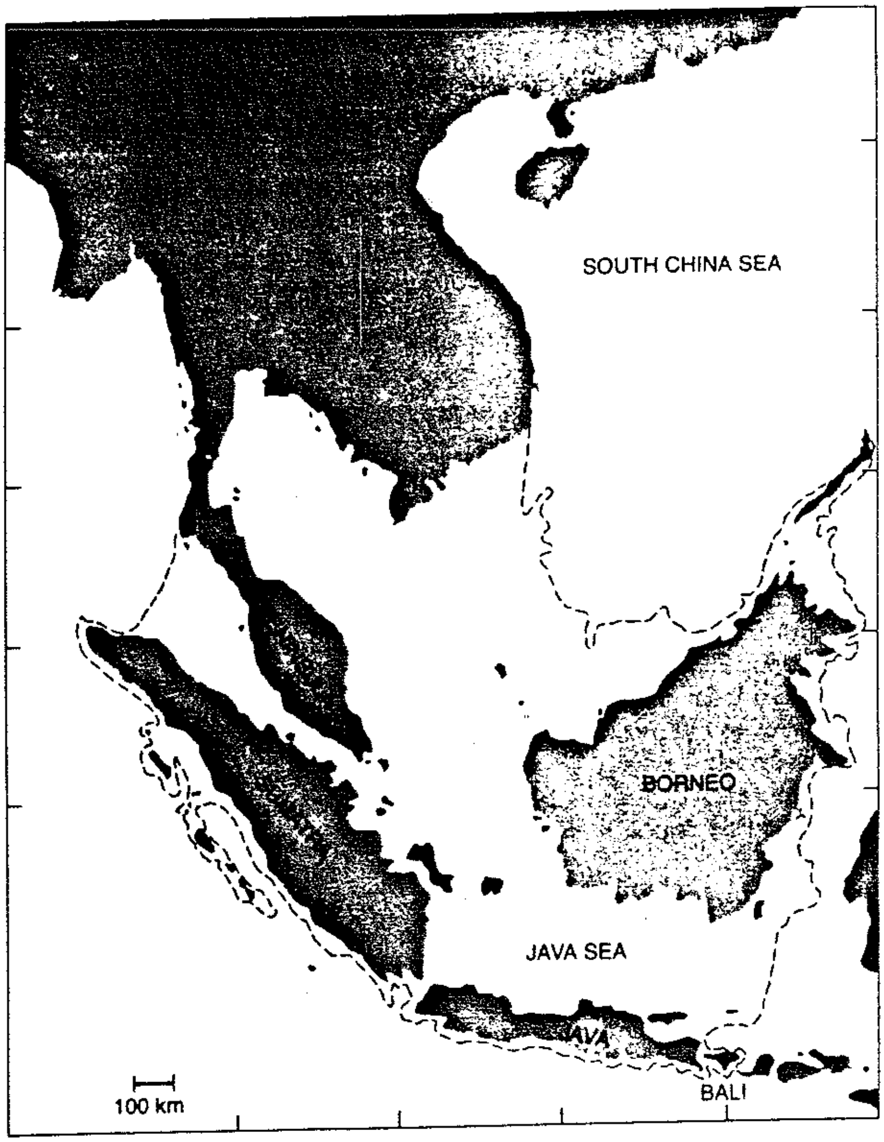

FIGURE 5. The Sunda Islands and the extent of the land surface of the Sunda Shelf during the last glacial period. The dashed line is the present 100 fathom contour and approximates the coastline of 18,000 years ago.

gence between the species area relation for the land mammal faunas of the Malaysian mainland and the Sunda Islands. Although the mainland curve is tenuously based on only two points, its z-value of 0.17 and that of the islands, 0.30, agree with theory and previous findings. Thus, the presumption is that island faunas all began near the upper curve and have since dropped to their present positions. The estimated species loss for

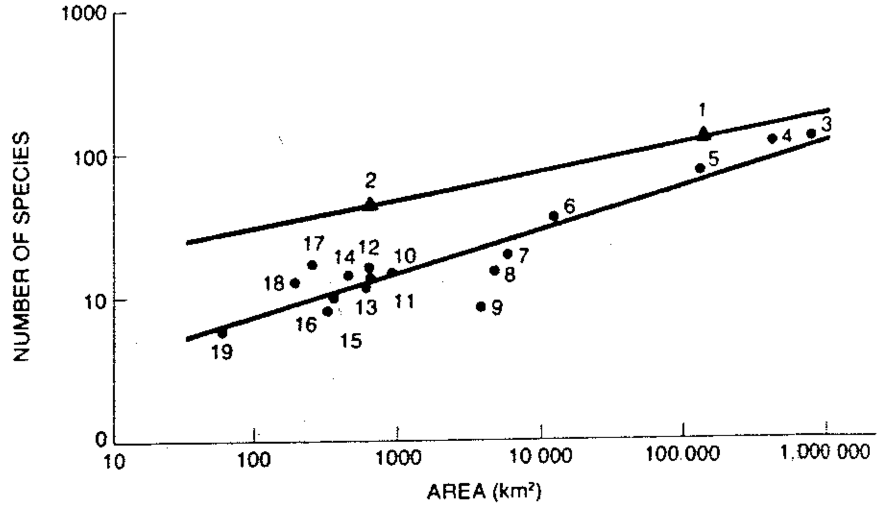

FIGURE 6. **Species-area relations for the land mammals (excluding bats) of the Malaysian mainland (upper curve) and Sunda Islands (lower curve). The upper curve ($S = 15.4\ A^{.17}$) is presumed to approximate the species-area relation of the Sunda Shelf prior to fragmentation by the rising sea level at the close of the Pleistocene. The lower curve ($S = 1.8A^{.30}$ by linear regression) differs as a result of fragmentation and collapse of isolate faunas. (1) Malay Peninsula, (2) Krau Game Reserve, Pehang, Western Malaysia, (3) Borneo, (4) Sumatra, (5) Java, (6) Banka, (7) Bali, (8) Billiton, (9) Siberut, (10) S. Pagi, (11) N. Pagi, (12) Sipora, (13) Singapore, (14) Tanabala, (15) Tanamasa, (16) Pini, (17) Penang, (18) Tuangku, (19) Bangkaru. (Data from Medway and Wells, 1971; Chasen, 1940)**

each island can thus be calculated as the difference between the projected initial number of species, S_0, and the present number of species, S_p. Table I shows the results of such calculations for the Greater Sunda Islands.

The species losses for these islands, the majority of which are species of large body size or high trophic level, are quite remarkable, especially because most of the islands are an order of magnitude larger than the largest existing nature reserves. Nevertheless, these figures alone probably provide only a crude view of the collapse process. If we could have directly monitored the loss of species from the time of initial isolation we would, according to theory, observe that the rate of loss would have been highest at first, decreasing exponentially to approach asymptotically a new equilibrium.

The prevailing evidence suggests that the loss of species is approximated by an exponential function, such as$-kS^n$, where k is the relaxa on

TABLE I. Estimated number of extinctions of land mammal species (excluding bats) since the formation of the Greater Sunda Islands.

Island	Area (km^2)	Initial number of species* (S_o)	Present number of species (S_p)	Extinctions** Number ($S-S_p$)	Percent $\left(\frac{S_o-S_p}{S_o}\right)$
Borneo	751,709	153	123	30	20
Sumatra	425,485	139	117	22	16
Java	126,806	113	74	39	35
Bali	5,443	66	19	47	71

* Initial number of species, S_0, are estimated from the species-area relation of mainland Malaysia.

** Total species loss is assumed to closely approximate or even underestimate extinctions. See text for more discussion.

parameter and *n* is an integer that might reasonably take on values from one to four, although two or three seems most probable on the basis of very limited data (Soulé et al., 1979). By using models of this general form, relaxation parameters or comparable measures of the magnitude of species loss with time have been estimated for a number of geographically and taxonomically divergent faunas (Diamond, 1972*b*; 1973; Terborgh, 1974*a*; 1974*b*; 1975; Case, 1975; Soulé et al., 1979). All of these findings show a tendency for smaller islands to have higher extinction rates. Also, the rate of species loss, as a proportion of the initial number of species and as a function of area and time, vary consistently in the manner predicted from intrinsic taxonomic differences. This will be discussed in more detail below.

Collapsing Reserves

The apparent universality in the general properties of the collapse process should allow extrapolation of these findings to nature reserves. One such attempt (Soulé et al., 1979) has been made using the large mammal species of the Sunda Islands as a model to predict the fate of similar species in East African reserves. Application of collapse theory to these reserves is particularly appropriate as insularization is nearly complete. In this study, relaxation parameters were calculated for several Sunda Island faunas to determine their relationship to island size. The size specific values were then applied to 19 East African national parks and game reserves to estimate species loss as a function of area and time. The results predict that the average reserve, which presently has 48 large mammal species and an area of about 4,000 km^2, will lose 11 percent of these in 50 years, 44 percent in 500 years and 77 percent in 5,000 years. Figure 7 shows the probable range of species loss trajectories for three of the national parks. This illustrates that as isolates, even the largest reserves in the world may be incapable of preserving most of their large mammal species without intensive management.

Extinction estimates have been calculated for other taxa in reserves using a similar approach. From his studies of bird faunas on tropical land-bridge islands Diamond (1972) predicted a loss of 51 percent for a hypothetical reserve of 7,800 km^2 in 10,000 years. This is smaller than predicted losses for the large mammals and probably results from smaller body size (allowing higher population densities) and higher colonization rates of birds, since collapse has both a colonization as well as an extinction component.

The theoretically predicted shapes of the colonization and extinction curves (Figure 4) as well as empirical evidence for their shapes approximated from actual data (Gilpin and Diamond, 1976) suggest a rather insignificant role for colonization (even where dispersal is possible) until species number nears equilibrium (Wilcox, 1978). For this reason, the net

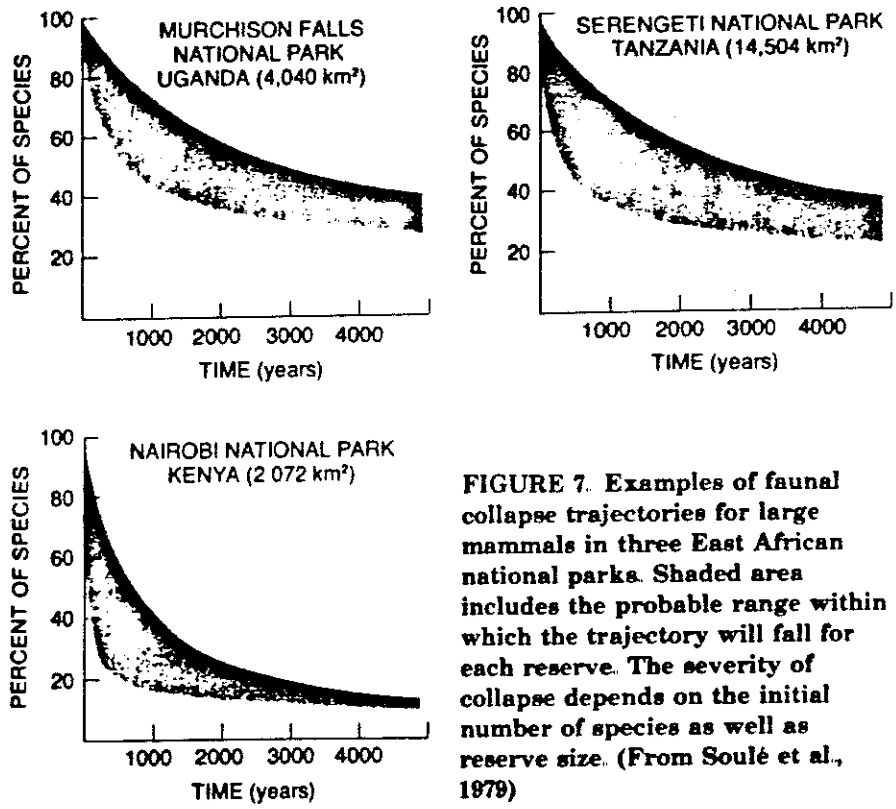

FIGURE 7. **Examples of faunal collapse trajectories for large mammals in three East African national parks. Shaded area includes the probable range within which the trajectory will fall for each reserve. The severity of collapse depends on the initial number of species as well as reserve size. (From Soulé et al., 1979)**

the world may be incapable of preserving most of their large mammal species without intensive management.

Extinction estimates have been calc[illegible] xa in reserves using a similar approach. From his stu[illegible] as on tropical land-bridge islands Diamond (1972) pre[illegible] percent for a hypothetical reserve of 7,800 km^2 in 10[illegible] smaller than predicted losses for the large mammals a[illegible] from smaller body size (allowing higher population d[illegible] r colonization rates of birds, since collapse has both a [illegible] as an extinction component.

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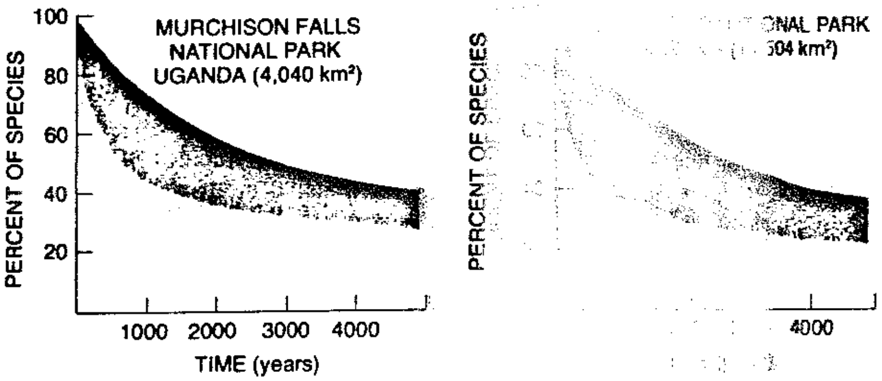

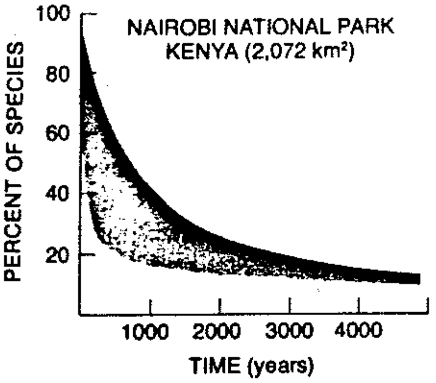

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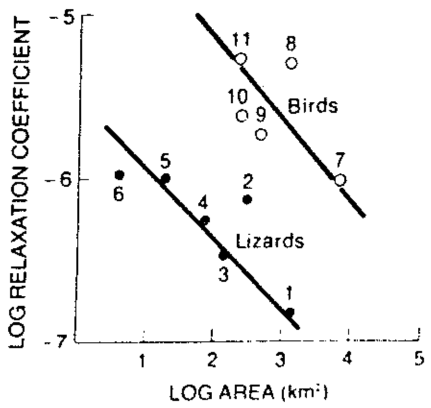

FIGURE 8. Comparison of relaxation parameters as a function of island area for lizard and bird faunas. The curves demonstrate the dependence of extinction rates on area, also the relatively lower collapse rates for lizards. Relaxation parameters are calculated as in Terborgh (1974*a*), except isolation times that are estimated as in Wilcox (1978). Lizard faunas: (1) Tiburon, (2) Cedros, (3) San José, (4) Espiritu Santo, (5) San Marcos, (6) Coronados (data from Soulé and Sloan, 1966). Bird faunas: (7) Trinidad, (8) Margarita, (9) Coiba, (10) Tobago, (11) Rey (data from Terborgh, 1974*a*).

species on an isolate. More convincing, however, is a comparison of different faunas on the same islands in the Gulf of California (Wilcox, in preparation). Reptile faunas of the land-bridge islands appear extremely supersaturated compared to their deep-water counterparts (Soulé and Sloan, 1966; Case, 1975; Wilcox, 1978), while the mammal faunas also appear supersaturated, but less so. Finally, the bird faunas show no evidence of supersaturation, presumably having already collapsed to their equilibria in the 10,000 or so years since the islands were formed (M. Cody, personal communication).

A second major consequence of heterogeneity in colonization and extinction rates among the vertebrate taxa are differences in the relative number of species maintained at equilibrium. Because of a combination of low colonization and high extinction rates, nonflying mammals will be depauperate in relation to other vertebrates in isolates. Indeed, the absence or small numbers of mammal species on most islands without a history of recent land-bridge connections is well known. The great dispersal advantage held by the birds and bats, however, may more than compensate for their high extinction rates in comparison with the reptiles and amphibians, particularly where dispersal barriers are barely surmountable by non-flying organisms. At equilibrium, therefore, bird and bat faunas will be relatively richer than those of reptiles and amphibians in extreme isolates.

These predicted differences in the relative number of species maintained at equilibrium are reflected in species-area relations. For example,

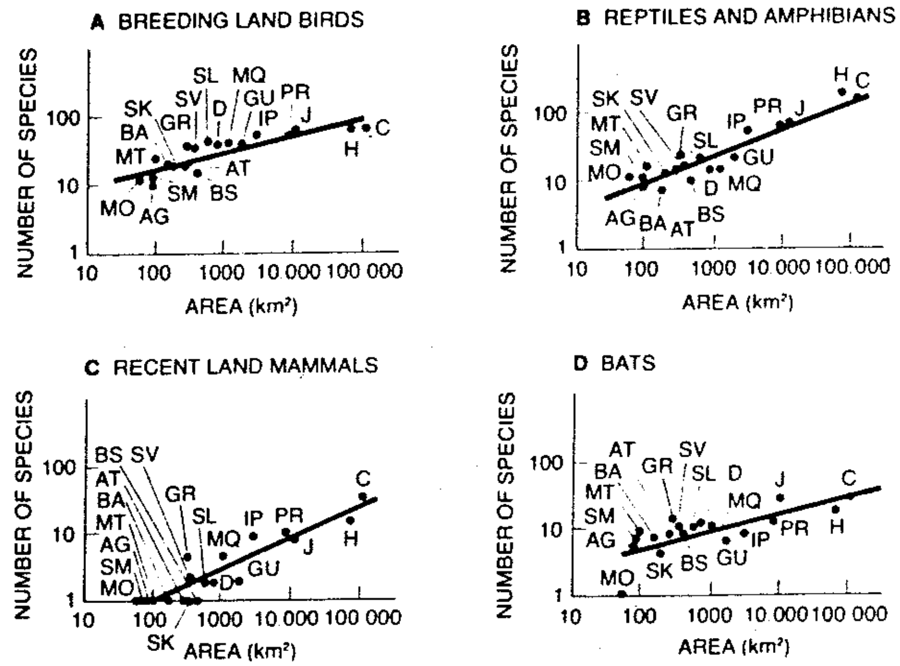

FIGURE 9. Species-area relations of four major vertebrate taxa on the same West Indian islands. The relative differences in the observed z-values follow from taxon-specific colonization and extinction rates. They suggest that consequences of habitat loss and insularization depend on metabolic rate, body size and dispersal ability. Species-area curves fitted by linear regression are as follows: (a) $S = 6.1A^{.24}$, (b) $S = 1.6A^{.38}$, (c) $S = 0.1A^{.48}$, (d) $S = 1.6A^{.24}$. (C) Cuba, (H) Hispaniola, (J) Jamaica, (PR) Puerto Rico, (IP) Isle of Pines, (GU) Guadeloupe, (MQ) Martinique, (D) Dominica, (SL) St. Lucia, (SV) St. Vincent, (BS) Barbados, (GR) Grenada, (AT) Antigua, (SK) St. Kitts, (BA) Barbuda, (MT) Montserrat, (AG) Anguilla, (SM) St. Martin, (MO) Mona. Recent Land Mammals include living and recently extinct native mammals. Many of the present mammal faunas include exotic species which have replaced native species. (Bird data from Bond, 1956, 1961 as compiled in Lack, 1976; reptile and amphibian data from Swartz and Thomas, 1975; mammal data from Varona, 1964)

size of a reserve necessary to insure the occurrence of a sufficient number of habitat patches occupied by a species, such that the probability of simultaneous extinction of the species in all patches is diminishingly small.

This unquestionably should be the approach used where minimum dynamic areas will be of realistic dimensions, given inevitable conflicting land use options. For example, communities of small vertebrates or arthropods adapted to patches of successional habitat would probably require minimum areas no larger than moderate sized national parks. For many species, however, particularly the larger vertebrates, minimum dynamic areas will be considered excessive given the myopic economic demands of most societies. Under these circumstances, the second approach will be required. Multiple reserves or fragments of undisturbed habitat will have to be manipulated as "artificial archipelagos" in order to minimize the probability of simultaneous extinction in each isolate. The second approach will, of course, not be successful in preserving those species incapable of inter-isolate dispersal, or those that cannot be transported successfully or introduced by man. It should be considered a last resort.

Detailed autecological studies are required to determine minimum dynamic areas and optimal design of artificial archipelagos. Here, biogeography will be most useful. The geographical distribution of a species reveals much about its ecological requirements. Diamond's (1976*a*) "incidence functions" are an efficient biogeographic method of defining the survival requirements of species among isolates. The studies of Moore and Hooper (1975), Forman et al. (1976) and those described by Terborgh (Chapter 7) on bird species distributions among disjunct habitat fragments should serve as models for determining preservation requirements of specific insular communities.

Non-avian species have received far too little attention in insular ecology. Perhaps the ease of study and exuberance of ornithologists have contributed to a disproportionate share of attention being focused on birds. Nevertheless, studies of a wider range of taxa are needed, both to test current theory and provide a basis for intelligent conservation decisions.

Of all the biological approaches to conservation, insular ecology is probably of the most immediate importance. The extent to which its lessons are heeded and its successful applications developed in the next few years will play an important role in determining the ultimate fate of this planet's biological diversity.

SUMMARY

The relevance of insular ecology to conservation stems from the similarities between natural isolates, such as islands, and the disjunct fragments of natural habitat resulting from expanding human exploitation of the earth's land surface. Habitat fragmentation can be dissected into two components: habitat loss and insularization. Each contributes to a reduction in the number of species supported, although different mechanisms are involved.

Studies suggest that habitat loss contributes in two ways: first, by excluding a portion of a fauna, particularly the rare or patchily distributed species; second, by increasing the extinction rate of the remaining species as a result of lower population sizes. Habitat insularization also contributes in two ways: first, by extinguishing species "protected" within an area through the removal of required resources outside the area; second, by reducing accessibility for, and sources of, colonists necessary to offset extinction events.

If a reserve were observed from its inception, three classes of these effects could be discriminated on the basis of time-scale. First, the decision to set aside any single area for preservation immediately excludes a number of species characteristic of the greater region as a whole. The proportion excluded is described by the species-area relation for samples. This *sample effect* amounts to the exclusion of about 30 percent of the regional fauna for each 10-fold decrement in area. The sample effect can be minimized by a system of strategically placed smaller reserves. However, other consequences must be heeded.

Short-term insularization effects will closely track encroachment of habitat contiguous to reserves resulting in the loss of self-sufficiency for species dependent on resources outside a reserve. Such species that might be mistakenly thought to be protected by their mere presence in a reserve, include non-breeding transients and populations that are breeding but marginally sustained by dispersal (rescue effect).

Long-term insularization effects describe the consequences of colonization-extinction disequilibria and climatic changes. Extinction is inevitable for any population, though the probability rises sharply with decreasing population size, or reserve area. The decreased colonization rate imposed by artifical dispersal barriers and fewer, more distant colonization sources will add to the collapse towards a new equilibrium with fewer species. Shifting climatic zones associated with the glacial-interglacial cycle will contribute further to extinctions unless reserves are large enough to include refugia.

Using land-bridge islands as models of faunal collapse suggests that large mammal faunas even in reserves of several thousand km^2 will begin to lose a very measurable number of species almost immediately. These losses will amount to as much as half of the initial reserve census of species in several hundred years and three-quarters in several thousand years. Even these estimates may be optimistic since they assume that the reserves will be left to themselves and not subject to poaching and other types of incursion or encroachment.

The rate of faunal collapse and the eventual number of species maintained at equilibrium in a reserve will depend not only on size and insularity of reserves, but also on taxonomic differences. Among the vertebrates, for example, mammals (excluding bats) have combined poor dispersal and high metabolic requirements (lower population densities on average). As a result, they are most vulnerable to extinction, manifesting the highest rates of faunal collapse and fewest numbers of species at equilibrium. Birds and bats, however, because of lower metabolic requirements and superior dispersal ability, are slightly less vulnerable to extinction, manifesting lower collapse rates and greater numbers of species at equilibrium. Reptiles and amphibians generally have much lower metabolic requirements than birds and mammals. As a result, they are, by far, the least vulnerable to extinction, and manifest the lowest collapse rates. In some natural isolates, reptiles and amphibians may maintain equilibrium faunas with nearly as many species as birds or bats. Under the conditions of extreme insularity often produced when humans impose dispersal barriers, however, nonflying vertebrate faunas in general will ultimately be thoroughly extirpated (barring human intervention).

Two primary approaches in insular ecology are suggested for future research and application. First, "minimum dynamic areas" should be defined, whose colonization-extinction equilibria are maintained internally. Second, since such area requirements will be excessive for many vertebrate communities, multiple disjunct reserves should be set aside and maintained as artificial archipelagos. For both approaches more autecological studies in insular systems are needed, especially of non-avian species.

The manageability of future reserves as well as the ultimate fate of biological diversity will depend to no small degree on the extent to which insular ecology is successfully applied in the next few years.

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Soulé, M.E., B.A. Wilcox and C. Holtby, 1979, Benign neglect: a model of faunal collapse in the game reserves of East Africa, *Biol. Conserv.*, 15, 259–272. Describes, hypothetically, the fate of large mammal species where there is a lack of conservation strategy which considers insular theory.

Global Warming

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ABSTRACT

The annual mean global surface temperature has increased by 0.5°C in the last hundred years One of the reasons for this increase could be the increase in 'greenhouse' gases such as carbon-di-oxide methane, nitrous oxide and chlorofluorocarbons. If these gases continue to increase at the same rate for the next forty years, then the global surface temperature can increase by 1.5 to 4.5°C These predictions are based on numerical simulations by climate models There is a large uncertainity in the predictions of these models because of the uncertainity in the nature of cloud-radiation feedback and ocean-atmosphere coupling. If a global warming above 2°C takes place it can cause a sea level rise of more than 50 cm which can inundate many caostal regions Global warming can also cause changes in climate pattern and hence affect global agricultural yields.

INTRODUCTION

The annual mean global surface temperature has increased by about half a degree centigrade in the last hundered years (Fig. 1). The six hottest years in this century occurred in the last ten years. What factors govern this global warming? Is this a part of natural climatic variability or is it on account of industrial or agricultural activities of human beings? The climate of the earth is governed by a complex interaction between solar radiation, atmosphere, ocean, hydrosphere and biosphere. We need to unravel the nature of these interactions in order to understand this phenomenon

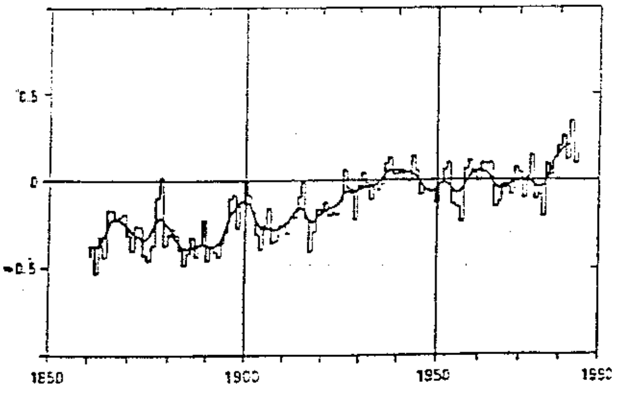

Fig 1 Global mean annual surface temperature change

RADIATION AND CLIMATE

This two major constituents of the earth's atmosphere, that is, nitrogen and oxygen are radiatively non-participating. Hence they do not have a direct impact on the earth's climate. On the other hand, three minor gases, namely water vapour, carbon-di-oxide and ozone play a dominant role in controlling the surface temperature of the earth. In the absence of these gases the earth's surface temperature would have been as low as -18°C. These three minor gases increase the annual mean global surface temperature to +15°C They are able to increase the surface temperature of the earth because they do not absorb most of the solar radiation but absorb strongly the infrared radiation emitted by the earth's surface. These gases trap infrared radiation from the earth in a manner similar to the glass in a greenhouse and hence are called greenhouse gases The other greenhouse gases in the earth's atmosphere are methane, chlorofluorocarbons, and nitrous oxide.

INCREASE IN THE ABUNDANCE OF GREENHOUSE GASES

The amount of carbon-di-oxide in the atmosphere has increased from 280 ppm (parts per million) to 350 ppm in the last hundred years (Fig 2). This increase is primarily on account of burning of fossil fuels and deforestation About half the carbon-di-oxide released in the atmosphere is absorbed by the oceans and the rest contributes to an increase of about 1.5 ppm per year. It is expected that the carbon-di-oxide content of the atmosphere will reach 60

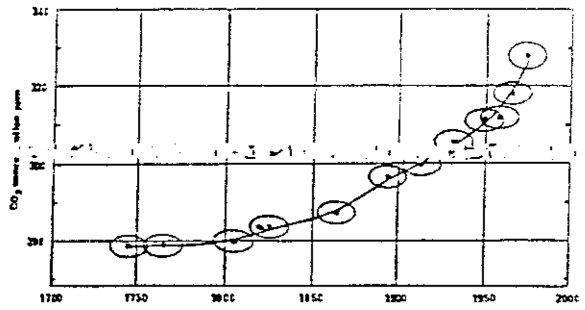

Fig 2 Atmospheric CO_2 concentrations measured in glacier ice formed during the last 200 years

Proceedings of the 26th Annual Convention and the Seminar on "Global Change" held during 15-17, March 1990, Indian Geophysical Union
Hyderabad INDIA (1991)

ppm by the middle or end of the next century depending upon the rate of fossil fuel use. The amount of methane in the atmosphere has increased from 0.8 ppm to 1.7 ppm in the last hundred years (Fig.3). The methane increase is attributed to increase in rice farming, fossil fuel burning and cattle. The amount of chloroflurocarbons in the atmosphere has been increasing at the rate of 5% per year in the last thirty years. These substances are used in refrigerators, air conditioners, aerosols, and solvents. The production of chloroflurocarbons has been restricted by the 1989 Montreal protocol since it causes a reduction of ozone in the stratosphere

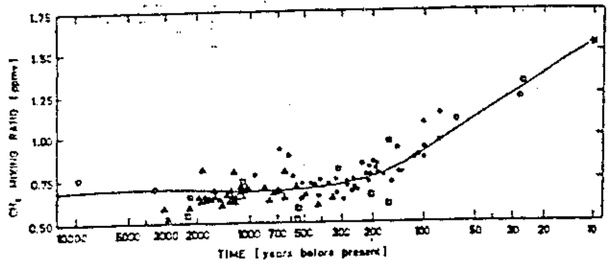

Fig 3 CH_4 mixing ratios measured in air trapped in ice cores

EFFECT ON CLIMATE

The increase in the abundance of greenhouse gases will increase the trapping of infrared radiation in the atmosphere. This should cause global warming if all the other factors affecting climate of the earth do not change. If the surface temperature of the earth increases this will increase evaporation and hence the water vapour content of the atmosphere and will enhance the greenhouse effect. The increase in water vapour in the atmosphere can cause an increase in cloudiness. An increase in cloudiness can cause extra warming or cooling of the surface

This is because clouds reflect solar radiation (and hence can cool the surface) and also trap infra-red radiation from the surface (and hence can warm the surface). Oceans occupy most of the earth's surface and hence influence the climate of the earth strongly. Oceans possess a large thermal inertia and therefore can delay global warming. The oceans absorb a lot of carbon-di-oxide and hence can control climate. Can we predict how these complex interactions between water vapour, clouds and ocean will respond to the increased trapping of infrared radiation by greenhouse gases? Climatologists use the basic conservation laws of physics and the computational power of supercomputers to predict the effect of increase in greenhouse gases. Climatologists have studied in great detail the effect of increase in carbon-di-oxide from 300 ppm to 600 ppm on the earth's climate. The car bon-di-oxide content of the atmosphere is expected to reach 600 ppm by the year 2080. The other greenhouse gases such as methane and chloroflurocarbons are more effective than carbon-di-oxide, because they absorb infrared radiation in the wavelength region 8 to 12 microns (one micron is one millionth of a meter) where other gases do not absorb. The amount of these gases can be converted to equivalent amount of carbon-di-oxide for the purpose of simplification of analysis. The equivalent amount of carbon-di-oxide in the atmosphere will reach 600 ppm by the year 2030.

RESULTS OF NUMERICAL SIMULATIONS

The simplest numerical model used to simulate the effect of doubling of carbon-di-oxide is the radiative-convective model. In this model the variation of temperature with height is calculated assuming radiative equilibrium. If the temperature profile so calculated is greater than the moist adiabatic lapse rate in any region, then the temperature profile in that region is modified to moist adiabatic lapse rate. This is known as convective adjustment. A review of 17 radiative-convective models by Schlesinger and Mitchell (1987) indicates that the global surface temperature can change by 0.5 to 4°C on account of the doubling of the concentration of carbon-di-oxide. There is such a large difference in the prediction of different models on account of the different assumptions made in these models. Some of the assumptions are with respect of variation of water vapour content, lapse rate of the atmosphere, and variations in cloud (amount, type and height). One way to avoid making some of these assumptions is to model the dynamical and thermodynamical changes occurring in the atmosphere. This can be done by the numerical solution of the partial differential equations governing the conservation of mass, momentum, energy and water vapour in the atmosphere. These models are usually three-dimensional. These are called General Circulation Models (GCM) and many groups around the world have developed such models. These models predict a temperature rise in the range 1.3 to 4.5°C on account of doubling of carbon-di-oxide content of the atmosphere from 300 ppm to 600 ppm. There is a large difference in the predictions of different models on account of the differences in the manner in which they model clouds and ocean-atmosphere coupling. Mnanbe and Wetherlad (1980) have compared a model with fixed clouds and another with variable clouds (internally determined) and indicate that both models predict a temperature rise of about 3°C on account of doubling of carbon-di-oxide. Washington and Mechl (1983) have also shown no difference in a model with fixed clouds and another with variable (internally determined) clouds

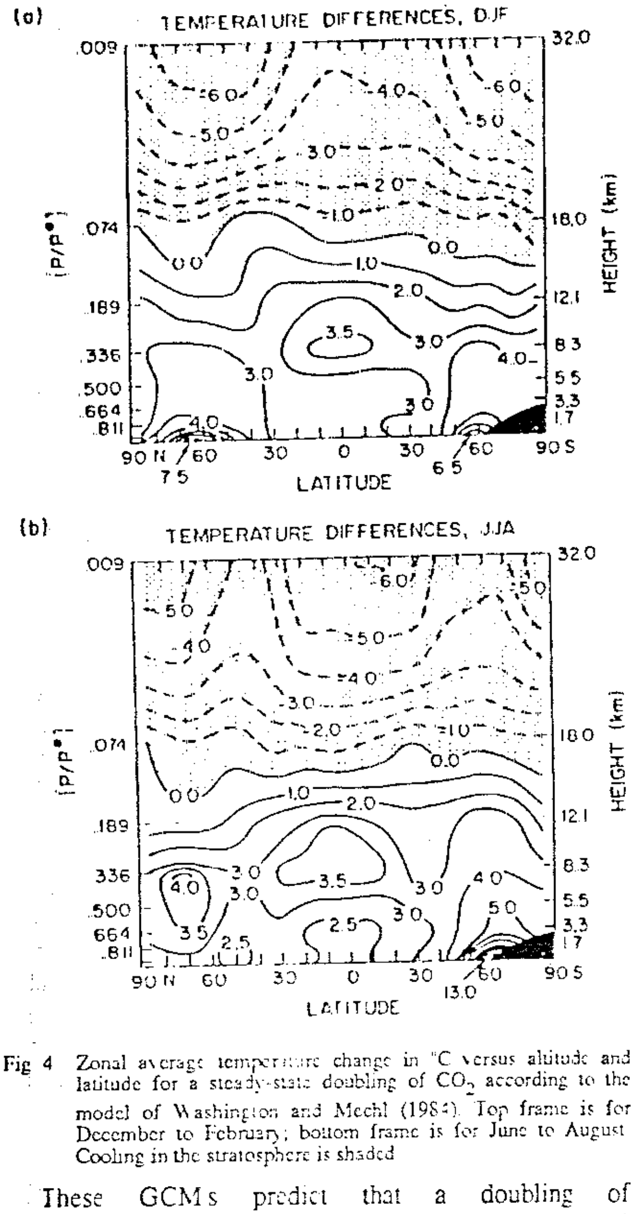

Fig 4 Zonal average temperature change in °C versus altitude and latitude for a steady-state doubling of CO_2 according to the model of Washington and Meehl (1984). Top frame is for December to February; bottom frame is for June to August. Cooling in the stratosphere is shaded

These GCMs predict that a doubling of carbon-di-oxide will increase the global annual precipitation by 3 to 13% Global warming will also cause an increase in evaporation Manabe and Wetherlad (1980) predict that soil moisture will increase equatorward of 35° latitude and decrease poleward of 35° latitude A decrease in soil moisture will cause an adverse impact in agricultural yields. The variation of global warming with latitude and altitude as predicted by Washington and Meehl (1984) is shown in Fig 4. We find that warming is more in polar region than in the tropics. This is on account of ice-albedo feedback Ice reflects most of the solar radiation (i.e., high albedo). When ice melts and becomes water, the latter absorbs most of the solar radiation Hence there is a large increase in surface temperature. Atmospheric layers above 10 km cool because as the amount of greenhouse gases increase more radiation is emitted to space by the layers above 10 km.

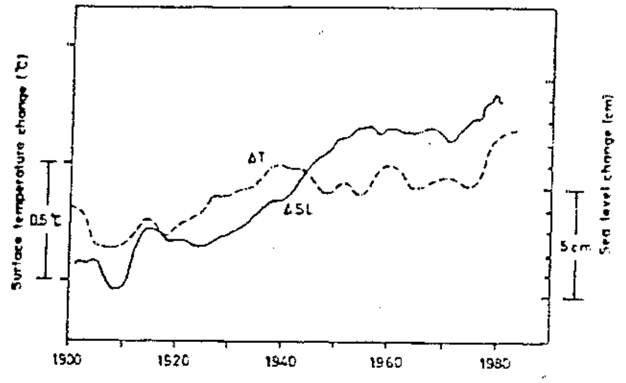

Fig 5 Comparison of changes in the global mean sea level with the global mean surface temperature

CONSEQUENCES OF GLOBAL WARMING

The most obvious effect of global warming is the rise in sea-level (Fig 5) The sea level will rise by about 15 cm for every degree rise in global surface temperature The changes in ice-sheets of Greenland and Antartica will tend to counterbalance and hence not contribute substantially to rise in sea level. A catastrophic collapse of the west Antarctic ice sheet might occur if the global warming exceeds 4°C This can cause a sea level rise of 5 meters in 200 years A gradual and monotonic rise in sea level will cause a disruption of human settlements near the coastline Countries such as Maldives and Bangladesh will be subject to large scale flooding There is, however, sufficient time for these nations to make contingency plan in such an eventuality. In tropical regions, the number and intensity of cyclones may increase.

There is no firm evidence to show that the increase in carbon-di-oxide and climatic change will have an adverse impact on different ecosystems The increase in carbon-di-oxide concentrations will increase the yield of major food and fibre crops The increase will be in the range of 10 to 50% The crops in the central regions of large continents will be subject to moiture stress and hence may contribute to a reduction in crop yields in these regions Paleoclimatic evidence indicates that a warmer earth will result in a wetter climate in the tropics and a drier climate in the interior of large continents The prediction of general circulation models as regards regional climate is not reliable because their resolution is too coarse

CONCLUSIONS

A global warming on account of increase in greenhouse gases of more than 1°C can be expected by the middle of the next century. This global warming can have adverse impact on agriculture and human settlement if the global warming is much more than 1°C. Present climate models are not in a position to resolve whether the global warming will be small (around 1°C) or large (around 4°C). By the beginning of next century, satellite and ground observations should indicate whether global warming is above natural climatic variations.

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