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Are Ant Workers Capable of Colony Foundation?

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In the ponerine ant *Harpegnathos saltator* both female castes reproduce sexually, but only queens disperse and independently start new colonies. Although incipient worker foundations have never been found in the field, mated workers of *H. saltator*, singly or in groups of three, proved capable of producing and raising adult offspring in the laboratory. Of 25 worker foundations 16 produced adult workers after 160 days, and two groups produced 110 and 167 workers after 1 year. Any mated worker has the option of remaining in the natal nest to rear closely related brood or of leaving to found a new colony. Reasons for the absence of worker foundations in nature can be attributed to differences in morphological and physiological specialization between the two female castes. Higher body reserves of queens compared to workers may be the essential factor for the absence of worker foundations in nature because they reduce the need to forage outside, and thus predation and parasitization risk and buffer periods of low food availability during foundation.

In ants the two female castes differ in both morphology and behavior. While sterile workers generally help to rear new offspring, queens disperse, establish new colonies, and then concentrate exclusively on reproduction (Hölldobler and Wilson 1990). Queens can found colonies either with or without the help of sterile workers, i.e., dependently or independently (Hölldobler and Wilson 1977). In a number of species of the subfamily Ponerinae, however, a queen caste does not exist, and reproduction is carried out by mated, egg-laying workers, which are called gamergates (Peeters and Crozier 1988; Peeters 1993). Studies have shown that such gamergate colonies propagate by fission, a dependent strategy of colony foundation. Except for a few anecdotal reports (Haskins and Whelden 1965; Ward 1981) it is not known whether gamergates are also able to establish new colonies independently. We investigated in the laboratory whether workers of the ponerine ant *H. saltator* retain the behavioral repertory for independent colony foundation, although this behavior may not necessarily be expressed.

In *H. saltator* both queens and gamergates reproduce (Peeters and Hölldobler 1995). The size dimorphism between queens and workers is small but distinct. Queens disperse by flight and found colonies alone. When the queen dies in the course of colony ontogeny several gamergates take over reproduction, but the colonies continue to produce winged queens and males every year (Peeters and Hölldobler 1995; Peeters et al. 1998). Based on our field data we suggest that colony propagation is achieved solely through these queens. Nevertheless our laboratory experiments demonstrate that workers are capable of raising new colonies on their own.

We excavated 75 *H. saltator* colonies in the western Ghats in southern India between 1991 and 1995. Twelve of these were used as stock colonies for the following experiments: Male cocoons had been added several weeks earlier, because *H. saltator* workers normally inbreed with males that eclose in their own nests (Peeters et al. 1998). Large numbers of young workers mate annually, but most of these are inhibited from producing eggs by the existing reproductives. To obtain the infertile workers required for our experimental groups we selected workers inside the nest chambers of the stock colonies because these are likely to be young and thus inseminated. To obtain newly differentiated gamergates we removed established gamergates from the various stock colonies, and after 2–3 weeks new reproductives had started to lay eggs and engaged in aggressive interactions, which made them clearly recognizable. To investigate the workers' abilities we isolated them in preformed nests (plastic boxes (19×9 cm) with a floor of plaster of Paris containing two circular chambers (4.5 cm diameter) which were covered with a glass plate) and distributed them in the following experimental groups: I, 10 single infertile workers; II, 5 groups each containing 3 infertile workers; III, 5 single gamergates; IV, 5 groups each containing 3 gamergates. We also collected four dealate queens walking on the ground in India, and one queen from an incipient nest in which she had already laid eggs. We followed the course of colony foundation by these queens in the laboratory to obtain baseline data for assessing the foundation success of workers.

Most of the worker and queen groups succeeded in producing and raising adult offspring; however, despite ad libitum supply of live crickets which they hunt, 20–40% of the workers in the experimental groups died before they produced adult offspring (Table 1). The successful worker foundations (n=16/25) produced between 2

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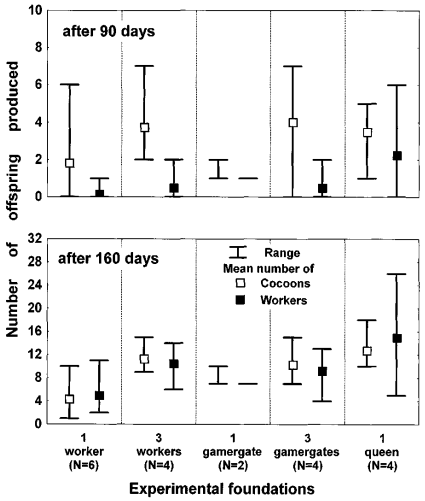

Fig. 1. Success of experimental foundations based on the number of cocoons and adult workers after 90 and 160 days of isolation (data on mortality can be found in Table 1). Initially sterile workers are indicated as *workers*. In the single gamergate foundations mean values are not given due to the small sample size. Worker and cocoon production were not significantly different between the different foundations after 90 days (Kruskal-Wallis test for workers, ANOVA for cocoons). After 160 days only cocoon production between single queens and single workers differed significantly ($P<0.05$, ANOVA with Tukey's test for unequal n)

Table 1. Mortality in each experimental group and founding success after 160 days

Initiated by	Infertile workers		Gamergates		Single queen
Group size	1	3	1	3	1
Number of groups	10	5	5	5	5
Mortality within 90 days[a]	2 (20%)	5 (33%)	2 (40%)	5 (33%)	1 (20%)
Unsuccessful foundation (no adult workers produced)	4[b]	1	3[c]	1	1

[a] No mortality occurred between 90 and 160 days
[b] Of the two surviving workers one produced only eggs within 160 days, and the other produced only two males
[c] One worker produced only males, thus she was probably not a gamergate

and 14 workers within 160 days (Fig. 1), and continued to grow. The results of 12 additional experiments were very similar to those described in Fig. 1, but these were not pooled with the other data since the workers had been collected from the same stock colonies, i.e., the data were not statistically independent. Two founding groups that consisted of one and three originally infertile workers, reached sizes of 110 and 167 workers, respectively, after 1 year. In the standardized experiments only cocoon production in single worker and single queen foundations differed significantly after 160 days of isolation ($P<0.05$, analysis of variance with Tukey's test for unequal n), but the following trend was apparent: productivity was lowest in single worker foundations, intermediate in groups of three workers, and highest in queen foundations (Fig. 1).

The initial developmental state of the ovaries (infertile workers versus gamergates) apparently did not affect the speed of colony foundation. Two groups revealed the high reproductive potential of workers: a single worker which was originally infertile produced two males within the first 23 weeks, suggesting that it was not mated. Another 13 weeks later, however, the first worker eclosed, indicating that the founding worker had mated with its son. In a second case a single gamergate had produced 6 workers before she died. These virgin workers produced males, and after several weeks new workers eclosed, indicating again that sons can mate with their mothers.

The laboratory conditions in which workers successfully produced and raised adult offspring were very artificial because foundations were provided with a secure nest chamber and foundresses hunted on crickets supplied ad libitum. Thus we think that these results cannot be extended to the natural situation. Indeed, we never collected worker foundations in the field. In 75 excavated colonies smaller colonies always contained a queen (Liebig et al. 1998), and colony founding by budding was never observed in the laboratory or in the field.

The ability of single ant workers to rear offspring in the laboratory has only been recorded anecdotally twice in the literature. Isolated virgin workers of *Rhytidoponera metallica* reared males, suggesting that isolated mated workers are similarly capable of producing workers (Haskins and Whelden 1965). In *R. chalybaea* an isolated gamergate produced three workers within 5 months, which was the same as that reared by a conspecific queen during the same period. However, founding groups of one to three workers have never been found in the field (Ward 1981).

Reasons for the absence of an alternative independent founding strategy by single workers or small worker groups become evident when considering the risks involved. In the natural situation foundresses are confronted with the risks of predation and parasitism, which can be substantial in foraging workers (Porter and Jorgensen 1981; Schmid-Hempel and Schmid-Hempel 1984; Hölldobler and Wilson 1990). Queens of the "higher" ants escape these problems by founding claustrally. They are able to rear their first offspring without foraging outside the nest chamber since they metabolize their body reserves. Indeed, the fat content of queens before mating is highest in those species exhibiting claustral founding (Keller and Passera 1989). Additionally, queens accumulate storage proteins before leaving their parental nest to found a new colony (Wheeler and Buck 1995). They also histolyze their flight muscles to feed the first generation of workers (Janet 1907), and, accordingly, the size dimorphism between queens and workers is greatest in species that establish new colonies claustrally (Stille 1996).

Queen-worker dimorphism is generally small in ponerine ants (Peeters 1993; Liebig et al. 1995), and the queens probably lack storage proteins (Wheeler and Martinez 1995). Independent foundation is generally semiclaustral, and queens regularly leave the nest chamber for foraging trips. *H. saltator* queens weigh 21.1±2.1 mg ($n=12$) and workers 12.3±2.3 mg ($n=28$), i.e., queens are 1.7 times heavier than workers. Since

flight muscle histolysis can provide additional body reserves (Haskins 1970), *H. saltator* queens are physically better specialized to found colonies semiclaustrally than workers. In addition to a reduction in foraging time, which decreases mortality risk, greater body reserves help to buffer periods of low or fluctuating foraging success. The significance of such fluctuations for semiclaustrally founding queens can be deduced from a comparison with solitary hymenopterans where fluctuations in food availability affect the number and size of offspring (Rosenheim et al. 1996; Strohm and Linsenmair 1997). The problem of fluctuating foraging success is best illustrated in the central limit theorem (Wenzel and Pickering 1991), which posits that fluctuations in the daily food intake of a colony increases with decreasing colony size, reaching a maximum in single-queen foundations.

In addition to drawing on their body reserves, *H. saltator* foundresses can buffer episodes of temporarily low foraging success by eating already present eggs or larvae which, however, increases the period until the eclosion of the first workers. In addition, their ability to store paralyzed prey (Maschwitz et al. 1979) reduces the number of foraging trips because larvae and foundress can use a single piece of prey for several days. Nevertheless, as soon as the prey has been eaten up, new foraging trips become necessary, and the foundress again faces fluctuating foraging success. Thus, trophic unpredictability is a further factor that may have led to the evolution of claustral foundation in ants in general.

Another general advantage of queen foundation over worker foundation is aerial dispersal by queens. Workers cannot colonize new localities or recolonize areas in a fragmented habitat where the former population became extinct. Every successful worker foundation would be close to her parental colony, where she would eventually compete for local resources.

The only conceivable scenario in which the founding behavior of workers could be expressed is the partial destruction of the parental colony. Although the nests of *H. saltator* are designed to protect against enemies and flooding in an area with heavy seasonal rains (Peeters et al. 1994), they can suffer accidental destruction. While this may be a relatively rare event, workers are capable of continuing the colony or starting a new one, either alone or with other nestmates and brood. Alternatively, the retention of the ancestral trait of independent colony foundation by workers can be explained simply by evolutionary inertia since they have evolved from species with totipotent females.

More generally, workers of *H. saltator* have fitness advantages when staying in their parental colony. Infertile workers gain by helping highly related nestmates, but there is also the chance to become a gamergate in a secure nest in which their relatives have already invested a lot. Although under laboratory conditions *H. saltator* workers show a remarkable behavioral plasticity in their ability to found colonies independently, under natural conditions they are clearly disadvantaged as colony foundresses compared to the queen castes. Thus the only successful strategy of workers seems to stay in a colony as hopeful future reproductives, although most of them remain sterile helpers.

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