REPRODUCTIVE COMPETITION AND BEHAVIOURAL CASTE DIFFERENTIATION IN THE NEOTROPICAL WASP POLISTES VERSICOLOR (HYMENOPTERA:VESPIDAE)

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SUMMARY

Behavioural caste differentiation into Sitters, Fighters and Foragers is demonstrated in the neotropical, primitively eusocial wasp Polistes versicolor using the technique of multivariate statistical analysis of time activity budgets of individually identified animals. While the basic pattern of social organisation in this species is similar to that reported for the old world primitively eusocial species, Ropalidia marginata and R.cyathiformis, an important new result is that the queens of the two pre-emergence colonies studied are Fighters while the queen of the post-emergence colony studied is a Sitter. Because worker-brood genetic relatedness is expected to be higher in post-emergence colonies compared to pre-emergence colonies, we argue that this result is another line of evidence supporting our hypothesis relating Sitter queens with low reproductive competition and Fighter queens with high reproductive competition.

INTRODUCTION

Social insects have become very attractive model systems for the study of reproductive competition, a prime theme of Sociobiology. (For recent reviews see Fletcher and Ross 1985; West-Eberhard 1979; 1981). It is now becoming clear that even in species with no morphological caste differentiation such as primitively eusocial wasps, there exists what might be called a behavioural caste differentiation (Gadagkar and Joshi 1983; 1984; Strassmann et al 1984; a similar phenomenon has been documented in primitively eusocial bees, see Brothers and Michener 1974). We have detected such a behavioural caste differentiation by statistical analysis of the patterns in which the members of a colony distribute their time between different behaviours. In two old world primitively eusocial wasps Ropalidia marginata (Gadagkar and Joshi 1983) and R.cyathiformis (Gadagkar and Joshi 1984) the members of a colony can be classified into 3 behavioural castes namely, Sitters, Fighters and Foragers.

The Sitters are wasps that spend a large proportion of their time sitting and grooming but seldom leave the nest or interact aggresively with their nestmates. Fighters are very alert to external disturbances by spending a large proportion of their time in sitting with their antennae raised and are also the most aggressive animals in their interactions with nestmates. Foragers are animals that spend a large proportion of their time away from the nest often returning with food or building material. They also show the least amount of aggressive interactions with their nestmates. An important feature of these studies is that the queen is also included in the analysis but data on egg-laying are not. The behavioural caste of the queen is therefore

not obvious prior to the analysis. As a matter of fact in all R.marginata colonies studied so far (Gadagkar and Joshi, 1983; Chandrashekara and Gadagkar, unpublished observations) the queen is a sitter while in all R.cyathiformis colonies studied so far (except in single foundress, pre-emergence colonies) the queen is a Fighter (Gadagkar and Joshi, 1984; Gadagkar, unpublished observations). We have interpreted this difference in the behavioural caste of the queen as an indicator of the levels of reproductive competition prevailing in the colonies (Gadagkar and Joshi, 1982; Gadagkar and Joshi, 1984; Gadagkar, 1985a). All the R.marginata colonies studied so far have been monogynous. In this species the queen almost never indulges in overt dominance behaviour by means of contact aggression but appears to exert queen control by means of more ritualised displays (or probably by means of pheromones). The non egglayers however show a dominance hierarchy in which the queen does not figure at all (Gadagkar 1980). This places R.marginata at a relatively advanced level in the evolution of sociality in the "polygynous family" route of social evolution (West-Eberhard,1978) and predicts a relatively low level of reproductive competition between queen and workers (Gadagkar and West-Eberhard, unpublished manuscript; Gadagkar and Joshi 1984). In contrast,some of the R.cyathiformis colonies we have studied have been polygynous. In both monogynous and polygynous colonies of R.cyathiformis, the queens actively indulge in overt dominance behaviour by means of contact aggression. The queen(or principal egg layer) is at the top of this dominance hierarchy (Gadagkar and Joshi 1982). Reproductive division of labour appears to be occassionally absent for, we have observed the same animals to forage as well as lay eggs (Gadagkar and Joshi 1982). Unlike in R.marginata, males are

sometimes produced early in the colony cycle and again, unlike in R.marginata, stay on with the colony for their entire life. Cannibalism is of frequent occurrence (Gadagkar, unpublished observations). All these facts taken together place R.cyathiformis at a relatively primitive or early stage in the "polygynous family" route to sociality (West-Eberhard 1978) and predicts a relatively high level of reproductive competition between queen and workers (Gadagkar and West-Eberhard, unpublished manuscript; Gadagkar and Joshi 1982; 1984).

One more line of evidence linking low reproductive competition with Sitter Queens and high reproductive competition with Fighter Queens is the fact that even in R.cyathiformis, the queen (egg layer) turns out to be a Sitter in single foundress pre-emergence colonies. In other words, when she has no other nestmates to interact with, even an R.cyathiformis queen is a Sitter and not a Fighter (Gadagkar and Joshi, 1984). In this paper we demonstrate the existence of a similar behavioural caste differentiation into Sitters, Fighters and Foragers in the Neotropical social wasps Polistes versicolor. In addition we provide a new line of evidence linking low reproductive competition with Sitter queens and, high reproductive competition with Fighter Queens.

MATERIALS AND METHODS

Study Animal

This study was conducted on three monogynous nests (two pre-emergence nests and one post-emergence nest) built on the eaves of sheds on Barro Colorado Island in Panama, (9 09'N, 79 51'W) (see Leigh et al 1982 for a detailed treatment of the ecology of this island) between November 1980 and February 1981. In all 240 h of observation

were conducted. All the adults of each colony were individually identified by marking with spots of coloured paint without removing them from the nest. New animals were marked upon their emergence and a census of all the animals present on each nest was taken at about 0600 hrs or after 2000 hrs, a time at which all the animals were expected to be on the nest. We found no evidence of animals shifting from one nest to another as reported by Itô (1984) for the same population. In all, sufficient data were available for 28 animals which are included in this analysis. Details regarding the nests and the animals associated with them are in Table 1.

Sampling methods

The sampling methods used in this study were adapted from Altmann (1974) as described earlier (Gadagkar and Joshi, 1983; 1984). Briefly, ad libitum sampling was used for obtaining preliminary information regarding the behaviour of the species and for constructing an ethogram. Instantaneous scanning of the behavioural states of all animals in a colony was repeated at a large number of randomly chosen times. Rare behaviours such as dominance and subordinate behaviour, bringing and exchange of food and building material etc., were quantified in separate 5 minute sessions, begun at randomly chosen times, during which every act of each of the chosen set of rare behaviours by every animal was recorded. All observations were made between 0800 and 1800 hours. Data were recorded in a pre-coded form on coding sheets in an 80 column format ready to be punched on computer cards. The data were analysed using the DEC 1090 computer facility at the Indian Institute of Science, Bangalore.

Table 1 Nests Studied, Animals associated with them and Periods of Observation.

Nest Code	Pre/Post Emergence	Code nos. of Associated Animals	Identity of Queen	Duration of Observation	No.of hours of Observation
J	Pre-Emergence	1-12	1	27 Nov 1980-3 Jan 1981	100
L	Pre-Emergence	13-18	13	22 Dec 1980-22 Jan 1981	80
M	Post-Emergence	19-28	19	12 Jan 1981-31 Jan 1981	60

Analysis of data

Analysis of data was performed as previously described (Gadagkar and Joshi, 1983; 1984). Briefly, data from the instantaneous scans were used to construct time activity budgets for each animal. Proportions of times spent in the six most common behaviours namely Sit and Groom, Raise antennae, Raise Wings, Walk, In cells and Absent from Nests were used for subsequent analysis. These behaviours accounted for (means± SD) 93.4 % of the wasps' time from 0600 to 1800 hours. Frequencies per hour of rare behaviours were computed from "all occurences of rare behaviours". The most frequent of these rare behaviours were Dominance display, Bring food, Snatch food, Lose food, Feed larva, Bring building material, Snatch building material and Lose building material. Our analysis is thus restricted to these. The names used for the sixteen behaviours for which data are presented in this paper are both self-explanatory as well as commonly used in studies of social insects. Besides, they have all been described previously (Gadagkar, 1980; Gadagkar and Joshi, 1983; 1984). They will therefore not be defined once again. Apart from these 16 behaviours, all instances of egg-laying seen during the observations were of course recorded and the queen was identified on the basis of this.. The proportions of time spent by each animal in each of the six common behaviours were subjected to principal components analysis (Anderberg 1973; Frey and Pimentel, 1978) as well as hierarchial cluster analysis (DeGhett, 1978).

RESULTS

The time activity budgets in Fig.1 show clearly that the 28 animals showed wide variation in the manner in which they allocated their time between the six behaviours, Sit and Groom, Raise antennae, Raise wings, Walk, In cells and Absent from Nest although they all spent a very similar amount of time in these six behaviours put together. In order to see if there are clusters of wasps showing particular types of behaviour patterns the method of principal components analysis is employed. The results of this analysis (Table 2) show that the first principal component accounts for 78.37% of the variance with Absent from Nest as its dominant term (Weightage = 0.8183). The second principal component accounts for 19.80% of the variance and has Sit and Groom as its dominant term (Weightage = -0.7254). Thus the first two principal components together account for 98.17% of the variance and we are therefore amply justified in considering only the first two principal components. Other advantageas of using the method of principal components analysis are discussed in Gadagkar and Joshi (1984). A two dimensional plot employing the first two principal components shows clearly that there are four clusters of wasps (Fig 2). A very similar (although not completely identical) set of clusters is obtained using the method of hierachial cluster analysis (Fig 3).

Interpretation of the clusters

We give below a biological interpretation of the clusters based on their mean behavioural profiles as well as by comparison of the patterns seen in *R.marginata* and *R.cyathiformis* (Gadagkar and Joshi, 1983; 1984). The results of the principal components analysis suggest that clusters I and II are characterised by low proportion of time in

Legend to Figure 1

Time activity budgets of 28 individually identified wasps from two pre emergence and one post emergence colony for six behaviours. The animals are arranged according to their colony affiliations begining with the queen of each colony. Thus animals 1-12 belong to colony J with 1 as their queen, animals 13-18 belong to colony L with 13 as their queen and animals 19-28 belong to colonu M with 19 as their queen.

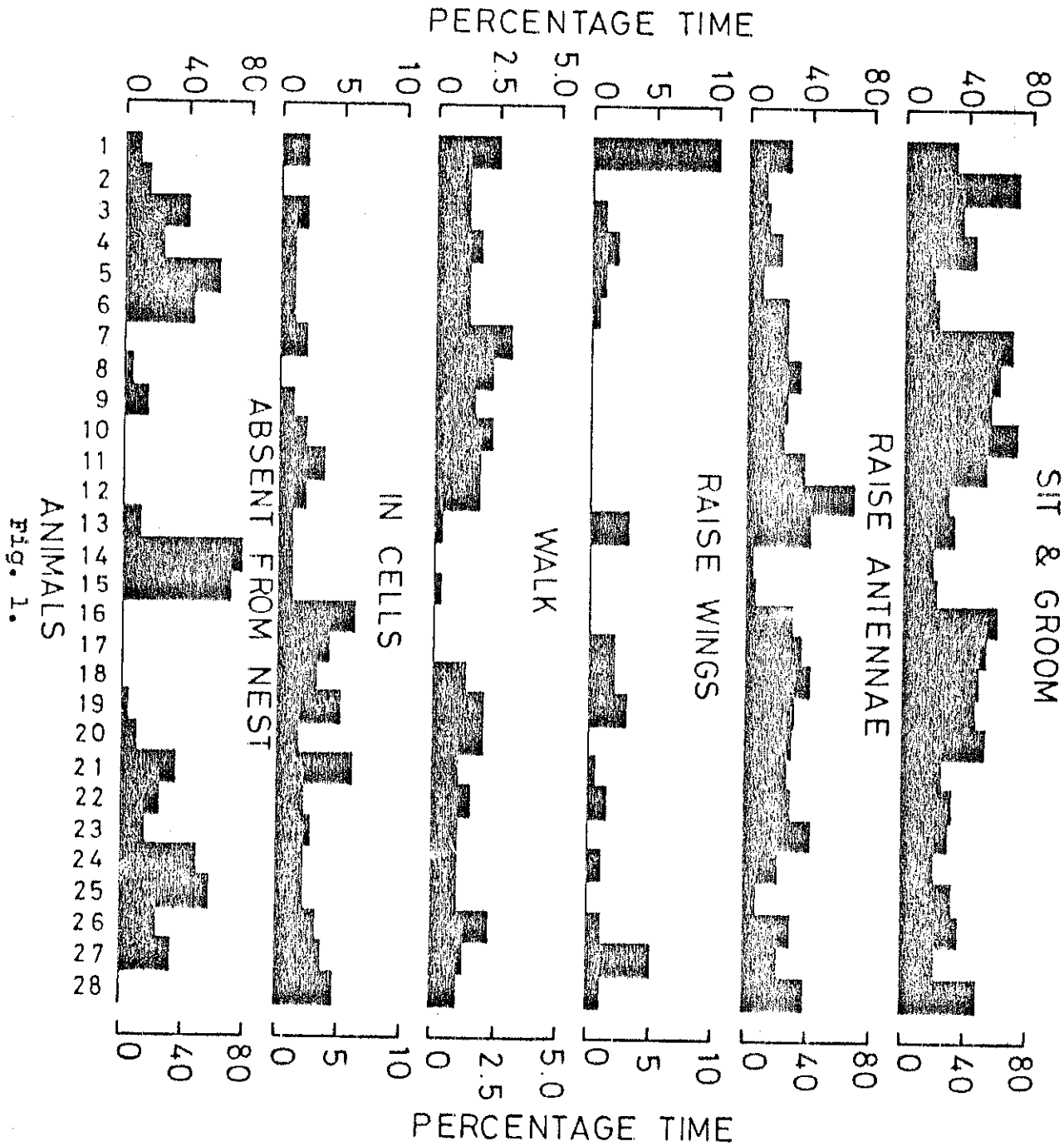
PERCENTAGE TIME
SIT & GROOM
RAISE ANTENNAE
RAISE WINGS
WALK
IN CELLS
ABSENT FROM NEST
ANIMALS
PERCENTAGE TIME

Fig. 1.

Table 2 Eigen vectors of principal components, Eigen values, percentage of variance, and cumulative percentage of variance.

Behaviour	Principal Components		
	1	2	3
Sit and Groom	-0.4602	-0.7254	0.4386
Raise Antennae	-0.3437	0.6749	-0.5974
Raise Wings	-0.0035	0.0471	-0.4255
Walk	-0.0115	-0.0055	-0.0275
In cells	-0.0158	0.0253	-0.1633
Absent from Nest	0.8183	-0.1239	0.4923
Eigen Value	0.0774	0.0196	0.0014
Percentage of Variance	78.37	19.80	1.43
Cumulative percentage of Variance	78.37	98.17	99.60

Legend to Figure 2

Behavioural castes of P.versicolor. 28 wasps from two pre emergence colonies and one post emergence colony are shown as points in the co-ordinate space of the first two principal components. The cluster boundaries are confirmed by the criteria of nearest centroid. Wasps 1 and 13 are the Queens of the two pre emergence colonies and wasp 19 is the Queen of the post emergence colony. Animals 2 and 12 are examples of occassional excentrics that we find in most colonies in all species whose significance we do not still understand.

denotes centroid.

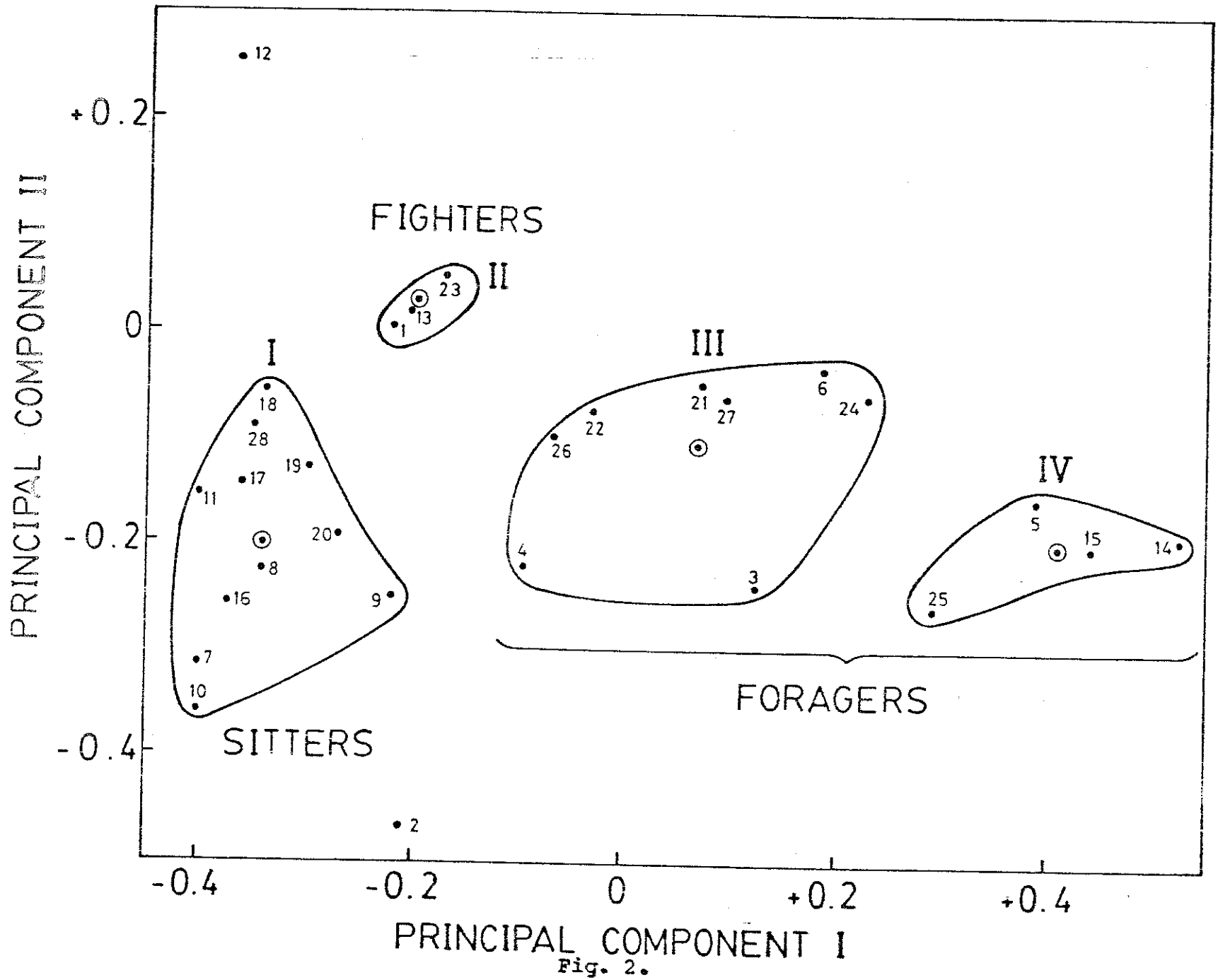
PRINCIPAL COMPONENT II
+0.2
0
-0.2
-0.4
FIGHTERS
II
I
III
IV
SITTERS
FORAGERS
12
23
13
1
18
28
19
17
11
20
8
16
9
7
10
2
6
21
27
24
22
26
4
3
5
15
14
25
-0.4
-0.2
0
+0.2
+0.4
PRINCIPAL COMPONENT I

Fig. 2.

Legend to Figure 3.

Hierarchial cluster analysis. Time activity budgets as shown in Fig.1 are used to calculate the pearson product moment corelation as an index of similarity between all pairs of wasps. The dendrogram is constructed using the single linkage algorithm.

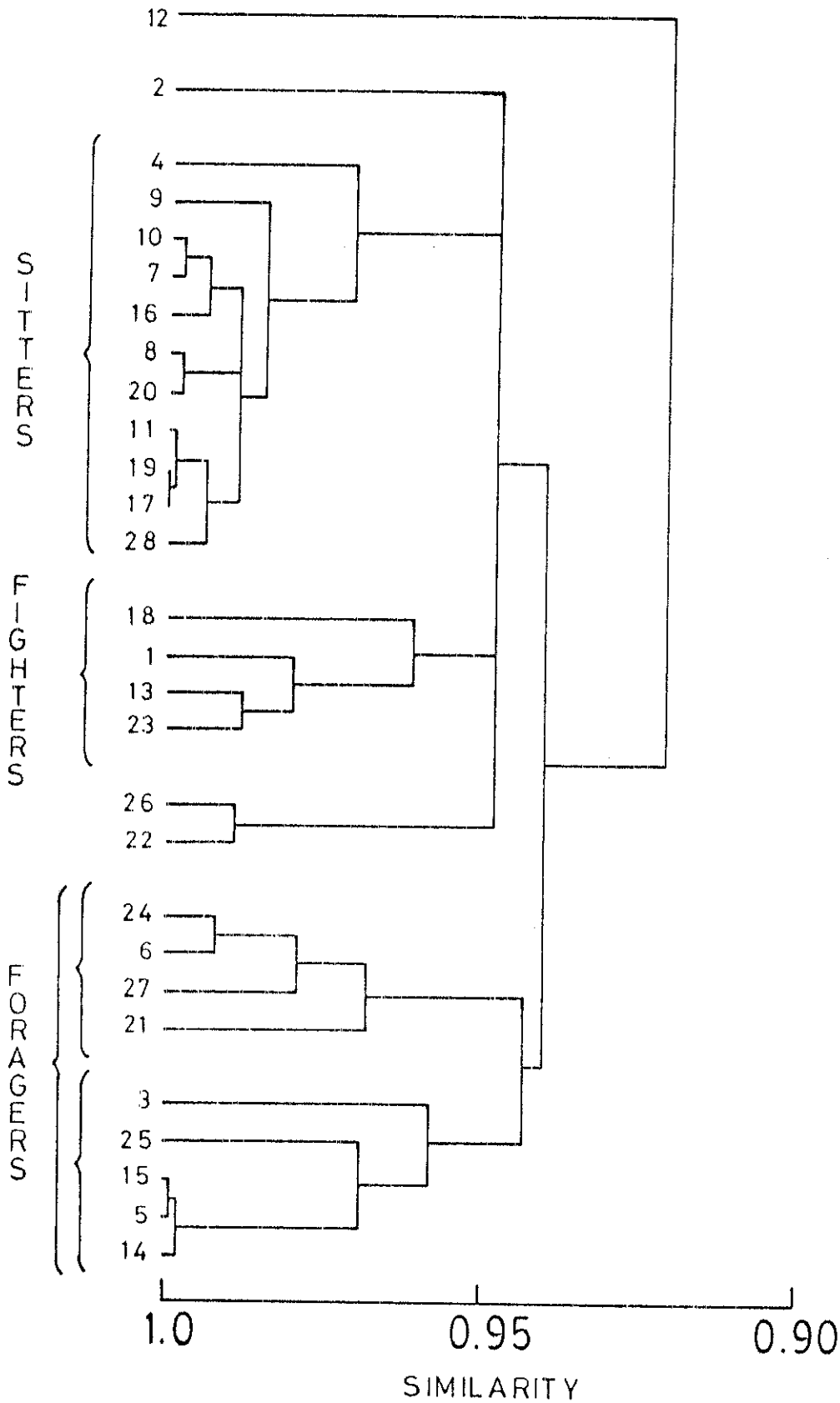
12
2
4
9
10
7
16
8
20
11
19
17
28
SITTERS
18
1
13
23
FIGHTERS
26
22
24
6
27
21
FORAGERS
3
25
15
5
14
1.0
0.95
0.90
SIMILARITY

Fig. 3.

being absent from the nest and conversely clusters III and IV are characterised by high proportions of time being absent from nest. This is because absent from the nest has the highest positive weightage in the first proncipal component and clusters I and II have negative amplitudes while clusters III and IV have higher amplitudes. Similarly cluster I is expected to be characterised by a high proportion of time in Sit and Groom. This pattern is confirmed by a computation of mean behavioural profiles of the clusters (Fig 4). Cluster I which is characterised by the highest proportion of time in Sit and Groom is termed Sitters. Cluster II is characterised by high proportions of time in Raise Antennae and Raise Wings. In other species that we have studied this is strongly correlated with a high frequency of dominance bahaviour. In these colonies of P.versicolor there was hardly any instance of dominance behaviour except in colony J where the queen (who belongs to cluster II) exhibited all the 12 cases of dominance behaviour seen (frequency = 0.97 per h). For this reason and in conformity with other studies we term this cluster Fighters. Clusters III and IV are characterised by high proportions of time in being absent from the nest and contain the only animals who were ever seen to bring food to the nest. These clusters are thus termed Foragers.

A number of behaviours which are suficiently rare so as not be included in the time activity budget analysis have been studied by computing the frequencies with which these behaviours were performed per hour per animal. Such data for the three behavioural castes (fig.5) show a number of interesting paterns. Foragers, Sitters and Fighters show increasing frequencies of Dominance display in that order. Sitters and Fighters were never seen to bring food but were

Legend to Figure 4.

Mean behavioural profiles (time activity budgets) of Sitters, Fighters and Foragers.

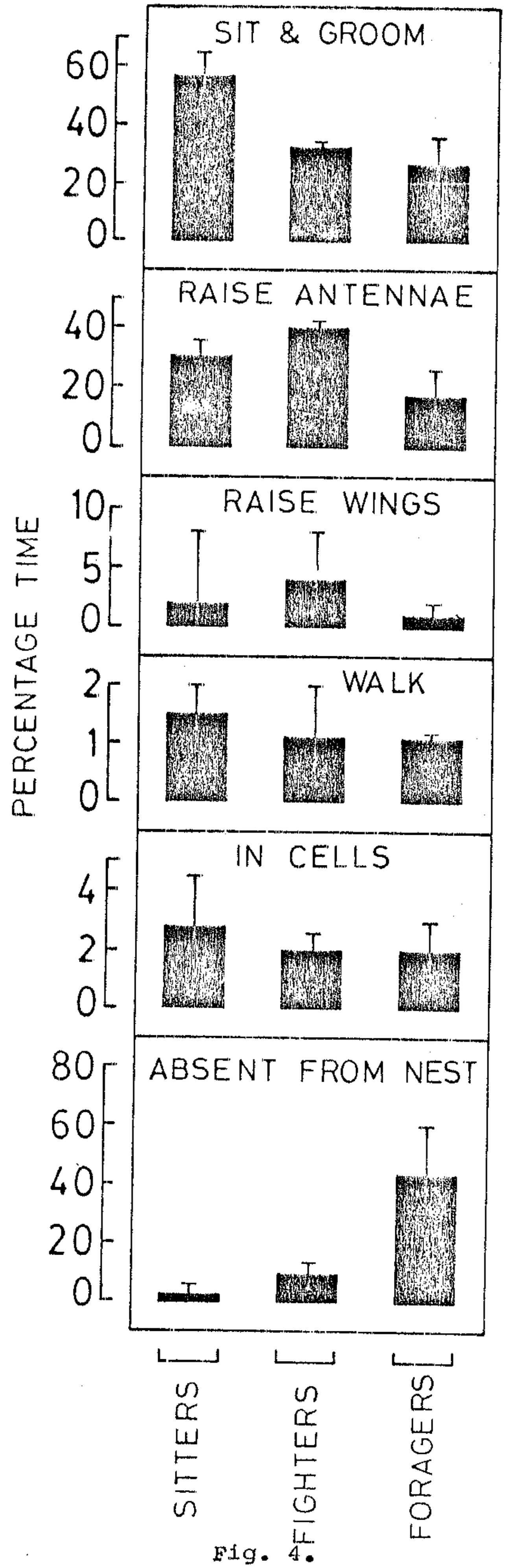

Fig. 4.

Legend to Figure 5.

Frequencies per hour per animal are shown for the three behavioural castes, Sitters, Fighters and Foragers for eight rare behaviours.

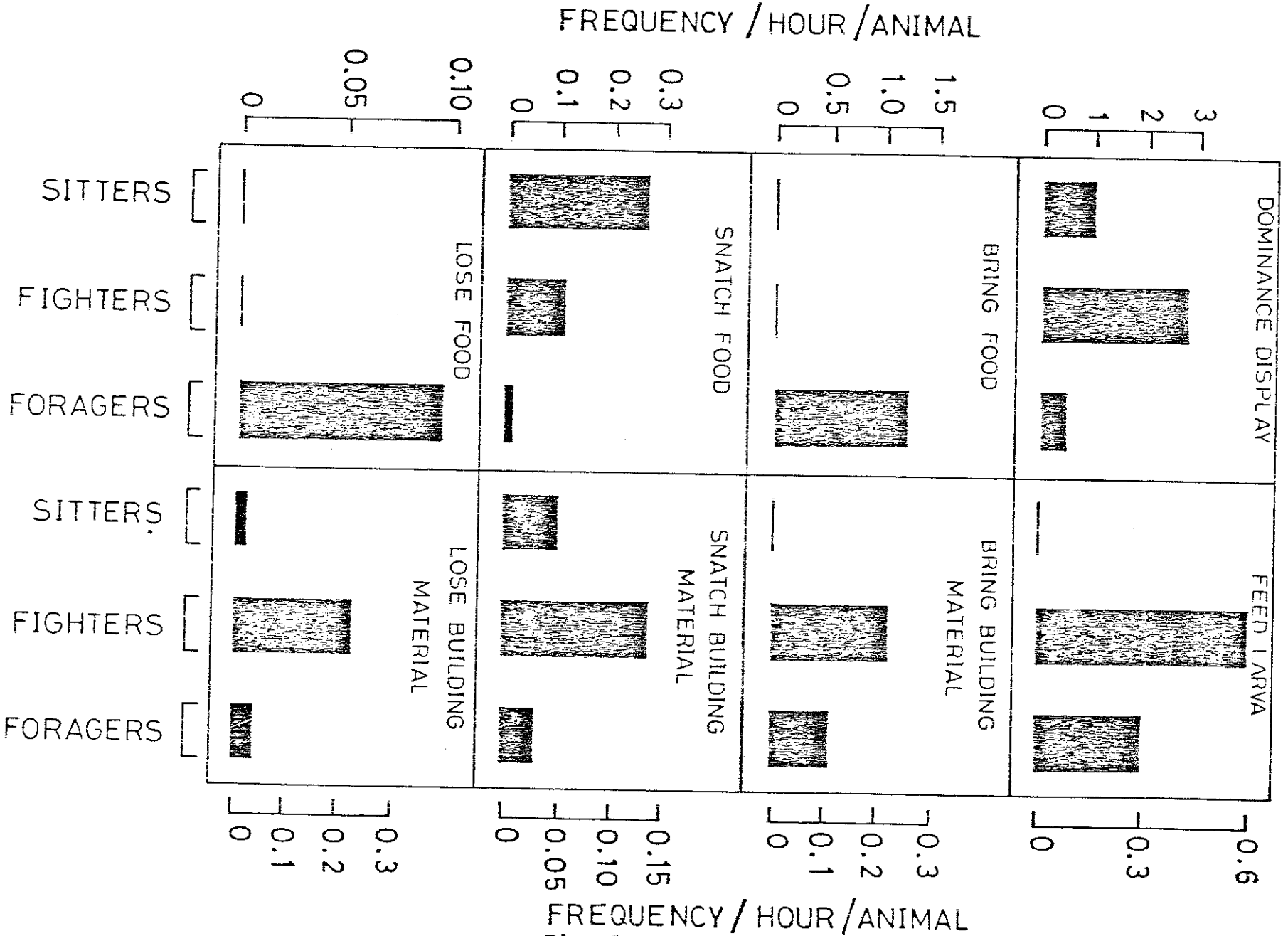
FREQUENCY / HOUR / ANIMAL
DOMINANCE DISPLAY
BRING FOOD
SNATCH FOOD
LOSE FOOD
FEED LARVA
BRING BUILDING MATERIAL
SNATCH BUILDING MATERIAL
LOSE BUILDING MATERIAL
SITTERS
FIGHTERS
FORAGERS
SITTERS
FIGHTERS
FORAGERS
FREQUENCY / HOUR / ANIMAL

Fig. 5.

certainly involved in snatching food from Foragers. Such food snatched from Foragers was never seen to be lost to other animals. Every act of losing food to another animal was only seen in a Forager. Both Fighters and Foragers were involved in feeding larvae but the Sitters were not. Fighters were conspicuously involved in matters connected with building material. They showed the highest frequency of bringing building material, snatching building material as well as losing building material. This is consistent with several reported cased where queens are known to bring only (or predominantly) building material to the nest (eg. Polistes fuscatus and P.canadensis: West-Eberhard 1969; P.gallicus: Pardi 1951; Mischocyttarus drewseni: Jeanne 1972) but apparently contradictory to Strassmann and Meyer's (1983) observation that a discriminant function that correlated negatively with foraging for pulp distinguished between pre queens and non queens in P.exclamans.

DISCUSSION

Multivariate analysis of time activity budgets of 28 individually identified P.versicolor wasps from 3 naturally occuring nests shows the presence of three behavioural castes which we have called Sitters, Fighters and Foragers. The pattern obtained here is almost identical to what has been reported earlier with two old world tropical wasps namely, R.marginata (Gadagkar and Joshi, 1983) and R,cyathiformis (Gadagkar and Joshi, 1984). In contrast to the latter species there are two clusters among what we call Foragers. We do not know if there is indeed any real difference in the social organisation of this species which leads to this pattern. We can see no interesting predictions or conclusions that can be made from this

difference and therefore do not wish to pursue the question at this time.

More interesting conclusions can be drawn by looking at the position of the Queens in the P.versicolor behavioural caste system. Of the three colonies studied two were pre-emergence colonies and the queens of both these colonies are Fighters (Animal 1 of colony J and Animal 13 of colony L). The third colony was a post emergence colony and the queen of this is not a Fighter but a Sitter (Animal 19 of colony M). It is important to know that this third colony however did have a fighter (Animal 23 of colony M) although the queen herself was not a Fighter. While it is true that we have so far studied only two pre emergence colonies and one post emergence colony, the difference in the position of the queen in the behavioural caste system begins to provide further evidence linking low reproductive competition with Sitter queens and high reproductive competition with Fighter queens. Our reasoning is as folows: pre emergence colonies are expectred to consist of a group of foundres females who are most likely to be Sisters (Bornais et al 1983;Post and Jeanne 1982; Ross and Gamboa 1981; for recent reviews see Gadagkar 1985b; Gamboa et al 1986). One of these foundresses assumes the role of the queen and the others become workers. If the workers (cofoundressess) are full sisters of the queen then they rear a brood of neices and nephews(average relatedness is equal to o.375). If the workers (cofoundressess) are less closely related to the queen then ofcourse they will rear brood that is even less related. The relatedness between workers and brood can thus be never greater than 0.375. In a post emergence colony on the other hand, subordinate cofoundresses begin to die out and the worker force is progressively replaced by the queen's daughters. When such

replacement is complete the workers consists entirely of daughters and thus rear a brood of brothers and sisters (average genetic relatedness is equal to 0.5). If the replacement is incomplete then the average genetic relatednes between workers and brood will lie somewhere between 0.375 and 0.5. We do not expect multiple matings by the queen to differentially effect worker brood genetic relatedness in pre and post emergence colonies. In general therefore worker-brood genetic relatedness will be higher in post-emergence colonies when compared to that in pre emergence colonies. Other things being equal workers in pre emergence colonies should hence be much less altruistic and should be selected to seek reproductive options of their own. Workers in post emergence colonies on the other hand should be relatively more altruistic and less likely to seek reproductive options of their own. In short we believe that queens face a greater threat of reproductive competition from their nestmates in pre-emergence colonies that in post- emergence colonies.

While interpreting the Sitter queens of R.marginata and the Fighter queens of R.cyathiformis we have argued that queens would tend to be Sitters if they face relatively little reproductive competition from their nestmates while they tend to be Fighters if they face relatively high levels of reproductive competition. The result that the queens of the two pre emergence Polistes versicolor colonies were Fighters and that the queen of the post emergence colony was a Sitter clearly buttresses our speculation.

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