Research article

Larval isolation and brood care in *Acromyrmex* leaf-cutting ants

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Abstract. The larvae of leaf-cutting ants are maintained within the fungus gardens of their colonies and are fed pieces of fungus by the adult workers. However, little else is known about the nature of the worker-larva interaction in these ecologically important ants. To examine whether workers can gauge the needs of individual larvae, we isolated larvae without adult workers for different lengths of time. We then placed workers with the larvae and recorded the type and frequency of the subsequent behaviours of the workers. Workers scraped the mouthparts of larvae, ingested their faecal fluid, fed them with fungal hyphae, transported them around the fungus garden and, most frequently, licked their bodies. The workers were also observed to 'plant' fungal hyphae on the bodies of larvae. Workers interacted more frequently with larvae that had been isolated without workers than with those that had not, but there was no effect of the length of isolation. The results suggest that the interactions are complex, involving a number of behaviours that probably serve different functions, and that workers are to some extent able to assess the individual needs of larvae.

Keywords: Acromyrmex, larvae, brood, disease, fungal mutualist.

Introduction

Cooperative care of young is a key feature of eusociality (Wilson, 1971). The brood of most ants, as well as that of bees and wasps, are more or less immobile and are entirely reliant upon adult workers supplying their needs, including being fed and cleaned. Unlike that of bees and wasps, ant brood are not kept in individual cells making it harder for adult workers to assess their needs. Larvae vary in their needs, depending on their size, caste-destiny and maturity, as well as how long ago and how well they were last cared for. In the fire ant *Solenopsis invicta*, for example, workers feed larvae trophallactically with standard quantities of food (Cassill and Tschinkel, 1995, 1996), but the rate of feeding depends upon both the size and hunger-level of a larva (Cassill and Tschinkel, 1995). Although immobile, larvae of some ant species are capable of 'begging' for food by stretching their heads (O'Neal and Markin, 1973; Agbogba, 1991; Creemers et al., 2003) and may adjust their intake according to the quality of the food offered (Cassill and Tschinkel, 1999).

The fungus-growing ants (Hymenoptera: Formicidae: Attini) consist of 12 genera, including the leaf-cutting ants (*Atta* and *Acromyrmex*) many of which forage more or less exclusively on fresh vegetation. Workers collect material for use as a substrate by the obligate, mutualistic fungus that they culture within their nests. In leaf-cutting species, the fungus has been shown to effectively metabolise plant polysaccharides, although apparently not cellulose (Bacci et al., 1995; Siqueira et al., 1998; Abril and Bucher, 2002). The fungus then produces nutrient rich structures called gongylidia, or staphylae when in clusters, which form the primary food source for the ant larvae (Quinlan and Cherrett, 1979). The fungus is also used as food by the adult workers (Bass and Cherrett, 1995; Silva et al., 2003), although these may satisfy part of their nutritional requirements with plant sap (Quinlan and Cherrett, 1979). The larvae of attine ants are normally found within the fungus garden and are often covered with a blanket of fungal hyphae such that they appear an integral part of the garden themselves (Weber, 1972; Schultz and Meier, 1995; Adams et al., 2000). They are immobile and apparently unable to feed themselves, being reliant on adult workers placing pieces of fungal material on their mouthparts (Weber, 1972). *Acromyrmex* colonies contain a wide size range of workers that exhibit distinct alloethism,

with the foraging being carried out by the largest individuals while the smaller workers tend the brood and fungus garden (Wetterer, 1999). Although caste destiny may be influenced by genotype (Hughes et al., 2003), it is almost certainly also dependent upon environmental factors. These include the temperature larvae are reared at and the food they receive, both of which are under the control of adult workers (Weber, 1972; Bollazi and Roces, 2002).

The cryptic nature of attine larvae means that there have been relatively few studies of the interactions between them and the adult workers. We set out to examine the behaviours shown by *Acromyrmex* workers towards larvae, and to determine whether the workers are able to adjust their behaviour according to the needs of the larvae.

Materials and methods

We collected four colonies each of *A. rugosus* and *A. balzani* in Botucatu, SP, Brasil (22º52'20''S; 48º26'37''W), and four colonies of *A. crassispinus* in Jaguariaíva, PR, Brasil (24º32'S; 49º57'W). The colonies were set-up in the laboratory in individual plastic containers with a 1 cm layer of dampened plaster at their base to keep the humidity inside the chambers at a high level. Each of these chambers was linked by tubes to a foraging arena and a garbage chamber. The laboratory was maintained at 24 °C, 70 % relative humidity, and the colonies fed on a diet of leaves: *Acalypha wilkesiana* for *A. rugosus* and *A. crassispinus*, or *Cynodon dactylon* var. *tyfton* for *A. balzani*.

Cassill and Tschinkel (1996) used ingested dye to mark *Solenopsis* larvae, and we adapted this methodology to mark *Acromyrmex* larvae. The dye consisted of 10 % glucose P.A. (p/v) and 2 % (p/v) of colouring nutrients (aniline) in distilled water. The addition of these colouring agents to the solutions in concentrations between 1 and 4 % has no effect on the amount ingested by *Solenopsis* larvae nor or the subsequent behaviour of workers towards the larvae (Cassill and Tschinkel, 1995) and we confirmed that this was also the case for *Acromyrmex* prior to the experiment (Lopes, unpubl.). Tufts of hyphae from the colony's fungus garden were dipped briefly (< 1 min) in the dye. Larvae were removed from the colony using forceps and fed under a dissecting microscope by placing tufts of dyed hyphae on their mouthparts using the tips of entomologic pins (n. 0-0). We observed larvae opening and closing their mandibles on the hyphae and the passage of dye through the digestive tract. Dye took approximately 10 hours to pass through the entire digestive tube and then spread through the haemolymph before degrading after approximately 72 hours.

To examine the effect of isolation and starvation on worker-larva interactions, we removed larvae from their colonies and marked them as above. We did this for larvae 0, 12, 24, 36 and 48 h prior to the experiment beginning and marked them with a different colour according to these time intervals (unmarked, red, blue, green and yellow respectively). We used only last instar larvae, distinguished by their darkened gut, which had no hyphal blanket covering their bodies. Marked larvae were then placed on small (approximately 5 cm diameter and 1 cm in height) pieces of mature fungus garden in sterile Petri dishes (90 × 15 mm) with a layer of moistened filter paper. The larvae were unable to feed upon the fungus because they were placed ventral side up, are immobile and are incapable of feeding for themselves (Weber, 1972). The fungus pieces never showed any signs of stress or contaminants during the short durations of the experiments. Each Petri dish contained two larvae that had been isolated for each of the five isolation periods, being distinguished by the colour of their dye. Three replicate Petri dishes were set-up for each of the four different colonies of the three species, to give a total of 36 experimental groups.

Larval groups were thus created that each contained two larvae that had been isolated for each of 0, 12, 24, 36 or 48 hours. Ten workers of

the smallest size class (1.2 to 1.6 mm for *A. balzani*, 1.0 to 1.2 mm for *A. crassispinus* and 0.7 to 0.9 mm for *A. rugosus*) were then taken from the fungus garden of the natal colony and placed in the Petri dishes. Worker: brood ratios of 1:1 in *Solenopsis* have been found to be sufficient for workers to meet the demands of all larvae (Cassill and Tschinkel, 1999). The Petri dishes were then observed for three 30 minutes observation periods starting 0, 45 and 90 minutes after the addition of the workers. The nature and frequency of behaviours by the workers towards the larvae were recorded during these periods. Behaviours were recorded as single occurrences regardless of their duration. The data were analysed using repeated measures analyses of variance, with observation period as the repeated measure, isolation period and species as factors, and with colony nested within species. A separate analysis was carried out for each of the behaviours recorded.

Results

Six behavioural acts were recorded by workers towards larvae:
1. Licking the body of larvae
2. Transporting larvae around the fungus garden
3. Feeding larvae with fungal hyphae
4. Ingesting faecal liquid excreted by larvae
5. Planting fungal hyphae on the body of larvae
6. Scraping the mouthparts of larvae

The licking of larvae was the most frequently recorded behaviour (Fig. 1). It was always preceded by the worker examining the body of the larva with its antennae and appeared to typically last until the entire body surface of the larva had been licked. The scraping of the mouthparts of larvae was carried out by workers using their mandibles. When larvae were transported, they were always moved within the fungus garden. Although *Solenopsis* workers may transport droplets of faecal fluid between their mandibles to the outskirts of the nest (Hölldobler and Wilson, 1990), the workers in our study were not observed to do this and ingested all the faecal fluid they collected. The planting of fungal hyphae on the bodies of larvae involved workers placing small pieces of hyphae upon the body of a larva, with the pieces eventually forming a complete blanket over the body. This behaviour only occurred after a larva had been thoroughly licked. The planting of hyphae was carried out in the same manner as when hyphae are planted on plant substrate for the cultivation of the mutualist fungus. The workers cut and transport hyphae with their mandibles and, after being placed upon the larval cuticle, the workers press the hyphae with their forelegs and antennae. Once larvae had a hyphal coat they were no longer licked by workers. Workers were not observed to tend hyphae once it had been planted on the bodies of larvae. In addition to the above six behaviours, workers frequently antennated larvae but the occurrence of this was not quantified. Larvae were also observed on occasion to move their heads and to extrude their mouthparts in the 'pouting' behaviour previously described by Weber (1972), but this also was not quantified.

The frequency of five of the six behaviours recorded changed significantly over the course of the three observation periods (licking: $F_{2, 240} = 88.9$, $p < 0.0001$); transporting:
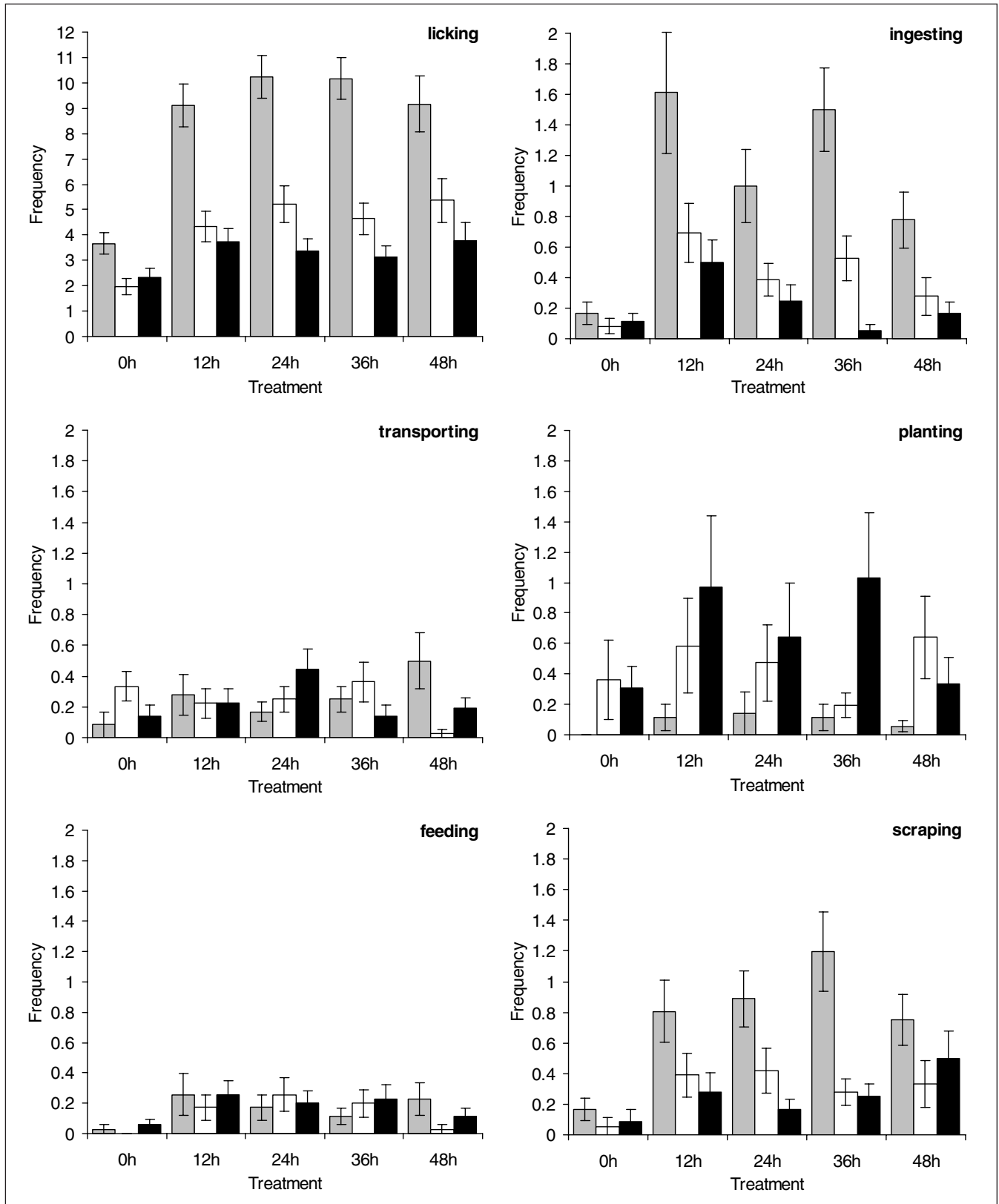
Figure 1. The mean (± s.e.) frequency of behaviours (licking body, transporting around the fungus garden, feeding with fungal hyphae, scraping mouthparts, ingesting larval faecal fluid, or planting fungal hyphae on body) observed by *Acromyrmex* workers towards larvae either 0–30 (grey), 45–75 (clear) or 90–120 (black) minutes after being placed together. The data are for larvae that had been maintained without workers for either 0 h, 12 h, 24 h, 36 h or 48 h. Note that the y-axis scale differs between licking and the other behaviours

$F_{2, 240} = 6.61$, p = 0.002; ingesting: $F_{2, 240} = 37.3$, p < 0.0001; planting: $F_{2, 240} = 9.52$, p = 0.0001; scraping: $F_{2, 240} = 26.6$, p < 0.0001), but the frequency of feeding did not ($F_{2, 240} = 0.651$, p = 0.522). Licking larvae, scraping their mouthparts and ingesting their faecal fluid, were all most frequent immediately after the workers were placed with them and decreased in frequency over the three observation periods (Fig. 1). The occurrence of workers planting fungal hyphae on the bodies of larvae became more common the longer workers were with the larvae (Fig. 1). Treatment (the period of time larvae had been isolated prior to workers being added) significantly affected the frequency of licking ($F_{4, 120} = 10.6$, p < 0.0001), transporting ($F_{4, 120} = 3.47$, p = 0.01), ingesting ($F_{4, 120} = 7.87$, p < 0.0001), and scraping ($F_{4, 120} = 5.94$, p = 0.0002). In all cases this was due to unisolated larvae being the recipients of fewer behavioural acts than larvae that had been isolated from workers (Fig. 1). There was no effect of the length of isolation and even unisolated larvae were the recipients of many occurrences of these behaviours. There was no significant effect of treatment on the frequency of workers feeding larvae ($F_{4, 120} = 2.27$, p = 0.065) or planting fungal hyphae upon the bodies of larvae ($F_{4, 120} = 0.682$, p = 0.606), but both these behaviours also occurred more often towards workers isolated for some time than towards control larvae (Fig. 1). The three species differed significantly in the frequencies of licking ($F_{2, 120} = 4.14$, p = 0.018), transporting ($F_{2, 120} = 16.2$, p < 0.0001), feeding ($F_{2, 120} = 3.62$, p = 0.03) and planting ($F_{2, 120} = 5.31$, p = 0.006), with *A. rugosus* workers engaging in the former three behaviours more often than the other species, while *A. crassispinus* engaged in planting of fungal hyphae more often than the other species. There were no differences between species in the frequencies of ingesting ($F_{2, 120} = 1.25$, p = 0.291) or scraping ($F_{2, 120} = 0.132$, p = 0.876). There were also no significant interactions between species and treatment for any of the behaviours (P > 0.05).

Discussion

Six behaviours by workers towards larvae were recorded and quantified: licking larvae, transporting them around the piece of fungus garden, feeding larvae, ingesting their faecal fluid, planting hyphae on their bodies and scraping their mouthparts. In addition, workers frequently antennated larvae and larvae occasionally pouted. Licking was the most frequent of the recorded behaviours while feeding and transporting were relatively rare. The frequencies of all six behaviours were greater when workers were interacting with larvae that had been isolated for a period of time than with the control larvae, but there appeared to be no effect of the length of isolation. For isolated larvae, the frequencies of licking, ingesting faecal fluid and scraping mouthparts all decreased over the course of the observations while the frequency of planting increased. Transporting and ingesting changed less markedly over the three observation periods.

Of the six behaviours recorded by workers towards the larvae, licking was by far the most frequent. It is possible that this behaviour may be a means by which a worker gains in-

formation about the larva, for example of its state of hunger. It is also likely that the behaviour plays a role in preparing larvae for incorporation in the fungus garden and in protecting larvae against disease. Important individual mechanisms of defence are grooming and the antibiotic secretions of the metapleural gland (Hughes et al., 2002; Poulsen et al., 2002). Larvae are unable to groom, have no metapleural gland and will therefore be exceptionally vulnerable to parasites. The frequent licking of larvae by workers may both ensure any microorganisms on their cuticle are rapidly removed and may cover the cuticle of larvae in compounds from the labial and mandibular glands, both of which have antibiotic properties in leaf-cutting ants (Kermarrec et al., 1986; North et al., 1997). The scraping of larval mouthparts by workers with their mandibles seems likely to also serve a hygienic function, as well as preventing the mouthparts of larvae being hindered by an accumulation of material. The frequencies of both licking and scraping decreased over the three observation periods. Larvae were not licked or scraped after they had had hyphae planted on them. The decreases in licking and scraping may therefore simply reflect the decreasing number of larvae without hyphae on them and/or the increasing cleanliness of larvae over the course of the observations.

The ingestion of larval faecal fluid (proctodeal trophallaxis) has previously been observed in the leaf-cutting ant *Atta sexdens* (Schneider et al., 2000), as well as a number of other ant species (Hölldobler and Wilson, 1990), and appears to be a relatively frequent behaviour. Trophallaxis between adult workers, in contrast, occurs only rarely in attine ants (Murakami and Higashi, 1997; Schneider et al., 1999). The ingestion of larval faecal fluid may simply be for hygienic reasons, keeping both the larvae and fungus garden clean of excreta. However, it seems likely that the workers may gain some nutritive benefit from the fluid. The contents of the larval hind gut originate from the Malpighian tubules and in *Monomorium* have been found to be rich in amino acids (Hölldobler and Wilson, 1990). Adult leaf-cutting ant workers require the products of the hydrolysis of plant polysaccharides, particularly glucose, to survive (Silva et al., 2003), but are lacking in the requisite enzymes to obtain these (D'Ettorre et al., 2002). Although the mutualist fungus does contain a certain amount of such compounds, *Atta sexdens* workers survive almost twice as long when provided with a diet of glucose as opposed to one of fungal material (Silva et al., 2003). Larvae have much larger quantities of digestive enzymes than adult workers (D'Ettorre et al., 2002), and will thus be better able than adult workers to digest fungal material. The fluid from their hind gut may therefore be both a source of digestive enzymes and of nutrients for the adult workers. It is notable that if colonies of leaf-cutting ants lack larvae then the workers become sluggish and the colony rapidly dies (Weber, 1972). Although this has been assumed to be due to larvae producing pheromones that unify the colony, it is also possible that larval faecal fluid is in fact a critical source of nutrients and/or enzymes for the adult workers.

It has previously been noted that attine larvae are generally located within the fungus garden and that they are often covered in a blanket of hyphae (Weber, 1972; Schultz and

Meier, 1995; Adams et al., 2000). In this study we observed workers actively placing fungal hyphae on the bodies of larvae and then pressing down the hyphae with their forelegs and mouthparts in a manner reminiscent of the way they plant hyphae in the fungus garden. This suggests that the occurrence of hyphae on larvae is not simply a consequence of their living within the fungus garden, but that it serves some purpose. It may be that it protects larvae against parasites or that it acts as camouflage against predators such as army ants (Weber, 1972; Swartz, 1998; LaPolla et al., 2002). Alternatively, it may be that either cuticular compounds produced by the larvae or saliva applied to their cuticle by workers during the act of licking, may promote fungal growth (Weber, 1956; 1972). Hyphae were only planted on larvae after they had been thoroughly licked and the frequency of planting was observed to increase over the three observations presumably because of the need for larvae to be licked first. It may be that larvae need to be clean before hyphae can be planted on them or that the saliva is necessary for fungal growth. Regardless, the fact that workers actively apply hyphae to larvae suggests that covering larvae with hyphae is in some way important to one or other party.

The frequencies of all six behaviours recorded were greater towards larvae that had been maintained without workers than towards control larvae. The difference was significant for licking larvae, transporting larvae, ingesting their faecal fluid and scraping their mouthparts, and was only marginally nonsignificant for feeding larvae. This difference suggests both that the isolation of larvae causes them to be associated with greater levels of whatever cues stimulate workers to care for them, and that workers are able to assess larval needs to at least some extent. Although attine larvae are immobile they can 'pout', or extrude their mouthparts, which can stimulate workers to feed them (Weber, 1972). It is also possible that they may emit pheromonal cues that could be volatile or nonvolatile, and that may perhaps be sensed by workers during the act of licking. The most obvious reason for workers to give more attention to larvae that have been isolated is because they are hungrier. *Solenopsis* workers, for example, adjust feeding rate according to the hunger-level of larvae (Cassill and Tschinkel, 1995). However, the fact the feeding rate was increased only slightly, and nonsignificantly, by larval isolation suggests that this was at most only part of the reason for the increased frequency of behaviour shown by workers towards isolated larvae. Hygiene, the removal of excreta and the preparation of larvae for incorporation in the fungus garden would seem to be more important reasons.

The fact that no differences were found between the different lengths of isolation, suggests that the cue(s) may be binary rather than providing more detailed information. Alternatively, it may be that all of the time periods for which larvae were isolated were at the extreme of what would naturally occur and that workers could not distinguish between such extreme levels. Several of the behaviours also became less frequent the more time workers had spent interacting with the larvae. This could relate to decreasing numbers of larvae giving off the cue(s) because more and more of them had been dealt with by workers or had been planted with

hyphae, or to individual larvae emitting reduced levels of the cue(s) once they had been given the attention they required. Further work is needed to elucidate the mechanism and reason for the observed increase in worker attention to isolated larvae. However the results demonstrate that *Acromyrmex* workers are to at least some extent able to assess and respond to the relative needs of larvae.

Acknowledgements

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