COLONY FISSION IN A SOCIAL WASP

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ABSTRACT

A colony of *Ropalidia cyathiformis* with eleven adult females experienced a period of high levels of aggression and continuously decreasing brood culminating in about half the adults leaving the parent nest to found a new colony nearby. The group that stayed back at the parent nest which we call the Loyalists and the group that left which we call the Rebels were rather evenly matched in numbers and age distribution. The Loyalists were relatively more dominant compared to the Rebels and the latter appeared to have behaved in a highly coordinated manner even before the actual colony fission. The fission resulted in an immediate increase in brood production in both the parent and the new nests thereby increasing the genetic fitness of both groups. We argue first that this phenomenon is a reflection of reproductive competition and second that it provides strong circumstantial evidence for kin recognition and communication.

INTRODUCTION

PRIMITIVELY eusocial insects are of special interest from the point of view of social evolution because, while they exhibit sterility and the extreme degrees of altruism characteristic of the highly eusocial ants and honey bees, they also show a remarkable degree of flexibility. The role of an individual in a colony is not fixed but appears to be determined by the social environment it finds itself in. Groups of females (foundresses) come together, relegate reproduction to the most dominant individual and the rest remain subordinate and sterile, working to feed and care for the offspring of the dominant female[1-3]. If the dominant female dies or is removed, however, one of the subordinate females ceases to work, and begins to lay eggs and thereby becomes the queen[4-7]. Since at least some of the subordinate females are potentially capable of becoming queens such a situation might be expected to foster a great deal of reproductive competition among nest mates.

Ropalidia, a genus representing such a primitive level of social evolution is abundantly distributed in India[8-12]. Here there appears to be scope for even greater levels of reproductive competition. On the one hand colonies are perennial and long lived and must therefore often outlive their queens providing opportunities for queen replacements. On the other hand new colonies are initiated throughout the year[12]. As a result, females emerging at anytime must have a finite chance of becoming queens.

During observations of two species, *R. marginata* and *R. cyathiformis* we noticed several behaviour patterns suggestive of reproductive competition. On one occasion, an individual became very aggressive and challenged the queen by biting, nibbling and chasing her. In this case both the queen and her challenger were missing the following day and the next most dominant female began to lay eggs[4]. We imagine however that such challengers must occasionally succeed in themselves becoming replacement queens. On several occasions we have seen single females go off on their own to start new nests. Most of such nests initiated by a lone founderess however fail after a short while. It appears therefore that emerging females have two reproductive options before them, (i) to leave the parent nest and initiate new nests on their own so that immediate egg laying is possible although the risk of failure is probably high, (ii) to stay on at the parent nest and challenge the queen; here the probability of succeeding in becoming the next queen is probably small but there is little chance of immediate nest failure; a certain amount of inclusive fitness on account of caring for siblings and other close relatives must therefore often be guaranteed.

Jeanne[13] has classified the sub-family polistinae into 2 behavioural categories namely those where new colonies are founded by one or more queens without the aid of a swarm of workers and those where new colonies are founded by a swarm of workers accompanying one or more queens. *R. cyathiformis* is believed to belong to the first group[13]. During longterm observations of a colony of *R. cyathiformis* however, we once saw a female behave in a manner most remarkable for a non-swarming species. She left her parental nest to initiate a nest but did so along with about half the adults on the parent nest who continued to remain subordinate and work for the new nest. The new nest subsequently became as large as the parent nest and produced several progeny. In this paper we analyse the behaviour of these wasps before and after the colony fission and interpret their behaviour in the context of reproductive competition, in an attempt to understand the causes and consequences of the colony fission as well as its probable mechanism.

MATERIALS AND METHODS

The study was conducted on a colony of *R. cyathiformis* that had built a nest on a metallic pole in the grounds of the Indian Institute of Science, Bangalore. All adults were marked with spots of coloured paint for individual recognition. Behavioural data were recorded using, the methods of instantaneous scanning and 'All occurrences of rare behaviours'[14]. (For further details see Gadagkar and Joshi[15,16]).

The data from the scans were used to assess the extent to which different animals coordinated with each other their times of being on and away from the nest. Yule's association coefficient between animals i and j given by the formula[17].

$$Y_{ij} = \frac{ad - bc}{ad + bc}$$

where a = probability that both animals i and j are on the nest

b = probability that animal i is on the nest and animal j is away from the nest

c = probability that animal i is away from the nest while animal j is on the nest

d = probability that both animals i and j are away from the nest

was chosen because it gives a value ranging from -1 to $+1$ irrespective of the actual time budgets. A value of $+1$ therefore means that the two animals synchronised their behaviour to the maximum extent possible within the constraints of their time-activity budgets while -1 indicates the maximum possible avoidance. A value of zero is equivalent to i and j choosing to stay on the nest or be away from it independent of each other.

The frequencies of the dominant and subordinate behaviours were computed from the 'all occurrences of rare behaviours' data. A nest map showing the location of brood in different stages of development was maintained on every other day. Observations were made between 19 February and 21 June 1980 for a total period of 225 hr during which 282 instantaneous scanning sessions in addition to *ad libitum* observations were performed between 5 a.m and 5 p.m. The data were analysed on the DEC 1090 computer facility at the Indian Institute of Science.

RESULTS

History of the colony and social organisation before fission

A colony of *R. cyathiformis* that had built a nest of 3 combs on a metallic pole at the Indian Institute of Science has been the focus of intensive study. Having shown that the three combs really belonged to a single colony[18], we made a detailed study of the social organization of this species[16,19]. Although the latter study included 8 colonies most of the animals studied belonged to the same colony with three combs which was described earlier[18] and is also the focus of the present study. The behaviour of individual wasps comprising this colony with reference to social organization has been described at length[16]. Briefly, we have constructed time activity budgets for individually identified animals and subjected these time activity budgets to multivariate statistical analyses such as principal components analysis and hierarchical cluster analysis. Using data on proportions of time spent in (i) sitting and grooming, (ii) sitting with raised antennae, (iii) sitting with raised antennae and raised wings, (iv) walking, (v) being in the cells of the nest and (vi) being away from the nest, we have shown that the animals belonged to three distinct behavioural clusters namely Sitters, Fighters and Foragers. Sitters spend a large proportion of their time sitting and grooming, Fighters spend a large proportion of their time sitting with raised antennae as well as show a high frequency of dominance behaviour while Foragers are characterised by a large proportion of time being spent away from the nest. A detailed discussion of the description and interpretation of such a behavioural caste differentiation is given elsewhere[16].

The colony fission

This colony had 11 adult female wasps and no males on 29 May 1980. On 30 May 1980, 5 female wasps left the parent nest to initiate a new nest about a meter away. Henceforth we will refer to the group that stayed back at the parent nest as Loyalists. It is significant that the two groups were rather evenly matched in numbers and age composition. The 6 Loyalists were 72, 58, 24, 10, 5 and 3 days old respectively at the time of fission while the 5 Rebels were 58, 37, 19, 17 and 8 days respectively (table 1). The Loyalists consisted of one Fighter, 2 Foragers and 3 Sitters while the Rebels had one Fighter and 4 Foragers (table 1). The Fighter among the Loyalists (animal No. 2) was the queen before the colony fission and continued to be the queen after the fission. The Fighter among the Rebels (animal No. 17) became the queen on the newly initiated colony.

Brood levels

The total brood (Eggs + larvae + pupae) on the parent nest had declined over time and reached its lowest point on 30 May, the day of colony fission. After the colony fission however, the brood on both the new nest as well as the parent nest increased quite rapidly (figure 1). We believe that the colony fission itself was the cause for the sudden increase in brood levels both because of the dramatic change in brood levels immediately following the colony fission and also because other factors such as a change in

Table 1 *Caste and age composition of loyalists and rebels*

Animal code No.[16]	Loyalist/ Rebel	Behavioural caste	Age in days at the time of fission
2	Loyalist	Fighter	72
6	Loyalist	Forager	58
16	Loyalist	Forager	24
21	Loyalist	Sitter	10
23	Loyalist	Sitter	5
24	Loyalist	Sitter	3
7	Rebel	Forager	58
12	Rebel	Forager	37
17	Rebel	Fighter	19
19	Rebel	Forager	17
22	Rebel	Forager	8

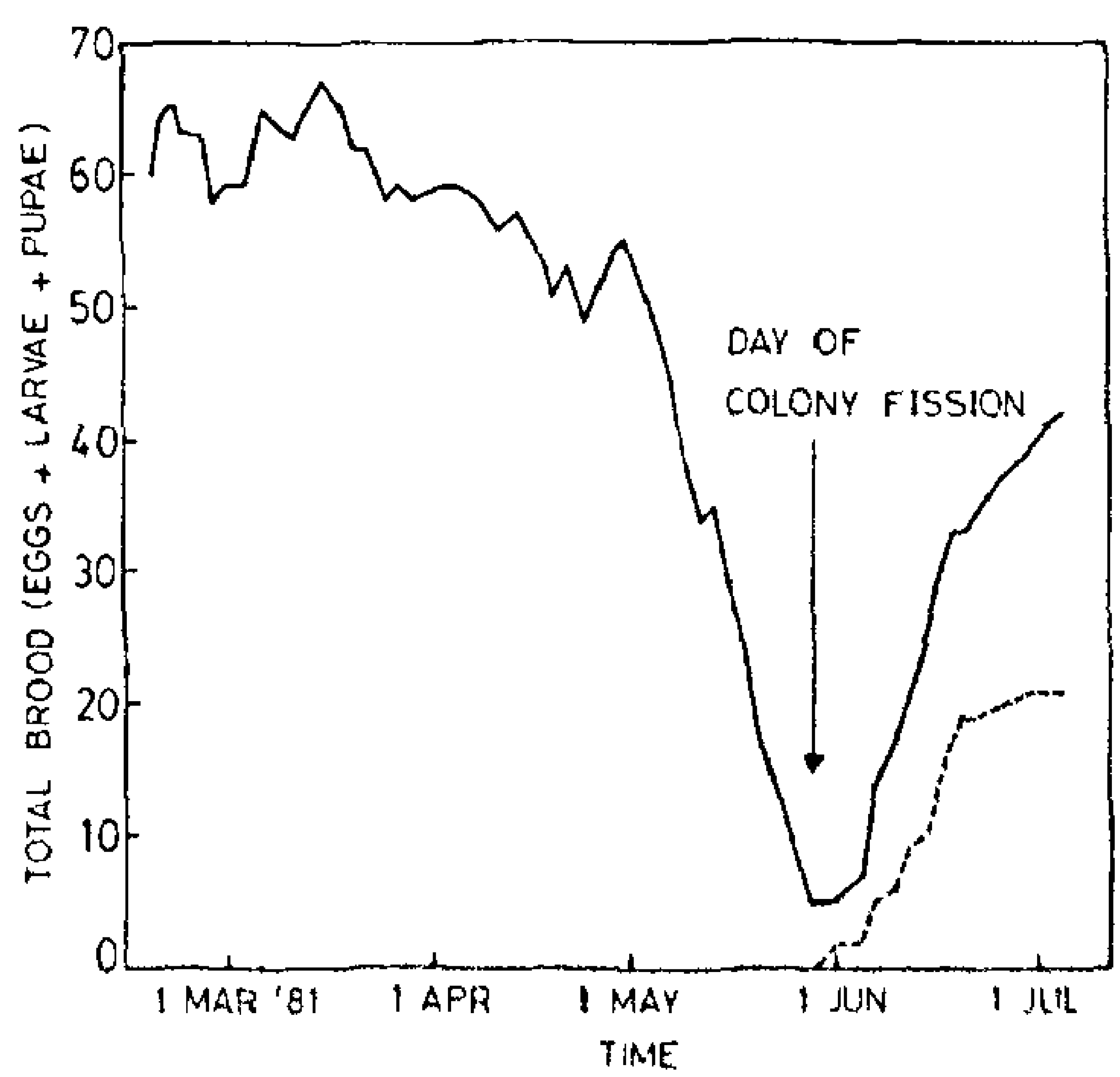

Figure 1. Total brood (eggs + larvae + pupae) on the three combs of the parent nest until 30 May, the day of colony fission (shown by arrow). After the fission, total brood on both parent nest and new nest put together (solid line) and brood on new nest alone (broken line) are shown.

environmental conditions can easily be ruled out. Several other colonies of *R. cyathiformis* in the vicinity did not show any such pattern of decrease in brood levels till 30 May 1980 followed by a sudden increase. It appears therefore that the colony fission increased the genetic fitness of both the queens. The inclusive fitness of the remaining animals in both groups also must have increased as long as they were at least marginally related to the queens.

Dominance Behaviour

There was no clear cut dominance hierarchy[3] on this colony at about the time of the split. It is therefore not possible to say for example if all the Rebels were subordinate to all the Loyalists. Nevertheless, mean frequencies per animal per hour of dominance and subordinate behaviour[16] within each group reveal interesting patterns (Figure 2). Among both Loyalists and Rebels, dominance as well as subordinate behaviour was relatively high before and declined after colony fission. Before colony fission the Loyalists showed a greater frequency of dominance behaviour than the Rebels while with subordinate behaviour the pattern was reversed. When these dominance behaviour frequencies are broken up, depending on towards whom they are directed (figure 3), we see that a high level of dominance behaviour was shown by the Loyalists towards the Rebels and 'others' while low frequencies were shown by the Rebels towards Loyalists and 'others'. No dominance behaviour was recorded between one Loyalist and another or between one Rebel and another. Here 'others' refers to wasps that were present before colony fission but had disappeared by the day of the split permitting therefore no classification into Loyalists or Rebels. One might thus argue that the Loyalists were the dominant group and the Rebels the subordinate group.

Coordinated behaviour patterns

As an index of coordination within each group before the split, we calculated Yule's association coefficients between pairs of wasps. We asked the question whether wasps within a group were

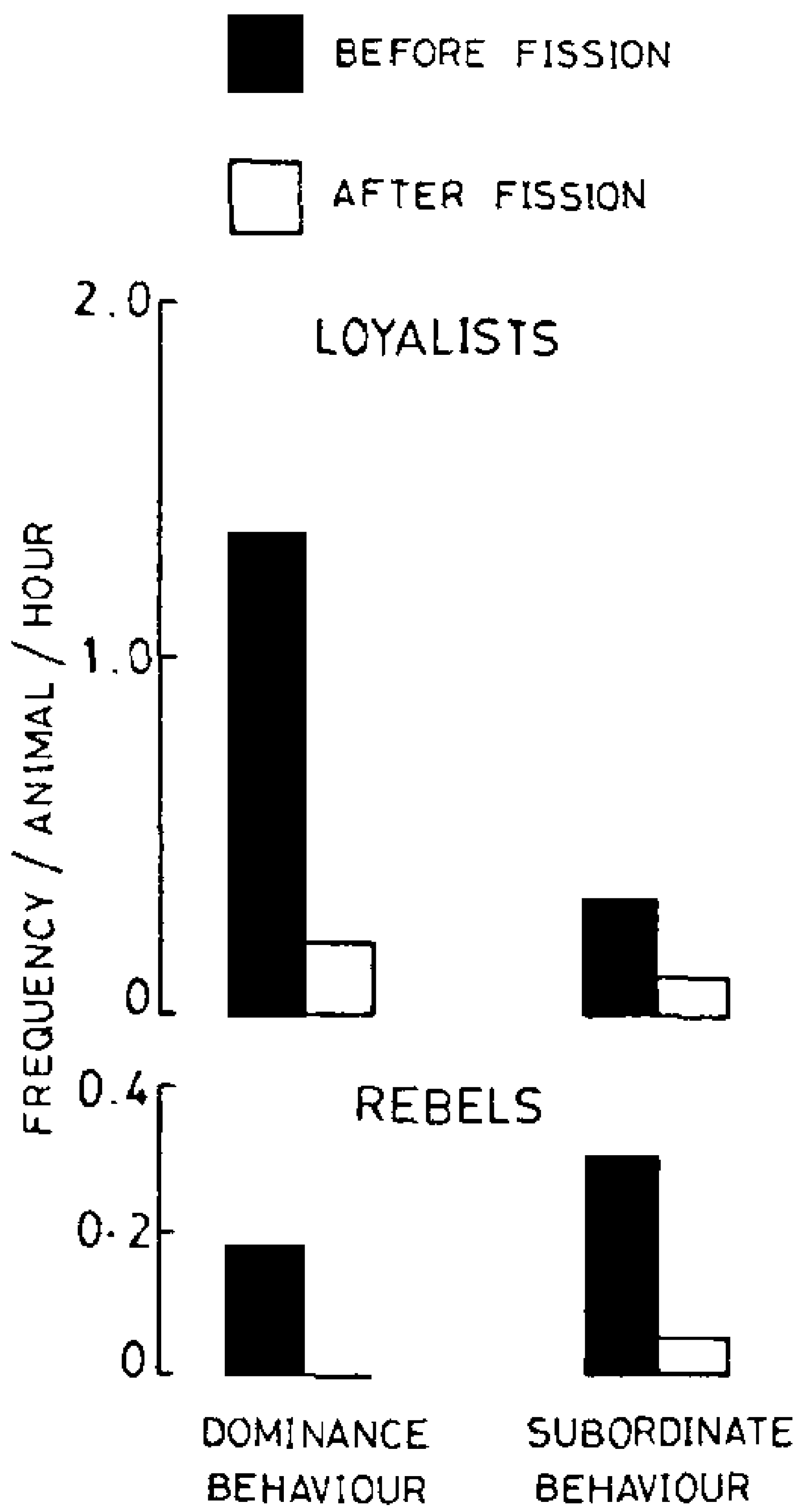

Figure 2. Mean Frequencies of dominance behaviour and subordinate behaviour per ànimal per hour shown by Loyalists (upper pannel) and Rebels (lower pannel) before (shaded bars) and after (open bars) the colony fission.

coordinated among themselves; for instance, did they synchronise their trips away from the nest?

The Rebels had a mean association coefficient of 0.69 with 5 pairs of wasps having a value of + 1. When the pairs were chosen such that wasp *i* was a Loyalist and wasp *j* was a Rebel the mean association coefficient was − 0.26 with 4 pairs of wasps having a value of − 1. The mean association coefficient of 0.69 among Rebels was found by Monte Carlo calculations to be significantly greater than zero ($P < 0.01$) (standard deviation = 0.10) suggesting that the Rebels synchronised among themselves their times of being on or away from the nest. Similarly the value of − 0.26 for Rebel Loyalist pairs was found to be significantly less than zero ($P < 0.05$) (standard

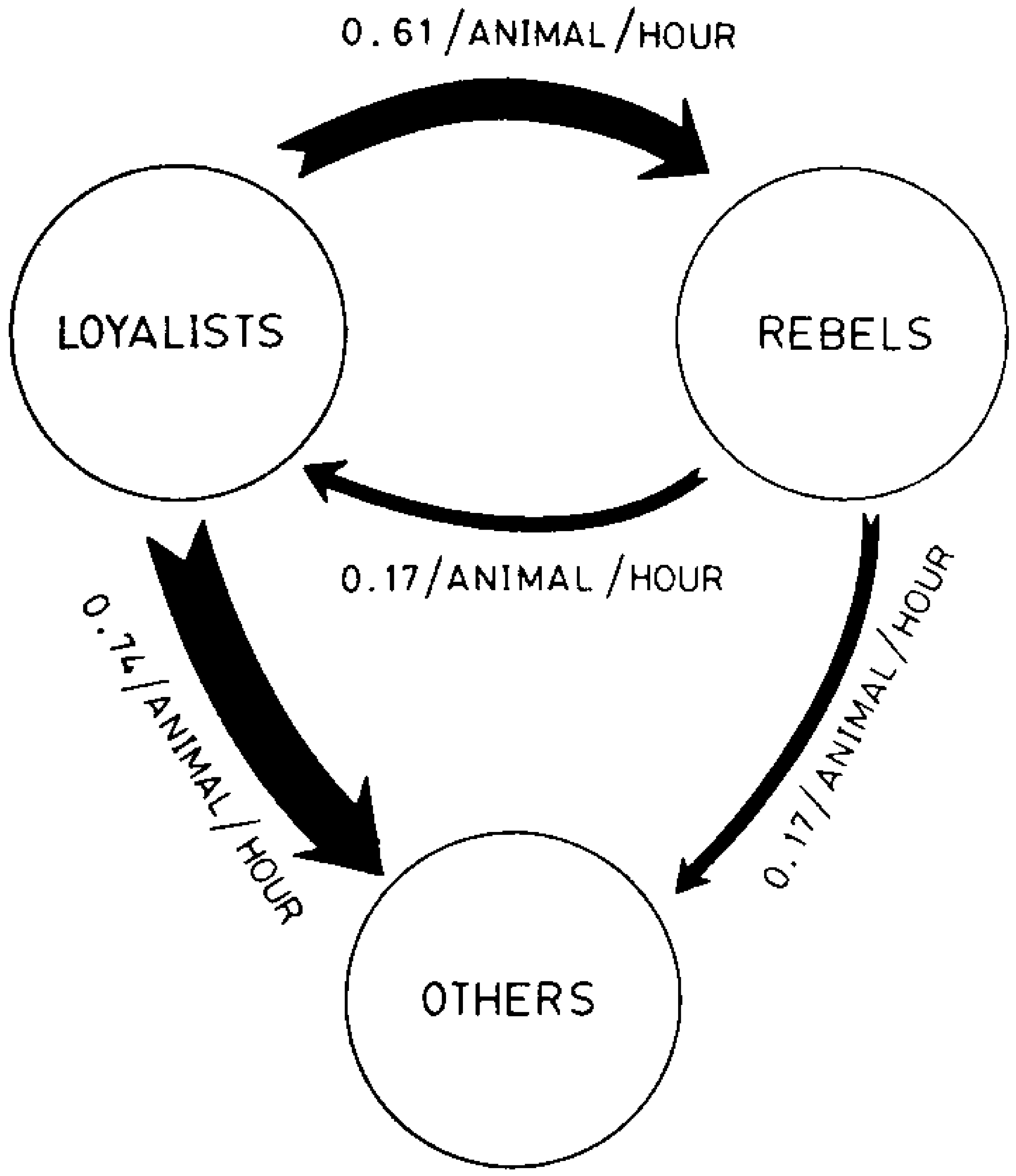

Figure 3. Break up of the frequency of dominance behaviour/animal/hr shown by Loyalists and Rebels towards each other and towards 'others'. Here 'others' refer to animals that were present before colony fission but had disappeared by the day of the fission and therefore could not be classified into Loyalists or Rebels.

deviation = 0.11) suggesting that the Loyalists and Rebels avoided each other.

DISCUSSION

We would like to interpret our results along the following interesting, (though speculative) lines. First we interpret the high level of aggression seen before the colony fission as a reflection of reproductive competition among the nest mates. Second, we suggest that the high level of aggression before the fission was responsible for the low level of brood. In short we suggest that a high level of reproductive competition led to high levels of aggression, decreasing thereby the efficiency of brood rearing in the nest. Such a situation we believe led to the emergence of a Rebel group that was largely subordinate but remained highly coordinated within itself, avoided members of the other group and eventually left the parent nest to initiate one of its own, an act that increased the inclusive fitness of both the Rebels and the Loyalists. Strassmann[20] studied a North American Social wasp *Polistes exclamans* where subordinate workers had the choice of staying with the queens' main nests or joining worker-initiated satellite nests and showed that as in the case of our study worker behaviour patterns increased inclusive fitness of both the queens and workers.

In our study the two groups were rather evenly matched in terms of the number of individuals and their age composition. Besides the Rebels appear to have behaved in a highly coordinated manner even before the fission. These two facts in our opinion suggest that individual recognition and communication must have played an important role in the process of colony fission.

There is growing evidence of individual recognition in social insects. In Polistes wasps, Gamboa and his group[21] have demonstrated that in a process that resembles imprinting newly emerged, wasps learn certain chemical cues from their natal nest or brood by means of which they later distinguish their nest-mates from non nest-mates. There is no evidence however for recognition of genetic relationship. In honey bees on the other hand, the environmental and genetic components of the recognition system have been well separated. Getz and Smith[22] showed that honey bee workers can distinguish between full and half sisters raised in the same hive. However, in these experiments each experimental bee was allowed to habituate to its full sisters before testing for ability to distinguish between full and half sisters. It is thus not clear if the bees can distinguish between full and half sisters in the same hive once they have been allowed to habituate to both classes of sisters. If kin recognition is involved in the colony fission of *R. cyathiformis* that we have studied, it must be of a kind that is not dependent on differential habituation. We do have reasons to believe that there may have been more than one genetic line among the eleven wasps at the time of the fission. This is because several females had simultaneously been laying eggs in this colony in the past[16-18]. We therefore believe that our results are highly suggestive of recognition of different genetic lines within a colony.

Communication by chemical means has been established by Jeanne[23] in a situation somewhat similar to our own. Polybiine wasps studied by Jeanne[23] initiate new nests by swarming, that is, the mass emigration of one or more queens and a number of workers to found a new colony. Swarming is also seen when a nest is abandoned and all the wasps move on to a new nest site. Jeanne[23] showed that swarming wasps of *Polybia sericea* apply a chemical substance by dragging their gasters over twigs and leaves and that these scent marks are later used by the swarm to orient itself. Although *R. cyathiformis* is classified among the non-swarming Vespids[13] it is possible that the 5 Rebel wasps may have used a communicatory mechanism similar to that of swarming *Polybia sericea*.

The conclusions drawn in this paper regarding the causes (reproductive competition and aggression) and mechanisms (kin recognition and communication) of colony fission are admittedly speculative. This is especially because only one instance of colony fission has been studied. But colony fission is an unpredictable event and even when a colony under study splits the departing adults may not always build a nest nearby. It may on the other hand be possible that colonies grown in large enclosures may undergo fission and produce daughter colonies within the enclosure. *Ropalidia* is an ideal system to exploit colony fission towards answering questions regarding evolution of sociality as well as communication and individual recognition. Its primitive level of sociality coupled with the occurrence of small and open, yet sometimes polygynous nests and the presence of such complex strategies as colony fission which increases the fitness of both groups is perhaps unparalleled.

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