Rank orders and division of labour among unrelated cofounding ant queens

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Young, unrelated queens may cooperate in colony founding (pleometrosis) in many species of ants. Whereas the founding queens of many 'advanced' species rely completely on body reserves in order to rear their first young, queens of the ponerine *Pachycondyla inversa* forage for food. In founding associations, only one queen specializes in this risky task. Here we show that the division of labour is strongly affected by aggressive interactions between cofounding queens: the dominant remains in the nest and guards the brood, whereas the subordinate is forced to leave and forage. The frequency of queen antagonism increased with the duration since food was last added to the foraging arena. Egg-laying rates did not differ significantly between nest-mate queens, but dominant queens destroyed and ate some of the eggs laid by subordinates.

Keywords: division of labour; colony founding; pleometrosis; social competition; Formicidae; *Pachycondyla*

1. INTRODUCTION

The elaborate division of labour in insect societies is a particularly impressive example of kin-selected cooperation. Some females forego reproduction and take over risky tasks such as colony defence and foraging. By thus helping a close relative increase the number or survival rate of its offspring they indirectly also maximize their own fitness (Hamilton 1964). Given the importance of relatedness between helper and the recipient of the help in inclusive fitness theory, it is not surprising that most mature insect societies are characterized by a significant non-zero relatedness among nest-mates (e.g. Bourke & Franks 1995; Crozier & Pamilo 1996) with the exception of some unicolonial or highly polygynous species (e.g. Kaufmann *et al.* 1992; Goodisman & Ross 1998). In contrast, relatedness is apparently not a major factor in the evolution of joint colony founding among ant queens (pleometrosis). In many species, unrelated queens work together when excavating a common nest burrow and rearing their first young (Hagen *et al.* 1988; Strassmann 1989; Sasaki *et al.* 1996). Once the first workers have eclosed, the cofoundresses typically become intolerant of each other, begin to fight and only a single queen survives per colony (Hölldobler & Wilson 1990; Heinze 1993; Choe & Perlman 1997; Bernasconi & Strassmann 1999). Jointly founded societies grow faster than founding colonies with a single queen and are thus believed to have an advantage in territorial contests with neighbouring colonies (e.g. Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Rissing & Pollock 1987; Sommer & Hölldobler 1995).

During the founding phase, queens of most species exclusively use tissue from their wing muscles, stored fat and protein reserves in order to rear their first young (claustral founding). In several species, however, founding queens leave their nests and forage (semi-claustral founding). The case of the desert leaf-cutter ant

Acromyrmex versicolor is of special interest because here unrelated queens cooperate during semi-claustral founding. Queens have to forage for leaves in order to cultivate a symbiotic fungus and cooperatively founded colonies appear to be more successful in initiating their fungus garden (Cahan & Julian 1999). One queen specializes in foraging while the other queens stay in the nest (Rissing *et al.* 1989). Once a forager, the queen remains in this task and is punished if she stops foraging (Rissing *et al.* 1996). Task allocation in *A. versicolor* does not appear to be regulated by aggressive interactions and it was suggested that, because the group succeeds or fails as a unit in competition with other such groups, an individual queen should be indifferent as to whether she takes over the more or less risky tasks (Rissing *et al.* 1989). Fighting about task allocation was selected against as it would decrease the success of the colony as a whole. Group selection has occasionally been invoked in order to explain pleometrosis in general (Dugatkin *et al.* 1992; Mesterton-Gibbons & Dugatkin 1992; but see Nonacs 1993) and the division of labour without social dominance in *A. versicolor* has been interpreted as a particularly strong case of group-selected cooperation (Wilson 1990; Dugatkin 1997; but see Pollock 1994).

Queen cooperation during semi-claustral founding has also been reported in Neotropical ponerine ants in the *Pachycondyla villosa* complex (Trunzer *et al.* 1998). As in *A. versicolor*, one queen per group specializes in foraging but, as we show here, the division of labour among *Pachycondyla* queens is achieved by aggression. The dominant queen coerces the subordinate into foraging and the frequency of these attacks increases with the time since food was last brought into the nest.

2. MATERIAL AND METHODS

Our study species was a ponerine ant belonging to the *P. villosa* group which is presumably identical to a taxon originally described by Smith (1858) as *Ponera inversa*. This taxon was later combined with *Pachycondyla villosa* var. *curvinodis* to form *Pachycondyla villosa inversa* (Emery 1904, 1911). Morphological, chemical and genetic

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analyses have suggested that *Pachycondyla villosa inversa* and *Pachycondyla villosa villosa* are two separate species (Lucas *et al.* 1999; Kolmer & Heinze 2000). A detailed revision of this species group has been prepared by C. Lucas, D. Fresneau and J. H. C. Delabie. Here, we preliminarily refer to the studied taxon as *Pachycondyla inversa*. Our studies are part of a collaborative project with these French and Brazilian researchers.

Colonies of *P. inversa* were collected from knot holes in cocoa trees and rotten cocoa pods at Centro de Pesquisas do Cacau, CEPLAC, Itabuna, Bahia, north-eastern Brazil in March 1998. The ants were housed in the laboratory in 19 cm × 19 cm × 9 cm plastic boxes with a plaster floor with two connected 3 cm × 3 cm × 1 cm chambers in the plaster covered by a glass plate serving as a nest. They were kept at room temperature and fed with live crickets and diluted honey at variable intervals (every one to six days). The plaster was regularly watered in order to maintain humidity.

All queens in the experimental colonies were individually marked with dots of enamel paint on the gaster for observations of behaviour. Behaviour was observed directly in 1 h sessions or after recording on video from April to September 1998. All instances of aggressive interactions (antennal boxing and biting), brood care, foraging, guarding the nest entrance, inactivity on or near the brood pile and nest maintenance were noted. In addition, we observed the behaviour in three groups each with two and three queens in more detail by focal and/or scan sampling (Altmann 1974) with a total observation time of 5–9 h per colony ('focus colonies'). Behavioural observations were ended after the eclosion of the first six workers. Egg-laying rates were determined by time-lapse video recordings over a total observation time of 168–336 h per colony, totalling 1440 h. Most queens were killed and dissected after the end of the observations.

We calculated the total duration of a certain behaviour for each queen during each hour of observation for statistical analysis and compared these data by Friedman's ANOVA or Wilcoxon matched-pairs test (Sachs 1992).

3. RESULTS

Out of a total of 52 founding colonies without workers, 26 had one queen (50%), 14 had two queens (27%), ten had three queens (19%) and two had four queens (4%). Queens engaged in aggressive interactions in all 26 pleometrotic associations. One individual attacked another by violent antennation, whereas the latter assumed a crouching posture with retracted antennae and/or attempted to escape, e.g. by leaving the nest. Aggressive interactions between queens in the six focus colonies resulted in clear dominance hierarchies (tables 1 and 2). Approximately 49.9% (527 out of 1057) of all attacks in the three-queen groups and 64.6% (126 out of 195) in the two-queen groups resulted in a clear winner–loser relationship. In the remaining interactions, the attacked queens did not react unmistakably to the attack. In none of the 1252 observed aggressive interactions did a queen that had previously shown clear submissive behaviour towards an attacker retaliate against the attack. Aggressive interactions continued after the emergence of workers until the end of our studies when approximately seven workers had eclosed. However, in mature colonies queen antagonism was only rarely observed (data not presented).

Table 1. Dominance interactions among cofounding queens in two-queen colonies of the ant *P. inversa*

(Only those interactions which resulted in a recognizable reaction by the ant attacked are included.)

founding colony	attacking queen	attacks against queen		total observation time (h)
		A	B	
PvII 21	A	—	65	5
	B	0	—	
PvII 129	A	—	44	5
	B	0	—	
PvII 190	A	—	17	7
	B	0	—	

Table 2. Dominance interactions among cofounding queens in three-queen colonies of the ant *P. inversa*

(Only those interactions which resulted in a recognizable reaction by the ant attacked are included.)

founding colony	attacking queen	attacks against queen			total observation time (h)
		A	B	C	
PvII 49	A	—	131	35	7
	B	0	—	76	
	C	0	0	—	
PvII 174	A	—	67	20	5
	B	0	—	44	
	C	0	0	—	
PvII 175	A	—	92	36	5
	B	0	—	26	
	C	0	0	—	

The frequency of aggressive interactions was significantly higher in three-queen groups (three two-queen groups, medians 6, 9 and 12 attacks h⁻¹, range 3–34 and total observation time 17 h and three three-queen groups, medians 26, 45 and 83 attacks h⁻¹, range 15–122 and total observation time 17 h) (Mann–Whitney *U*-test with medians, *n*₁ = *n*₂ = 3, *U* = 0 and *p* = 0.05). The return of low-ranking queens from the arena (see below) into the nest often initiated aggressive interactions between all three queens until the lowest ranking queen had again left the nest or at least moved to the nest entrance.

Subordinate queens generally performed foraging trips at a much higher frequency than dominant queens, whereas the latter rested with extended legs on or near the brood pile ('brood guarding'). The queens assuming the middle position in the hierarchy in three-queen groups also had frequencies of foraging between those of the two other queens. Observations in the six focus colonies corroborated these qualitative results. Only the dominant queens exhibited brood-guarding behaviour (Wilcoxon matched-pairs test for two-queen groups, *t* = 0.00 and *p* < 0.05 for each colony and Friedman's ANOVA for three-queen groups, χ^2 = 10, 10 and 8 and *p* < 0.02 for each colony) (table 3). Although all queens of focus colonies were occasionally observed outside the nest, low-ranking queens left the nest for significantly longer periods than high-ranking queens (two-queen groups, *t* = 0 and *p* < 0.02 in two groups and *t* = 4 and *p* = 0.09 in colony PvII 21 and Friedman's ANOVA for

Table 3. Time-budget (i.e. percentage of time spent in various types of behaviour) of queens in founding colonies in *P. inversa* (A, B and C denote queens of decreasing dominance status. Note that data for exact time-budgets were only collected in part over a shorter period of time than for foraging or for the determination of dominance hierarchies in tables 1 and 2. As some types of behaviour are not included in the table (e.g. resting), the totals do not add up to 1.00.)

founding colony	queen	brood guarding	brood care	nest maintenance	guarding nest entrance	total observation time (h)	foraging	total observation time (h)
PvII 21	A	0.284	0.179	0.023	0.002	5	0.069	7
	B	0.000	0.007	0.071	0.044		0.328	
PvII 129	A	0.333	0.100	0.038	0.006	5	0.037	8
	B	0.000	0.000	0.002	0.000		0.434	
PvII 190	A	0.211	0.150	0.000	0.140	6	0.099	8
	B	0.000	0.008	0.138	0.082		0.587	
PvII 49	A	0.435	0.148	0.000	0.000	6	0.001	9
	B	0.000	0.225	0.030	0.111		0.169	
	C	0.000	0.037	0.049	0.098		0.568	
PvII 174	A	0.157	0.086	0.000	0.000	5	0.073	6
	B	0.000	0.103	0.002	0.080		0.298	
	C	0.000	0.013	0.000	0.000		0.682	
PvII 175	A	0.163	0.234	0.000	0.011	5	0.006	7
	B	0.000	0.135	0.020	0.007		0.351	
	C	0.000	0.019	0.027	0.000		0.535	

three-queen groups, $\chi^2=17.2$, 11.6 and 0.65 and $p < 0.01$ for each colony). In only one out of 48 observation sessions of 1h each did a dominant queen spend more time outside the nest than a subordinate (PVII 21). The lowest ranking queens typically undertook less brood care than the higher ranking queens (table 3).

A positive correlation was found in the three three-queen groups between the frequency of dominance interactions and the time elapsed since the last addition of food (table 4). The failure to detect such a correlation in two-queen groups was probably due to the much lower aggression rate in these colonies (tables 1 and 2).

The egg-laying rates were extremely low and, therefore, probably did not differ between subordinate and dominant queens (table 5) (two-queen groups, median dominant queens 0.43 eggs day⁻¹, subordinates 0.27 eggs day⁻¹ and total observation time 600 h, Mann–Whitney *U*-test, $U=3.5$ and $p=0.663$ and three-queen groups, median dominants 0.29 eggs day⁻¹, subordinates 0.21 eggs day⁻¹ and total observation time 840 h, Kruskal–Wallis *H*-test, $\chi^2=0.90$ and $p=0.637$) or between queens in two- and three-queen groups ($U=14.5$ and $p=0.141$). However, dominant queens regularly attacked egg-laying subordinates and occasionally robbed and ate their eggs, while these behaviours never occurred in the opposite direction (Fisher’s exact test, two-tailed $p=0.0008$ and total observation time 1440 h). In order to escape attacks, subordinates were observed laying their eggs outside of the nest four times after having been attacked by the dominant queen. On one occasion an egg-laying subordinate was chased out of the nest by the dominant and attacked when attempting to return with a newly laid egg. A foraging worker later carried the egg into the nest without being attacked by the dominant queen.

Dissection of some of the queens at the end of the observations (both queens from each of the two two-queen colonies and five queens from two of the three-queen colonies) proved that their ovaries were all well developed and that their spermathecae contained sperm.

4. DISCUSSION

Our study provides clear evidence that the division of labour among cofounding queens in *P. inversa* results from social competition. Cofoundresses of *P. inversa* engage in aggressive interactions and the dominant forces the subordinate to leave the nest and forage. Furthermore, the dominant also feeds on the eggs laid by the subordinate and harasses her during egg laying. The subordinate therefore presumably produces less offspring than the dominant during these early stages of colony ontogeny.

Dominance interactions have been suggested as underlying the division of labour in foundress associations in wasps (Pratte 1989; Strassmann 1989) and in small ant societies (Bourke 1988; Ito & Higashi 1991). However, in all these cases, the interacting individuals were typically close relatives. In contrast, cofounding queens of *P. inversa* are unrelated. The band-sharing coefficient of multilocus DNA fingerprints of cofounding queens (0.34 ± 0.09) was similarly low to that of individuals taken from different colonies (0.31 ± 0.09) and differed strongly from that of nest-mate workers in monogynous societies (0.90 ± 0.12) (Trunzer *et al.* 1998; B. Trunzer, J. Heinze and B. Hölldobler, unpublished results). To our knowledge, this is the first observation of dominance interactions among unrelated individuals in eusocial insects leading to a clear-cut division of labour.

Subordinates regularly returned to the nest with prey and, though harassed by the dominant, also attempted to lay their eggs in the nest. Why then did they not instead abscond from the nest and found their own colony solitarily if they were forced to leave and forage anyway? Assuming that subordinate queens behave in an adaptive way, the benefits from joint founding must outweigh the costs of being a subordinate (e.g. Robertson *et al.* 1998).

Optimal skew theory (e.g. Reeve & Ratnieks 1993) provides a framework for understanding the outcome of social interactions between individuals. In particular, the behaviour of unrelated cofounding queens is thought to

Table 4. Correlation (Spearman's rank correlation r_s) of the frequency of aggressive acts per hour and the duration since last feeding in two- and three-queen groups of *P. 'inversa'*

colony	number of queens	number of observation sessions	r_s	p
PvII 21	2	5	0.154	0.800
PvII 129	2	5	0.102	0.870
PvII 190	2	7	-0.250	0.600
PvII 49	3	7	0.890	0.008
PvII 174	3	5	0.950	0.014
PvII 175	3	5	0.950	0.014

depend on their respective fighting abilities, the ratio of productivity of a group to that of a solitary individual and the magnitude of ecological constraints. Increased group productivity and strong ecological constraints have previously been suggested to favour pleometrotic associations in social insects, for example faster colony growth (Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Rissing & Pollock 1987; Sommer & Hölldobler 1995; but see Pfennig 1995; Jerome *et al.* 1998), increased protection against predators and usurpation (Gamboa 1978; McCorkquodale 1989; Balas & Adams 1996) and a shortage of nest sites (e.g. Pfennig 1995). Though empirical data from the field do not exist for *P. 'inversa'*, pleometrosis might be associated with similar advantages (Trunzer *et al.* 1998).

If ecological constraints are large, a queen with low fighting ability might still benefit from joint nesting even if she is forced to specialize in dangerous tasks and some of her eggs are destroyed by the dominant. It is often assumed that foraging is more risky than brood guarding. However, *Pachycondyla* queens have a powerful sting for deterring predators (Schmidt *et al.* 1980; Starr 1985) and the mortality rate of foraging queens is possibly not very high. Furthermore, *Pachycondyla* feed opportunistically on insect prey (e.g. Fresneau 1994) which are often large enough to be shared with other individuals but which cannot be stored. Foraging costs are therefore probably not much higher for a subordinate in a pleometrotic association than for a solitary queen.

Whether egg eating and harassing during egg laying in this early phase affects the future reproductive success of a subordinate is currently unclear. However, what might tip the scale very strongly towards pleometrosis in *P. 'inversa'* is that, in striking contrast to most other cooperatively founding ants, the queen number in founding associations is not regulated to monogyny after the eclosion of workers. In most species, queens begin to fight when the first workers have eclosed and all but one queen is finally killed or expelled from the nest (Bartz & Hölldobler 1982; Heinze 1993; Choe & Perlman 1997). However, pleometrosis in *P. 'inversa'* leads to primary polygyny and cofounding queens still coexist without much aggression once the colony has become mature and sexuals are produced (Trunzer *et al.* 1998). As expected from optimal skew theory (Reeve & Ratnieks 1993), reproduction is quite evenly partitioned among the unrelated queens in polygynous societies of *P. 'inversa'* (Trunzer 1999). Interestingly, cooperative founding among unrelated queens in *A. versicolor* results similarly in primary polygyny (Rissing *et al.* 1989), suggesting that it pays for a queen to take over

Table 5. Number of eggs laid by individual queens in foundress associations of *P. 'inversa'* during the observation period and number of egg-laying events during which a queen was either harassed or attacked by another queen, laid her egg outside the nest or after which the egg was eaten by another queen ('disturbed egg laying')

	number of eggs laid			disturbed egg laying			observation time(h)
	A	B	C	A	B	C	
PvII 21	4	5	—	0	3	—	168
PvII 129	3	3	—	0	1	—	264
PvII 190	3	1	—	0	1	—	168
PvII 49	4	3	0	0	1	—	336
PvII 174	1	3	2	0	2	2	168
PvII 175	5	3	0	0	3	—	336

foraging only if she does not risk being expelled from the nest after successful founding. Pleometrosis in semi-claustally founding ants might therefore be a suitable model system for testing optimal skew theory.

Our observations also fit the hypothesis that energetically costly antagonism among queens is only possible after the colony has changed from a closed- to an open-energy system (Rissing & Pollock 1986). Ant queens which found claustrally typically begin to fight only after the first workers have started to forage and carry in new resources. Newly founded colonies of *P. 'inversa'* are open systems due to foraging by the subordinate and social competition is therefore possible.

The results of our study differed from those of a previous analysis of pleometrosis in the same population of *P. 'inversa'* (then referred to as *P. villosa*) (Trunzer *et al.* 1998). In this investigation, the division of labour among queens appeared to be achieved without queen antagonism, similar to the relationships in *A. versicolor*. Furthermore, egg-laying rates were much higher. Both discrepancies are probably explained by differences in the provisioning of the laboratory colonies with food. Whereas the colonies studied by Trunzer *et al.* (1998) were fed every two days, in our study food was added after longer intervals and less regular intervals. In colonies with three queens at least, the frequency of attacks significantly increased with the time since food was added to the arena. Less favourable conditions might therefore lead to more frequent aggression (and, thus, to more intensive foraging by the subordinate queen) and make dominance relationships among queens more obvious for an observer. Similarly, food shortage accentuated the reproductive dominance of one queen in polygynous colonies of *Myrmica rubra* (Sommeijer & Van Veen 1990). The apparent lack of overt aggression among queens in foundress associations or mature polygynous colonies does not therefore necessarily mean that dominance relationships do not exist at all. Division of labour may instead result from subtle and difficult-to-observe interactions among cofoundresses (Bernasconi & Keller 1998; see also Choe & Perlman 1997). Therefore, group selection alone does not always explain apparent altruistic behaviour of unrelated queens.

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