



Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*

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Ant larvae may increase their fitness by trying to increase their food intake, since adult morphology and quality depend on nutritional conditions during juvenile development. As larvae are legless and dependent upon workers, some sort of begging signal can be expected. We studied larval begging behaviour in the ant *Gnamptogenys striatula*. Workers preferentially fed larvae that were either near the food or performed a typical swaying behaviour. In this swaying behaviour, larvae raised their head and neck, and gently reached and waved towards workers or food items. Swaying duration was not, however, correlated with distance to food. In a separate experiment, hungry larvae swayed more than well-fed larvae, suggesting that swaying is an important element of begging for food. Acquiring extra food through begging probably allows *G. striatula* larvae to manipulate their future reproductive options.

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Solicitation for food is a widespread phenomenon among animals, and it has been a topic of discussion ever since Trivers (1974) introduced his idea of parent–offspring conflict. Because of relatedness asymmetries, he argued, young are selected to acquire more resources than a parent is selected to give. Each young animal values itself more highly than it values its siblings, and therefore should demand a disproportionately large share of parental investment. For a parent, in contrast, provisioning one of its offspring critically influences the trade-off between fitness returns from this versus other offspring, and from current versus future reproduction (Trivers 1972, 1974). Subsequent conflicts, however, can arise only when both parents and offspring have the opportunity to affect the allocation outcome, behaviourally or by other means. Some sort of offspring begging for more resources is therefore expected in many family systems with parental care.

Recent biological signalling theories focus mainly on the costs and benefits of begging behaviour, and consider whether begging is an honest signal of need or quality (Godfray 1991, 1995; Kilner & Johnstone 1997) or serves more manipulative or competitive purposes (Macnair &

Parker 1979; Parker 1985; Royle et al. 2002). Apart from burying beetles (e.g. Smiseth & Moore 2002) empirical studies on begging and food solicitation have focused largely on vertebrates, with special attention to bird family systems (e.g. Kilner 1995; Mondloch 1995; Price & Ydenberg 1995; Smiseth & Lorentsen 2001; Whittingham et al. 2003). Our study is one of the first on begging in ant societies. Furthermore, we studied a social model system, which might provide valuable insights into the fitness consequences of begging.

The prime difference between the offspring of the majority of birds or mammals and those of ants is that ant larvae mature in a highly social context. In the social Hymenoptera, the division of reproductive labour generates two types of female concerned with procreation: one for offspring production and one for offspring nurture. Application of parent–offspring models may therefore prove to be complex. First, nonreproducing workers may experience low costs of parental care since they are not endangering future reproductive success. Furthermore, through indirect fitness returns of rearing relatives, little conflict or even cooperation between caregivers and offspring may evolve (Rauter & Moore 1999). For reproducing (noncaring) females, low investment costs may temper conflicts with their developing offspring. On the other hand, the consequences of the social system may also intensify the conflict: a female's direct fitness benefit from her own reproduction will always exceed the indirect fitness returns of worker behaviour (Wenseleers et al. 2003), so that she favours being a reproductive. Whether

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she prefers a reproductive role relates to the female's reproductive potential, which in turn is based on dissimilarities in adult body size or morphology (Wheeler 1994): in many eusocial Hymenoptera a highly adapted queen morph with a larger body and more ovarioles than those of the workers occupies the reproductive position(s). In other species, this dimorphism may be less clear. In more 'primitive' ponerine ant colonies where monomorphic workers compete for full reproduction, reproductive fate depends on differences in body condition or morphology (Peeters 1997; Blatrix & Jaisson 2001; Peeters & Ito 2001). However, in all ants (with a few possible exceptions, see Ashe & Oldroyd 2002) these adult features are not genetically based, but are determined during larval development (Wilson 1971). Hence they are known to depend on developmental conditions in the larval stages. In many social Hymenoptera, nutrition, possibly combined with other environmental or social factors, can profoundly influence the future adult morphology of a developing larva (Wilson 1953; Wheeler 1986; Wensleers et al. 2003). From a larval point of view, this effect of nutrition enables important evolutionary opportunities for controlling personal future fitness.

However, larvae of social Hymenoptera are legless and depend on worker nurturing. Manipulating resource provisioning by workers might thus affect their later reproductive fate (Bourke & Franks 1995; Bourke & Ratnieks 1999). Therefore, and inspired by other animal species with parental care, existence of some sort of begging signal has been hypothesized (Nonacs & Tobin 1992; Bourke & Franks 1995; Bourke & Ratnieks 1999). The possible conflict over reproductive fate might thereby intensify larval competition over resource allocation.

Few empirical studies have characterized begging or hunger signalling in Hymenopteran larvae. Obvious signals communicating hunger can be found in various species of vespine wasp larvae (Matsuura & Yamane 1984), which scrape their mandibles against the cell walls to attract workers with food (Ishay & Schwartz 1973), whereas nonscraping larvae often reject food (Yamane 1976). Saliva drops (Delage 1968; Brian 1977) or anal secretions (Le Masne 1953; O'Neal & Markin 1973) of some Hymenopteran larvae appear to contain valuable nutrients, and might be used to attract nearby workers. Whether this evokes feeding, however, is not known. In ants, Cassill & Tschinkel (1995) suggested that nonvolatile chemical cues signal hunger in fire ant larvae, *Solenopsis invicta*, and Brian (1977) described *Myrmica* larvae flexing their head or whole body to attract workers in food-deprived colonies. In some species, certain behavioural signals associated with feeding have been described (Le Masne 1953; Brian 1956; Wheeler & Wheeler 1976), but in most cases they are believed only to communicate a readiness to feed to the workers, after antennal contact or on being offered food (Le Masne 1953; Brian 1956). Creemers et al. (2003) showed that workers preferentially feed *Myrmica* larvae with an upward-bending head. To add to our knowledge for ants, we studied behavioural displays related to feeding in *Gnamptogenys striatula* larvae.

Larval control of reproductive fate is especially likely in the South American ponerine ant *G. striatula*. All the

workers are potentially reproductive, and a limited number of workers will mate and start to reproduce when queens are absent (Blatrix & Jaisson 2000; Giraud et al. 2000). These 'gamergates' make up 4–15% of the workforce of 372 ± 299 females ($N = 51$ colonies, Blatrix & Jaisson 2000, 2001). Although workers normally possess two or four ovarioles, workers with four ovarioles are more likely to become a gamergate than workers with few ovarioles. Blatrix & Jaisson (2001) showed that although 40.1% of workers have fewer than four ovarioles ($N = 3121$), this is the case in only 6.6% of gamergates ($N = 243$). As larval diet affects adult morphology in social insects, larvae could potentially benefit from better nutrition. However, *Gnamptogenys* workers control how retrieved food items are distributed by placing food and immobile larvae together (e.g. Gobin et al. 1998; personal observation). In nature, the ratio of workers to larvae varies considerably (median 4:1; quartiles 2:1 and 7:1; $N = 34$ colonies; Blatrix & Jaisson 2001).

We predicted that larvae would try to control their individual food intake by behavioural signals to the nursing workers to stimulate feeding. We tested two central hypotheses, in parallel with two predictions common to most recent begging models. (1) Parents supply resources in relation to begging signal intensity. We traced and observed a feeding act by a worker and related it to the preceding larval behaviour. Larvae that were fed were compared with larvae that were not fed. (2) Begging intensity reflects offspring need, usually defined as hunger state. For this purpose we compared the behaviour of fed larvae with that of larvae that were food deprived for a short period.

METHODS

Colonies of the abundant species *Gnamptogenys striatula* were collected in 1999 in the Santa Rosa National Park, Acguanacaste, Costa Rica, with permission from the Ministry of the Environment and Energy (MINAE). We worked with 11 queenless colonies, in which several mated workers reproduced. Each colony was kept in a plaster nest at $25 \pm 2^\circ\text{C}$ with $75 \pm 15\%$ relative humidity and a 12:12 h light:dark regime. Water and live crickets or mealworms were provided ad libitum in the foraging area daily.

To collect larvae for the experiments, we carefully opened the nest cavities and picked up larvae with a soft paintbrush. We chose larvae of similar length, as these are at the same developmental stage before differentiation (Wheeler 1991). We measured the larva's longest body length (± 0.04 mm) in the relaxed position under a binocular microscope. When workers were collected, we chose those that were nursing the brood, thus ensuring good brood-rearing capabilities.

Number of Ovarioles Related to Larval Feeding

In experiment 1, we verified whether a larger food supply for *G. striatula* larvae during their development

results in development of more ovarioles (inspected in the adult stage). We sampled larvae (1.0 ± 0.2 mm) from 11 colonies. Each larva was placed separately in a small plastic cup with a plaster bottom in which an interior nest cavity was hollowed out (ca. 1×1.5 cm), together with five workers from another randomly selected colony (to exclude familiarity with the larvae). Adults do not discriminate between larvae of their own and other colonies (Blatrix & Jaisson 2002). The cups were closed, randomly divided into two groups and marked correspondingly. Group F was fed ad libitum with small (± 1 cm) live mealworms, so that fresh food was always available. Group H was fed only twice a week with equally small mealworms. Preliminary trials showed that this latter food regime was the minimal required for larval development. In both F and H groups, some larvae ($N = 11$) died shortly after transfer from damage caused by manipulation. The set-up was repeated until we had seven replicates in each group. Once a larva was encapsulated in its cocoon, workers were again given ample food.

We killed the adults that emerged in each group (F and H) by freezing within a day of eclosion. They were subsequently dissected under a Wild microscope at $20\times$ magnification. We summed the ovarioles in both ovaries and compared data sets with a nonparametric two-tailed Mann–Whitney U test (significance threshold of 0.05, unless otherwise indicated). The limitation in available colonies and brood resulted in the multiple use of some colonies. As *G. striatula* is highly polygynous, it is unlikely that two random larvae have the same parents, thus we feel safe to treat our replicates as independent. Our design is, however, far from ideal, as we cannot fully exclude effects of pseudoreplication; there may be important nongenetic differences between colonies.

Worker Feeding Related to Larval Behaviour

In a second experiment, we tested whether decisions in food allocation by workers can be related to differential behaviour of the larvae. To correlate specific larval behaviour with feeding acts by workers, we videotaped eight experimental replicates. The conditions of these replicates were chosen to maximize the chance of observing larval behaviour and associated feeding, without compromising image resolution (e.g. when nests are too big). Each replicate represented a unique team of workers and larvae from different colonies. Larvae and workers were prepared as follows.

Twelve workers from a randomly selected colony were collected and placed in an observational nest. This consisted of a transparent plastic petri dish filled with a thin layer (± 4 mm) of plaster. A small hole (ca. 1×1.5 cm) was left in the plaster so that the bottom was visible to allow filming from underneath. A piece of plastic foil covering the plaster formed an interior nest cavity. The workers were kept with water but without food in this nest for 72 h. Food deprivation motivates workers to acquire food in social insects (Rinderer & Baxter 1978; Cartar & Dill 1990; Schulz et al. 1998). We therefore assumed that

a short period of food deprivation would enhance the workers' response to possible begging signals from larvae.

For each replicate, we collected seven larvae from one randomly chosen colony (but different from that of the 12 workers to exclude familiarity). They were set aside in an isolation nest with three nursing workers for 24 h. To increase hunger and possible begging behaviour, we did not provide food. These larvae were 1.8 ± 0.2 mm long, a minimum for distinguishing behaviour in detail.

After the 24 h of isolation, we transferred the seven larvae to the observational nest, where the workers moved them inside the nest within 15 min. We then added a fresh, decapitated (so the haemolymph was easily accessible) mealworm. A thin paper strip attached to its tail end, and fixed to the plaster in the foraging area, forced the workers to bring the larvae to the food and not vice versa. This facilitated the observations of individual feeding. The petri dish was placed on a support, above a camera with its lens directed upward. We videotaped for 3 h during daytime (0800–2000 hours).

During the videotaping, workers performed a wide range of actions, some concerning themselves (eating, resting, leaving or entering the interior nest) and some with other workers or larvae (grooming, walking over some or all larvae, having antennal contact with each other or with larvae, replacing larvae, bringing a larva to the food item or taking a larva away from the food item). In the square nest, the larvae were mostly kept in an opposite corner from the food item. When a larva was picked up by a worker and obviously placed with its mouthparts against the food, we considered it 'fed'. Multiple larvae can be fed by either a single or multiple workers. The food item was large enough to accommodate all larvae for simultaneous feeding.

Videotapes were analysed as follows. As soon as the feeding of a larva started, we noted which of the larvae were fed and which were not fed during the next 5 min. Then we monitored the behaviour of all larvae (fed and nonfed) for the 5 min preceding the feeding of the first larva. We analysed consecutive feeding events per videotape, taking care to avoid overlap between the time blocks. We distinguished two clear larval behaviours. We recorded the duration of the first, a gentle poising and reaching towards the food or the workers, which we termed 'swaying'. The second, which we named 'stretching', was an obvious and rhythmic stretching of the whole body. However, this behaviour was rare and so was not included in statistical analyses. We also noted the distance between each larva and the food item to detect any influence of position on the feeding behaviour of the workers. Distances were measured (± 1 cm) on the monitor, representing an actual accuracy of about 0.8 mm.

All larvae used in the experiment were reared in their experimental groups to exclude replicates containing male larvae from further analysis. This, however, was never the case.

The data were analysed with a Generalized Linear Model (GLZ) with a binomial error structure and logit link. We used replicate number as a factor to test for the effects of swaying duration and stretching (continuous variables nested in replicate), using distance to food as a covariate.

Interactions of each variable with replicate and between variables were never significant ($P > 0.40$), and neither was the variable 'stretching' so these were dropped from the final model (Verbeke & Molenberghs 2000).

Larval Behaviour Related to Hunger

The second central hypothesis, that food-deprived larvae differ behaviourally from well-fed larvae (in the presence of food and workers), was tested in a third experiment. To correlate larval behaviour with hunger status, we set up six experimental replicates in a similar manner to the one described above, except for food availability of the larvae in the 24-h isolation period before videotaping: we provided abundant dead crickets and fruit flies and made sure the nursing workers fed the larvae. Larvae were then transferred to the observation nests and filmed for 3 h. We analysed three periods of 5 min of each videotape: one at 25 min, one at 1 h and 25 min, and one at 2 h and 25 min after transfer. During these three periods, we noted the duration of swaying of all larvae and calculated mean values per larva per min. Stretching was rare and excluded from analysis. Larvae that were not clearly visible or eating during our observations were not included in the analysis.

For comparison with food-deprived larvae, we reanalysed videotapes from experiment 2, where the larvae were food deprived for 24 h before the videotaping in an analogous manner. The data for swaying were analysed in a repeated measures ANOVA, with replicate number and feeding status (H = hungry, NH = nonhungry) as categorical predictors (replicate number nested in feeding status), and consecutive periods (1–3) as repeats.

We conducted experiments 2 and 3 consecutively, so we cannot exclude a temporal influence on our results. However, as both experiments were carried out within a month in a room with constant environmental conditions (temperature, light, humidity), we assume temporal effects to be minimal.

RESULTS

Number of Ovarioles Related to Larval Feeding

All larvae in both groups developed into workers; no queens were obtained. Larvae that were fed frequently developed into workers with more ovarioles than larvae that were fed less frequently. Six of seven well-fed larvae (group F) developed into adults with four ovarioles, and one had two ovarioles. In group H only two of seven adults had four ovarioles, whereas four had two, and one had three. Although the result was significant (Mann-Whitney U : $U = 11.0$, $N_1 = N_2 = 7$, $P = 0.05$), some larvae originated from the same colonies and might not provide independent data. When we used colonies as replicates ($N = 5$), the trend was not significant ($U = 5.5$, $N_1 = N_2 = 5$, $P = 0.11$).

Worker Feeding Related to Larval Behaviour

Although swaying duration varied between replicates, within replicates it differed significantly between fed and nonfed larvae, as did distance to food (Table 1). Fed larvae swayed for longer (Fig. 1), or were nearer to the food (fed: median 16 mm, 25th and 75th quartiles 10, 21 mm; nonfed: 22 mm, 13, 26 mm) before feeding.

Larval Behaviour Related to Hunger

Food-deprived larvae swayed for significantly longer than well-fed larvae (repeated measures ANOVA: $F_{1,65} = 23.07$, $P < 0.001$; Fig. 2). No significant change in swaying duration was found over time (during subsequent periods; $F_{2,10} = 1.86$, $P = 0.18$).

DISCUSSION

Food is important for the juvenile development of most organisms, and is often the prime issue in parental care conflicts. In Hymenoptera, and specifically in ants, larval diet is often pivotal for overall morphological development, including the features critically correlated with fecundity (Wilson 1953; Wheeler 1986, 1994; e.g. *Camponotus pennsylvanicus*: Smith 1942; *Bombus terrestris*: Ribeiro et al. 1999; *Apis mellifera*: Evans & Wheeler 1999). Given the conflict over reproductive fate, food availability might thus strongly affect the future fitness of a larva.

Although not conclusive, our data suggest that nutrient availability during the larval stages affects the ovariole number of adult workers. The ovariole number is important for reproductive success in *G. striatula*: the reproductives of two natural and six experimental colonies had significantly more ovarioles than the workers (Blatrix & Jaisson 2000, 2001). We therefore conclude that higher food availability during larval development increases an ant's reproductive options.

In the worker feeding experiment, we identified swaying as a possible begging behaviour or signal of hunger to workers. Within replicates, the workers preferentially fed larvae that swayed for longer. These allocation decisions cannot be influenced by differential relatedness with the larvae, as kin discrimination is absent in *G. striatula*.

Table 1. Worker feeding related to swaying duration and distance of larvae from food

	df	Log likelihood	Chi-square	P
Intercept	1	-33.64		
Distance	1	-31.32	4.64	0.031
Swaying duration	1	-31.11	0.42	0.52
Replicate	7	-26.12	9.98	0.19
Replicate (swaying duration)	7	-8.88	34.49	<0.001

GLZ: Likelihood Type 1 test with binomial distribution and logit link function.

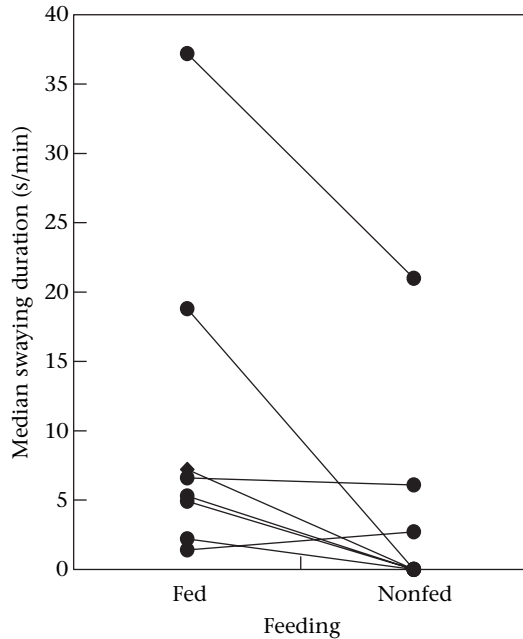


Figure 1. Total swaying duration of *G. striatula* larvae. For each replicate (= colony), medians are given for larvae fed by workers and for larvae that were not fed by workers in the 5 min before the first feeding.

(Blatrix & Jaisson 2002). We thus assume that swaying stimulates feeding behaviour by workers.

The distance of a larva to the food item also affected its likelihood of being fed, as workers preferentially chose nearer larvae. This is similar to many bird species, where spatial position in the nest is known to affect food allocation decisions (Rodríguez-Gironés et al. 2001). The relative position of bird siblings is determined through jostling competition, which takes place largely in the

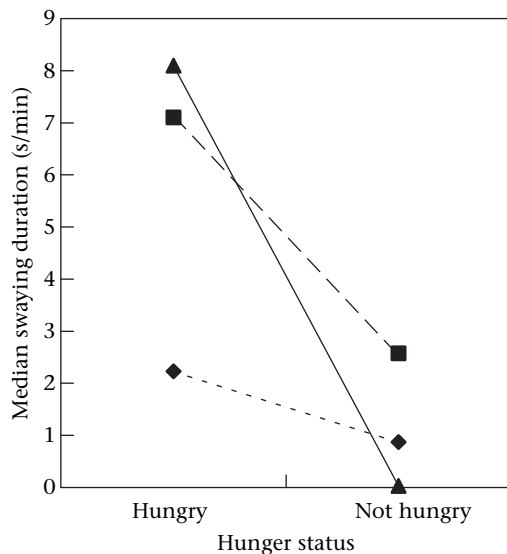


Figure 2. Total swaying duration of food-deprived larvae versus well-fed larvae of *G. striatula*. - - - -: first 5-min period of analysis; - · - · -: second period; —: third period.

absence of the parents. Such direct sibling competition is impossible in ants, because larvae are largely immobile. Even though larvae can shift position slightly, it is obvious that the workers decide their relative spatial location. The absence of an interaction between swaying duration and distance to food excludes the possibility that nearer larvae just begged more, for example because they smelled the food. Workers shuffled larvae after the food was added. From our experiments, however, we cannot determine whether workers position larvae according to their hunger status.

Further evidence for the importance of swaying as a begging signal was obtained in experiment 3, in which food-deprived larvae swayed significantly more than well-fed larvae. Swaying thus probably communicates hunger. We can thus conclude that swaying is an aspect of begging behaviour in *G. striatula* larvae. This is different from the only other quantified begging behaviour in ants. In *Myrmica rubra*, workers respond to an immobile, stretched posture of begging larvae (Creemers et al. 2003), rather than to movement. We cannot of course exclude other, accompanying hunger signals (e.g. chemical cues, Cassill & Tschinkel 1995).

Some signalling models (e.g. Godfray 1991, 1995) assume offspring begging signals are an honest reflection of true need when parents (workers in our case) have active control over resource allocation. Our empirical results support two of the three predictions of honest signalling models (the third was not tested), as formulated by Kilner & Johnstone (1997). The first prediction states that offspring need will influence begging intensity and the second predicts a relation between parental resource provisioning and begging signal intensity. We might therefore conclude that the begging signals of *G. striatula* larvae are honest communication of hunger from larvae to nursing workers. In the context of potential reproductive conflicts, however, larval begging is believed to be a dishonest signal, used to manipulate workers into giving them more food than the minimum required for survival, to improve their later reproductive opportunities. Discriminating between the two mechanisms on empirical grounds, however, is complex as quantitatively equivalent results are obtained under both honest and dishonest signalling models (Parker et al. 2002; Royle et al. 2002).

Relatedness asymmetries between the members of highly polygynous ant colonies such as those of *G. striatula* could shape totally different begging mechanisms to those in other animal family systems. Conflicts between a colony's reproductives and its brood are likely to be less important in polygynous species. Although policing of larvae by reproductives has been suggested in some species (Masuko 1986; Keller et al. 1989), we prudently assume, in view of the large colony sizes of these species, that the reproductives' share of parental investment is mainly restricted to egg laying, whereas allocation decisions are made mainly by the workers (Bourke & Ratnieks 1999). Workers, on the other hand, form a third and important party of interest, and add complexity to the classic parent-offspring models. In systems with cooperative resource provisioning by more than one caretaker, honest nestling begging can be expected for regulation of individual provisioning rates.

Begging can then allow caretakers to respond adaptively to short-term changes in brood size and partner effort (Wright & Cuthill 1990; Ottoson et al. 1997; Wright 1998; Wright & Dingemanse 1999). On the other hand, workers potentially oppose the larvae's demands. There may be several reasons for worker–larvae conflict in ants (Nonacs & Tobin 1992; Ratnieks & Reeve 1992; Bourke & Franks 1995), all of them shaping the balance of power between the two parties, and so shaping the evolutionary possibilities of an honest/dishonest pathway.

First, as in nonsocial systems, resources in ant colonies are limited and have to be shared with all colony members. Because workers control foraging and brood care, limited resources may lead to potential larvae–worker conflict over resource allocation. Second, manipulation by larvae could lead to excess production of reproductives (Bourke & Ratnieks 1999), which would overexploit the colony's workforce (Wenseleers et al. 2003). The kin structure in a colony might discourage workers bringing up new, possibly less-related, potential reproductives. Finally, as in nonsocial systems, offspring may compete with each other for the best care. Further studies are needed to evaluate whether, and to what degree, each of these conflicts affects the degree of honesty during communication.

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