

Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*

K. SOMMER* & B. HÖLLDOBLER

Theodor-Boveri Institut, Biozentrum, Zoologie II, Am Hubland, D-97074 Würzburg, Germany

(Received 6 December 1993; initial acceptance 11 February 1994;
final acceptance 27 September 1994; MS. number: 4539)

Abstract. After the nuptial flight, queens of *Lasius niger* occur in very high densities on the ground. Queens in this study avoided areas frequented by workers of established colonies, leading to additional clumping of nest foundations. In the field 18% of colony foundation-nests contained more than one queen (pleometrosis). Queens showed neither preference for nor avoidance of pleometrotic founding, indicating that foundress associations are facultative, promoted by crowding and intense inter-colony competition. Indeed, under laboratory conditions brood raiding occurred. In this situation groups of queens had an advantage because they produced more workers initially and the colony with the most workers was more successful in brood raids. The queens in a colony fight until only one is left alive. Removal of workers delayed fighting and addition of workers led to premature fights, indicating that the presence of workers induces fighting amongst the queens. As soon as workers started to forage, additional queens negatively affected colony productivity: colonies with three or four queens produced fewer workers than colonies with one queen. Workers also influenced the outcome of queen–queen interactions, by preferentially feeding the most fertile queen, which was therefore the most likely to survive. Neither weight of the queens by the time of the nuptial flight nor injections of juvenile hormone affected the outcome of fights between queens.

© 1995 The Association for the Study of Animal Behaviour

The founding of new colonies is a critical stage in the life cycle of ant societies. In fire ants, *Solenopsis invicta*, for example, 80% of all incipient nests perish before the first workers have a chance to forage (Tschinkel 1987). This might be why, in a considerable number of monogynous species, young queens cooperate during the founding phase (pleometrosis), although one could argue that selection should favour solitary claustral founding (haplometrosis) instead of the sharing of reproduction with other queens (Hölldobler & Wilson 1977). This is especially intriguing, because in most cases where pleometrosis has been analysed in great detail, the queens seem to join each other without respect to relatedness (Rissing & Pollock 1988; Hölldobler & Wilson 1990). Only Nonacs (1990) showed that related queens of *Lasius pallitarsus* were more successful in rearing workers than unrelated queens. The major advantage that does accrue to multiple founding queens is that they produce larger initial broods and

worker forces in less time than the solitary founding queens. This effect has been documented across a wide variety of ant genera, including *Lasius* (Waloff 1957), *Solenopsis* (Markin et al. 1972; Tschinkel & Howard 1983), *Tapinoma* (Hanna 1975), *Messor* (Taki 1976) and *Myrmecocystus* (Bartz & Hölldobler 1982). It has recently been shown for several species that colonies starting with larger initial worker forces are more successful in brood raids directed against other incipient colonies (Bartz & Hölldobler 1982; Rissing & Pollock 1986; Tschinkel 1987). In most pleometrotic founding groups the queens behave amicably at the beginning, but they show increasing agonistic behaviour towards each other after the first workers have eclosed (Hölldobler & Carlin 1985; Rissing & Pollock 1987). In *Myrmecocystus mimicus* a hierarchy among the queens is established and workers expel the lower-ranking queens from the colony (Bartz & Hölldobler 1982). The factors that determine which queen survives in foundress associations are still poorly understood (for recent reviews see Hölldobler & Wilson 1990; Heinze 1993; Herbers 1993). In the present study we investigated pleometrosis in

*Present address: c/o Prof. N. E. Pierce, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A.

Lasius niger with special regard to the factors favouring foundress associations and the reduction in the number of queens.

MATERIAL AND METHODS

Lasius niger is a common formicine ant in the holarctic region (Wilson 1955). Adult colonies are usually monogynous and contain up to 10 000 individuals.

In the study area near Würzburg (northern Bavaria, Germany) nuptial flights occur between July and September. Immediately after the mating flights in 1990, 1991 and 1992 we collected hundreds of queens, which had already shed their wings, for laboratory experiments. In other areas we investigated 50 founding nests under limestone rocks 1 day after the nuptial flights to obtain data on naturally occurring haplometrosis and pleometrosis.

The ants were kept under a 12:12 h light:dark cycle. No food was provided to founding queens. When workers appeared colonies were fed honey-water and cockroaches.

To investigate whether queens show a preference for haplometrosis we conducted 20 choice tests, in which individual queens were released into an arena (diameter 15 cm) connected to two nest chambers. One chamber was empty while the other contained one queen. In a second set of choice tests ($N=18$) we tried to determine whether queens differentiate between queens on the basis of their weight. Queens were weighed immediately after the nuptial flight and then placed in nest chambers. In these experiments one chamber contained a lighter queen and the other a heavier one. After 24 h we noted, for both choice tests, which chamber the test queen had chosen. Each queen was used only once for a choice test.

A similar arena arrangement was used for observing the interactions between incipient colonies ($N=11$). Food was offered in the arena to which workers from different nest chambers had access. The number of workers present in the different nest chambers was noted twice a week.

To compare the amount of brood produced by single queens versus groups of queens, freshly mated queens were placed in nest chambers ($9.6 \times 3.2 \times 2.9$ cm), the bottoms of which were covered with plaster of Paris. The queens were either kept singly ($N=22$) or in groups of two to

six ($N=22$). Owing to early death of their queens nine groups had to be omitted from the calculations. We counted the number of brood and workers twice a week.

To investigate whether queens avoid territories of established colonies, a colony containing over 200 workers was given access to a foraging arena the floor of which was covered with filter paper (diameter 50 cm). After at least 2 weeks had passed all workers were removed and half of the arena was covered with fresh filter paper. We released 20 post-nuptial queens into the arena ($N=8$) and noted their positions 24 h later.

To compare worker production after the addition of workers and to test the hypothesis that additional queens are an energetic burden on a colony, 21 single queens and 21 groups of four queens were given 10 workers, 30 pupae, 30 larvae and 50 eggs. Brood and workers were counted twice a week.

To investigate whether the presence of workers was the key factor eliciting antagonistic behaviour in the queens, workers were removed daily from 20 founding groups each containing two queens. After 75 days we noted in how many groups the foundresses were still together compared with 18 groups where the workers were not removed. In a second set of experiments 12 groups of two queens were given three workers, 10 pupae and 10 larvae after the nuptial flight. We noted when the queens started to fight. The control groups ($N=10$) reared their own workers.

We observed egg laying and interactions between queens and workers in 15 groups consisting of two or four individually marked queens under a stereomicroscope (Carl-Zeiss, magnification 10 times) during 1-h observation periods. Observations started within 1 week of the nuptial flight and ended when only one queen remained. In addition long-term video-recordings (Panasonic AG 67720 recorder; camera Panasonic F15) were analysed during repeated playbacks. The queens were weighed after the nuptial flight and again after the colonies were provided with food.

To test for the influence of weight on the outcome of fights among queens, 42 queens were weighed after the nuptial flight and placed in an arena in pairs. We noted which queen survived the ensuing fight. In addition we tested whether the weight of queens was correlated with successful brood rearing. Queens ($N=58$) after the nuptial flight were weighed and placed singly in nest

chambers. After 76 days we noted which queens had reared workers and their weight was compared to that of queens that had not reared workers at that time.

To investigate the influence of juvenile hormone on the outcome of fights between queens, we injected one of two queens with 1 μ l juvenile-hormone-I (Sigma) dissolved in 1 μ l triolein (Sigma; 99%), between two abdominal tergites with a microinjection needle and micromanipulator. The other queen received triolein without juvenile hormone. The queens were separated for 1 h after the injection before being placed together. We noted which queen won the fight. We used 27 pairs of queens. Injections were carried out only once because of the complicated procedure; we therefore used juvenile-hormone-I, in preference to juvenile-hormone-III because the former degrades more slowly. We used injections rather than a topical application to avoid transfer of juvenile hormone between queens.

To test for the influence of juvenile hormone on egg laying we applied juvenile hormone topically with a Hamilton syringe. Queens ($N=10$) were kept singly in this experiment. Juvenile-hormone-III (Sigma) was dissolved in acetone (Merck, 1 μ g/1 μ l) and 1 μ l was applied to the abdomen. Controls ($N=15$) received only acetone.

RESULTS

Frequency of Pleometrosis

One day after the nuptial flight nine out of 50 nests found under stones in the field contained more than one queen. Five nests contained two queens, three nests had three queens and one nest had five queens.

In 11 out of 20 choice tests in which queens could either join a founding queen or establish the nest alone they chose the latter showing neither preference for nor avoidance of pleometrosis ($\chi^2=2.0$, $df=1$, $P>0.1$). In the second set of tests nine queens joined the heavier queen ($\bar{X} \pm SD=2.9 \pm 1.4$ mg) and nine joined the lighter queen (3 ± 1 mg; Mann-Whitney $U=37.5$, $P>0.8$).

In all 11 experiments where interactions among incipient colonies were studied raiding occurred and the colony with the most workers ($\bar{X} \pm SD=31.7 \pm 29.5$) adopted brood from the colony with fewer workers (9.3 ± 7.6 ;

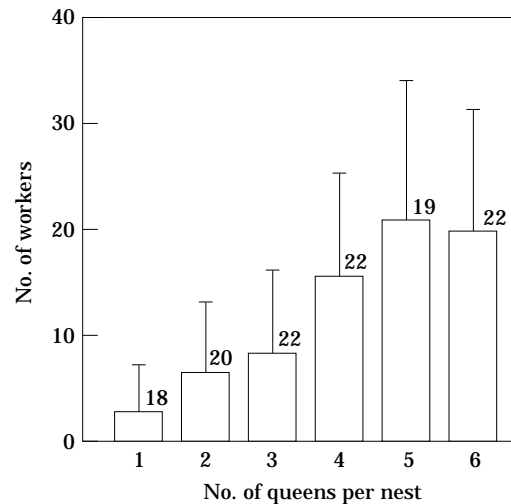


Figure 1. Mean number (\pm SD) of workers in founding groups with one to six queens at day 60. Numbers indicate number of groups.

Mann-Whitney $U=23$, $P<0.05$). Workers and queens of the defeated nests did not appear to join the raiding nest.

After 60 days groups of two to six queens produced significantly more workers than single queens ($N=18$; Fig. 1; Mann-Whitney $U=106$, $U=111.5$, $U=39$, $U=26$, $U=23.5$, respectively, for groups of two, three, four, five and six queens, $N_s=20$, 22, 22, 19, 22, $P<0.05$).

In laboratory tests, freshly mated queens avoided areas marked by workers of an established colony. One day after they were placed in an arena in which workers had foraged, a mean of 15.9 ($SD=3.6$) queens were found in the section that had not been frequented by workers and 4.1 ($SD=3.6$) in the part visited by workers (Mann-Whitney $U=0.05$, $N_1=N_2=8$, $P<0.001$).

Reduction in Queen Number

Small colonies with four queens reared fewer workers within 9 days ($\bar{X} \pm SD=15.8 \pm 4.1$) than colonies with only a single queen (21.7 ± 4.0 ; Fig. 2; Mann-Whitney $U=63.08$, $N_1=N_2=21$, $P<0.001$). After 32 days this effect was even more pronounced. Single queen colonies had 34.5 ($SD=9.6$, $N=21$) workers whereas colonies with at least three queens had only 18.6 ($SD=8.2$) workers ($N=14$; Fig. 2; Mann-Whitney $U=59.91$, $P<0.001$).

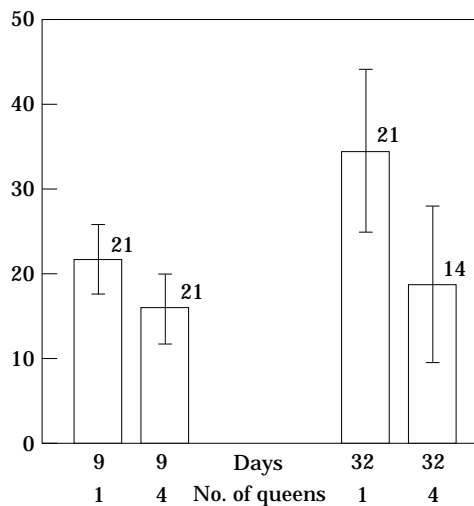


Figure 2. Mean number (\pm SD) of workers produced by single queens and groups of four queens after the first workers had emerged and food was given. Numbers indicate number of groups.

Removal of workers or adding workers to groups of queens demonstrated that it is the presence of the workers that induces queen fighting. In the experimental groups significantly more queens were still together after 75 days (Fig. 3a; 15 out of 20) than in control groups in which workers remained (5 out of 18; $\chi^2=8.47$, $df=1$, $P<0.01$). Groups of queens that were given workers started fighting after 39 ($SD=13.9$) days whereas queens

rearing their own brood did not fight until 61.6 ($SD=13.8$) days (Fig. 3b; Mann-Whitney $U=14.5$, $N_1=12$, $N_2=10$, $P<0.01$).

Observations revealed that queens started to fight after the first workers appeared. These fights could last for several hours and led in general to the death of all but one queen. Workers frequently joined the fights without showing any preferences for particular queens. The number of eggs laid by queens differed substantially within groups (Table I). In 12 out of 15 groups, egg laying was not equally distributed among queens. In addition, in 10 colonies in which the frequency with which queens were fed by workers was compared, workers fed preferentially the most fecund queen (Fig. 4; Spearman's rank correlation: $r_s=0.641$, $P<0.001$) which was also more likely to win fights and remain the sole surviving queen. In six out of seven groups the queen that was fed preferentially won the fights. In all 11 groups in which queens had been weighed a significant weight difference between the heaviest ($\bar{X} \pm SD=34.8 \pm 5.3$ mg) and the lightest queen (25.8 ± 4.1 mg; Mann-Whitney $U=9.48$, $P<0.01$) was found after 25 days. The same queens did not show significant weight differences directly after the nuptial flight (20.6 ± 3.5 mg and 18.7 ± 2.3 mg, respectively; $U=37.96$, $N_1=N_2=11$, $P>0.1$).

The weight of queens 1 day after the nuptial flight had no influence on the outcome of fights. In 20 out of 42 cases the lighter queen remained the sole survivor. The average difference in weight

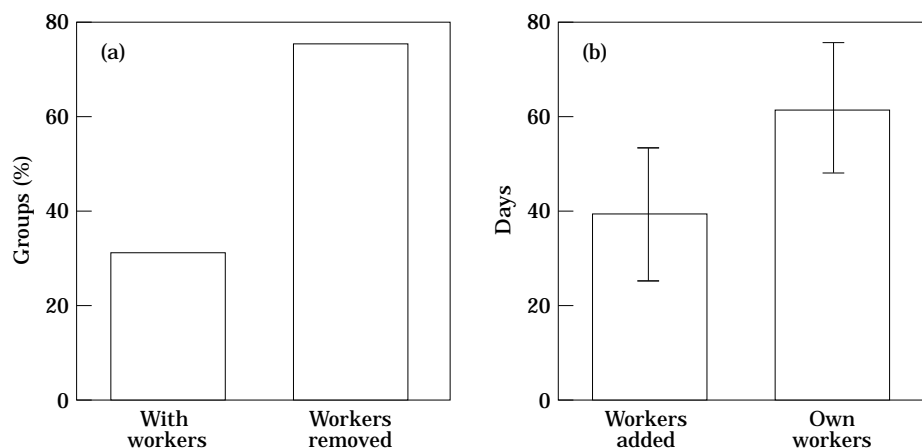


Figure 3. (a) Percentage of groups of queens still together after 75 days when workers were removed daily or left with the queens. (b) Days (\pm SD) after which queens started to fight when they were given workers and brood (added; $N=12$) or had to rear their own workers (own; $N=10$).

Table I. Number of eggs laid by the queens (A, B, C, D) in foundress groups and the time they were fed by workers (in groups 1–10) during the observations

Group	Number of eggs				χ^2	Time fed (min)				χ^2
	A	B	C	D		A	B	C	D	
1	0	30	1	1	80.75***	0	11	3	3	15.71***
2	17	3	0	0	40.24***	18	11	0	8	18.03***
3	18	51	41	15	32.42***	28	54	36	19	19.41***
4	1	12	14	23	19.60***	0	0	4	0	12.00**
5	2	10	1	11	13.47**	5	6	14	9	5.77
6	11	3	2	3	11.09*	10	0	0	0	90.00***
7			14	28	4.60*			23	42	5.56*
8			13	36	10.79**			11	27	64.06***
9			13	16	0.31			6	11	1.47
10		73	95	78	4.31		44.5	125.5	37	69.79***
11	43	70	3	100	94.32***					
12	15	35	0	69	74.89***					
13			11	13	2.00					
14			27	46	4.95*					
15			62	27	13.75***					

Groups consisted of two to four queens. Total observation period differed between groups. Asterisks indicate a significant (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) difference in egg laying and time fed by queens.

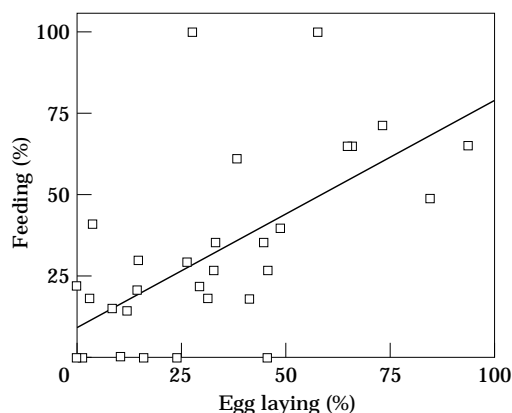


Figure 4. Correlation between the relative amount of time workers spent feeding a queen and the proportion of eggs laid by that queen in groups of two or four workers (10 groups included).

between the two queens when the lighter queen won ($\bar{X} \pm \text{SD} = 1.2 \pm 1.1$ mg) did not differ from that when the heavier queen won (1.5 ± 1.2 mg; Mann-Whitney $U = 295$, $P > 0.4$). Additionally, the weight of singly founding queens at the time of the nuptial flight did not correlate with successful brood rearing. Queens that had reared workers after 76 days weighed on average 27.9 mg ($\text{SD} = 2.2$, $N = 18$) at the time of the nuptial flight

and queens without workers weighed 28.3 mg ($\text{SD} = 1.7$, $N = 12$; $U = 373$, $P > 0.8$).

Juvenile hormone injection did not increase the chances of queen survival: in only 10 out of 27 cases did the queen given juvenile hormone win ($\chi^2 = 1.81$, $df = 1$, $P > 0.1$). Juvenile hormone application led to a decrease in egg laying ($\bar{X} \pm \text{SD} = 7.0 \pm 6.6$ eggs, $N = 10$) compared with the controls (37.9 ± 12.3 eggs, $N = 15$; Mann-Whitney $U = 17.16$, $P < 0.01$).

DISCUSSION

Founding of new colonies by several queens rarely leads to primary polygyny (Hölldobler & Wilson 1990; Heinze 1993). Usually all but one queen are eliminated; thus pleometrotic founding groups eventually become monogynous colonies. The current evidence indicates that queens in foundress associations are not closely related (Rissing & Pollock 1988) which in part explains why fierce competition among queens is so prevalent.

After nuptial flights *L. niger* queens occur on the ground in very high densities. Our experiments showed that queens avoid areas that were frequented by workers of established colonies. This can result in additional clumping of nest foundations in the field. Avoidance of foraging areas of

established colonies by founding queens has also been shown for *Messor semirufus* (Kawecki 1992).

In the field we found approximately 18% of all colony foundations of *L. niger* to be pleometrotic. In choice tests in the laboratory queens showed neither avoidance of nor preference for pleometrotic colony founding. Foundress association in *L. niger* is thus facultative, possibly promoted by crowding and intense inter-colony competition. Indeed, *L. niger* colonies are highly territorial (Czechowski 1984) and under laboratory conditions brood raiding between incipient colonies can be readily elicited. In such situations pleometrotic founding groups have an advantage, because they initially produced more workers in less time and colonies with a larger worker force were usually more successful in raiding other incipient nests. Similar relationships have previously been described in other ant species (Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Rissing & Pollock 1987; Tschinkel 1987).

Reduction in queen number in pleometrotic founding groups of *L. niger* occurred after the first workers appeared. The queens fought with one another and the workers sometimes participated in the fights without particular discrimination. We demonstrated that the presence of workers is an important factor triggering the commencement of fighting among the queens: removal of workers could prolong the amicable queen association, while adding workers resulted in premature fighting. This supports the 'closed and opened energy' concept proposed by Rissing & Pollock (1986) which suggests that queens should not fight until workers start to bring food into the colony. In fact, we demonstrated that after adult workers eclosed from their pupae and started foraging, additional queens negatively affected the development of the colony. Growing colonies with three or four queens produced fewer workers than colonies with only one queen. Obviously this has a negative effect on the initial advantage gained by brood raiding and therefore exerts a high pressure on queens to eliminate supernumerary reproductive females. In addition, during colony founding queens rely on the histolysis of their wing muscles and their large fat reserves (e.g. Keller & Passera 1989) to feed the brood, and therefore more queens can provide more energy to rear brood. However, at the time the first workers eclose, queens have nearly exhausted their fat reserves

(Tschinkel 1993) and are therefore of no more value to other queens.

Workers not only trigger the outbreak of queen fighting, but also influence the outcome of queen-queen interactions. We demonstrated that they preferentially feed the most fertile queens and it is likely that these queens have a greater chance of winning owing to a substantial weight gain. Although workers should support their own mother, there is no convincing evidence that ants do so (Carlin 1989) and we have no indication that this is the case in incipient colonies of *L. niger*. Since queens frequently also eat eggs during the initial founding phase one should expect differential oophagy, discriminating between own and foreign eggs as shown for *Polistes fuscatus* (Downing 1991). However, egg discrimination does not seem to occur in founding queens of *L. niger* (Sommer & Hölldobler 1992). The best strategy for workers, therefore, is to support the most fertile queen because this queen is more likely to be their own mother (Forsyth 1980; Bartz & Hölldobler 1982).

The question arises which factors lead to differences in fertility between queens and how these can be quantified. Tschinkel (1988) showed for *S. invicta* a positive correlation between the number of eggs laid and weight but no correlation between the number of progeny produced and weight (Tschinkel 1993). Our results for *L. niger* indicate no correlation between the probability of rearing workers and queen weight at the nuptial flight. However, queen weight could be important if queens have to hibernate without workers. In choice tests, queens showed no preference for lighter queens, indicating that this might not be an important factor. This is supported by the fact that queen weight at the nuptial flight had no influence on the outcome of conflicts. This is contrary to the results obtained by Nonacs (1992) with *Lasius pallitarsus*. He showed that queens preferentially joined lighter queens. The weight differences in our experiments could have been too small to reveal such effects. On the other hand, if queen weight is important and queens are able to assess competitiveness arising from weight differences, a lighter queen should leave the nest unless mortality among queens preceding worker eclosion is high.

In most insects egg laying is regulated by juvenile hormone (Koeppel et al. 1985). Our experiments suggest that juvenile hormone inhibits egg

laying in *L. niger* after the nuptial flight, in contrast to investigations in, for example, *S. invicta* (Vargo 1992) in which juvenile hormone application did not correlate with egg laying. Injection of juvenile hormone also did not increase the chances of a queen surviving in foundress groups; in contrast in *Polistes gallicus* (Röseler et al. 1985) juvenile hormone increases the probability of becoming dominant. Although fertility plays a major role in the outcome of queen competition in *L. niger* foundress groups, its physiological basis remains to be investigated.

ACKNOWLEDGMENTS

We thank Jim Costa and the two referees Laurent Keller and Alain Lenoir for several helpful comments on the manuscript. The work was supported by the Deutsche Forschungsgemeinschaft (Leibniz prize given to B.H.).

REFERENCES

- Bartz, S. H. & Hölldobler, B. 1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behav. Ecol. Sociobiol.*, **10**, 137–147.
- Carlin, N. F. 1989. Discrimination between and within colonies of social insects. *Neth. J. Zool.*, **39**, 86–100.
- Czechowski, W. 1984. Tournaments and raids in *Lasius niger* (L.) (Hymenoptera, Formicidae). *Annls Zool.*, **38**, 81–91.
- Downing, H. A. 1991. A role of the Dufour's gland in the dominance interactions of the paper wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). *J. Insect Behav.*, **4**, 557–565.
- Forsyth, A. 1980. Worker control of queen density in Hymenopteran societies. *Am. Nat.*, **116**, 895–898.
- Hanna, N. H. C. 1975. Contribution à l'étude de la biologie et de la polygynie de la fourmi *Tapinoma simrothi phoenicium* Emery. *C. r. hebd. Séanc. Acad. Sci., Paris, Sér. D.*, **281**, 1003–1005.
- Heinze, J. 1993. Queen–queen interactions in polygynous ants. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 334–361. Oxford: Oxford University Press.
- Herbers, J. M. 1993. Ecology determinants of queen number in ants. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 262–293. Oxford: Oxford University Press.
- Hölldobler, B. & Carlin, N. F. 1985. Colony founding, queen dominance and oligyny in the Australian meat ant *Iridomyrmex purpureus*. *Behav. Ecol. Sociobiol.*, **18**, 45–58.
- Hölldobler, B. & Wilson, E. O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* **64**, 8–15.
- Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Belknap Press.
- Kawecki, T. J. 1992. Young queens of the harvesting ant *Messor semirufus* avoid founding in places visited by conspecific workers. *Insectes soc.*, **39**, 113–115.
- Keller, L. & Passera, L. 1989. Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). *Oecologia (Berl.)*, **80**, 236–240.
- Koepe, J. K., Fuchs, M., Chen, T. T., Hun, L.-M., Kovalick, G. E. & Bries, T. 1985. The role of juvenile hormone in reproduction. In: *Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 8* (Ed. by G. A. Kerkut & L. I. Gilbert), pp. 165–205. Oxford: Pergamon.
- Markin, G. P., Collins, H. L. & Dillier, J. H. 1972. Colony founding by queens of the red imported fire ant *Solenopsis invicta*. *Ann. entomol. Soc. Am.*, **65**, 1053–1058.
- Nonacs, P. 1990. Size and kinship affect success of co-founding *Lasius pallitarsis* queens. *Psyche*, **97**, 217–228.
- Nonacs, P. 1992. Queen condition and alate density affect pleometrosis in the ant *Lasius pallitarsis*. *Insectes soc.*, **39**, 3–13.
- Rissing, J. K. & Pollock, G. B. 1986. Social interactions among pleometrotic queens of *Veromessor pergandei* (Hymenoptera: Formicidae) during colony foundation. *Anim. Behav.*, **34**, 226–233.
- Rissing, S. W. & Pollock, G. B. 1987. Queen aggression, pleometrosis and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Anim. Behav.*, **35**, 975–981.
- Rissing, S. W. & Pollock, G. B. 1988. Pleometrosis and polygyny in ants. In: *Interindividual Behavioral Variability in Social Insects* (Ed. by R. L. Jeanne), pp. 179–222. Boulder, Colorado: Westview Press.
- Röseler, P.-F., Röseler, I. & Strambi, A. 1985. The role of ovaries and ecdysteroids in dominance hierarchy establishment among foundresses of the primitively social wasp, *Polistes gallicus*. *Behav. Ecol. Sociobiol.*, **18**, 9–13.
- Sommer, K. & Hölldobler, B. 1992. Pleometrosis in *Lasius niger*. In: *Biology and Evolution of Social Insects* (Ed. by J. Billen), pp. 47–50. Leuven: Leuven University Press.
- Taki, A. 1976. Colony founding of *Messor aciculatum* (Fr. Smith) (Hymenoptera: Formicidae) by single and grouped queens. *Physiol. Ecol. Japan*, **17**, 503–512.
- Tschinkel, W. R. 1987. The fire ant, *Solenopsis invicta*, as a successful 'weed'. In: *Chemistry and Biology of Social Insects* (Ed. by H. Eder & H. Rembold), pp. 585–588. München: Verlag J. Peperny.
- Tschinkel, W. R. 1988. Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. *Physiol. Entomol.*, **13**, 327–350.
- Tschinkel, W. R. 1993. Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.*, **33**, 209–223.
- Tschinkel, W. R. & Howard, D. F. 1983. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.*, **12**, 103–113.

- Vargo, E. L. 1992. Mutual pheromonal inhibition among queens in polygyne colonies of the fire ant *Solenopsis invicta*. *Behav. Ecol. Sociobiol.*, **31**, 205-210.
- Waloff, N. 1957. The effect of the number of queens of the ant *Lasius flavus* (Fab.) (Hymn., Formicidae) on their survival and on the rate of development of the first brood. *Insectes soc.*, **4**, 391-408.
- Wilson, E. O. 1955. A monographic revision of the ant genus *Lasius*. *Bull. Mus. comp. Zool. Harv.*, **113**, 1-201.