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Claustral colony founding is limited by body condition: experimental feeding increases brood size of *Lasius niger* queens (Hymenoptera: Formicidae)

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ABSTRACT

Ants can found colonies in different ways. One is by claustral colony foundation, when fertilized queens typically have enough nutrients reserved in their bodies to raise the first 'nanitic' worker generation without any foraging activity. This colony-foundation strategy evolved in response to selective pressures (e.g. predators), but it limits the number of nanitic workers. We, therefore, assumed that fed queens might initially rear more nanitic workers, although feeding might also be associated with risks and stress. In this study, we analysed the effects of stress and different diets during the colony-foundation period on the success of colony founding by claustral black garden ant *Lasius niger* (Hymenoptera: Formicidae) queens. Our findings confirm that regularly fed claustral ant queens raise more pupae and workers, reflecting that limited brood size is a cost of safety behaviour for claustral ant queens. There is another notable aspect of our findings for laboratories: in order to maximize the size of the nanitic worker generation, they can feed claustral ant queens with crickets.

Keywords: black garden ant; carbohydrate; colony-founding strategies; diets; laboratory ant colonies; protein; starvation; stress; sugar

INTRODUCTION

Colony foundation is a fundamental but risky period in the lives of ant queens. After mating, fertilized queens adopt different strategies to found colonies (Hölldobler and Wilson 1990). Two main types of colony founding have been distinguished: independent (semi-claustral or claustral) (Keller and Passera 1989, Sommer and Hölldobler 1995, Brown and Bonhoeffer 2003, Johnson 2006) or social parasitic (temporary or permanent) (Buschinger 1986, 2009).

The basically ancient, semi-claustral form of independent colony foundation means that queens leave the nest and search for food to nurture their larvae because they cannot store enough nutrients in their relatively small bodies (Johnson 2002, Brown and Bonhoeffer 2003). Given this need to search for and find food, only well-fed regular forager/hunter semi-claustral queens can raise their offspring successfully (Brown and Bonhoeffer 2003, Johnson 2006). However, when semi-claustral ant queens are foraging for food, their mortality rates increase significantly because of predators, which puts a strong selective pressure on them (Hölldobler and Wilson 1990, Brown and Bonhoeffer 2003).

In order for a queen to be able to manage exposure to high food stresses and starvation until the arrival of nanitic (the first, small, short-lived) workers without having to leave the nest and put herself at risk of falling prey to predators, she needs to store nutrients in her body (Hölldobler and Wilson 1990, Brown and Bonhoeffer 2003). A queen with a suitable amount of reserved nutrients does not need to forage and can remain in her nest for weeks. This behavioural pattern is the claustral colony-founding strategy. The queen raises her brood by metabolizing specially accumulated body reserves and histolysing the flight muscles (Brown and Bonhoeffer 2003, Johnson 2006, Matte and Billen 2021).

The transition from semi-claustral to claustral colony foundation was an essential step in the evolution of colony foundation (Aron and Passera 1999, Brown and Bonhoeffer 2003, Madsen

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and Offenberg 2017), but there are also some examples of the reverse transition (Peeters and Molet 2009). It seems that claustral colony foundation is safer and more beneficial, but these benefits can have costs. The drawbacks of this strategy can be the limited amount of nutrients and resources inside the bodies of the queens (Jönsson and Jonsson 1997, Johnson 2006) and the higher feeding costs from the side of the maternal colony (Keller and Passera 1989). Furthermore, bigger and heavier queens are more noticeable to predators than smaller ones, and it is more difficult for them to colonize more distant areas (Keller and Passera 1989, Hölldobler and Wilson 1990, Brown and Bonhoeffer 2003).

Ants are good laboratory model organisms (Hölldobler and Wilson 1990, Czechowski and Pisarski 1992). The possible consequences of providing or not providing food for claustral ant queens also has implications for researchers who seek to develop strong ant colonies within a short period of time. On the one hand, providing food helps queens to establish stronger colonies; on the other hand, feeding can disrupt colony establishment and also poses risks of accidents. For example, disturbed queens often eat the brood, food waste can be a breeding ground for infection, the brood and adults can be stuck in the honey/sugar water, and ants can escape and be harmed during feeding (A.T. and N.S., personal observations). Nevertheless, the possibility cannot be ruled out that claustral queens eat some food in the wild (Brown and Bonhoeffer 2003), if the opportunity arises, e.g. if some small animals (such as arthropods or worms) enter their chamber or if some root aphids start living in their nest.

The aforementioned issues raise an interesting question: would providing food for claustral ant queens increase the number of nanitic workers or would feeding disrupt the colony-foundation strategy that has evolved?

In order to monitor which nutrients are most influential in the colony-foundation period of the queens, we must be aware of the nutritional demand of the ants. In most ant species, two main types of nutrients should be provided to rear fit individuals: carbohydrates and proteins (Markin 1970, Sorensen and Vinson 1981, Cassill and Tschinkel 1999, Csata and Dussutour 2019), but the nutritional demands of larvae and workers are different (Cassill and Tschinkel 1999, Dussutour and Simpson 2008a).

We predicted that feeding would restore the semi-claustral feature of ant queens, i.e. they would take advantage of the opportunity to eat. In this study, we sought to determine whether providing carbohydrate-based food supplements and/or protein-based food supplements would influence the success of colony foundation by claustral ant queens, measured by the number of developed pupae and nanitic workers.

MATERIALS AND METHODS

Model organism

Lasius niger (Linnaeus, 1758) (Hymenoptera: Formicidae) is one of the most common and widespread species of ant in the Palaearctic region (Seifert 2020). This ant is an opportunistic, abundant species, which can be found in different habitats, including urban areas and human homes (Wilson 1955, Seifert 1992). The nuptial flights of *L. niger* happen on hot summer afternoons, when weather conditions are anticyclonic, with low wind speed. At this time, masses of copulating ants can be seen in the air (Boomsma and Leusink 1981, Seifert 2018). After mating, males die, whereas the successfully fertilized females remove their wings and start digging holes in the ground. The queens obtain enough sperm for a lifetime during the process of copulation (Lafleur 1941). Given that *L. niger* queens follow the claustral colony-founding strategy (Sommer and Hölldobler 1995), and hundreds of them can be collected within an afternoon around the campus of the University of Debrecen (A.T. and N.S., personal observations), we chose this well-known species as a model organism for our study.

Experimental details

Two hundred and forty *L. niger* queens were collected during the afternoon of 6 July 2021 within the area of the campus of the University of Debrecen (47°33′21″N, 21°37′18″E; 130 m a.s.l.). Ants were put into 12 mm × 100 mm glass test tubes immediately. The bottom halves of the tubes were filled with water and separated by wet cotton wool (Hölldobler and Wilson 1990). These tubes with the queens were kept in a dark and stress-free place at room temperature (24.5 ± 0.5°C) for the entire study. The queens were separated randomly into eight different groups (Fig. 1; Supporting Information, Appendix S1). Each group consisted of 30 queens.

These groups differed in the combination of diets and treatments they were given. Four diets (sugar, cricket, both, and none) and three feeding frequencies (once at the beginning, once weekly, and never) were applied during the experiment (Fig. 1, Supporting Information, Appendix S1). The sugar (carbohydrate) diet was based on a 1.75 mol dm^{-3} sucrose solution (Detrain and Prieur 2014), and tap water was used as a solvent. All the ants (queens and, later, young colonies) that belonged to this group received a standard 3 μL droplet measured by automatic pipette directly into the test tube. In pre-tests, this volume was found to be optimal and drinkable for a queen or a small colony within a short period of time. The cricket-based (protein) diet was ensured in the form of juvenile Jamaican field crickets, *Gryllus assimilis* (Fabricius, 1775) (Orthoptera: Gryllidae), 2–3 mm in size. We used this species as a natural crude protein source because the dry matter of this insect contains 55.6% crude protein (Mlček *et al.* 2018), and it is a frequently used feed in myrmecological studies (Vogt 2003, Gavilanez-Slone and Porter 2013, Advento *et al.* 2022, van Wilgenburg *et al.* 2022). The third type of dietary treatment was a combination of the previous two (hereafter ‘combined diet’). The chambers of all the queens that were given food were cleaned regularly to avoid infection. Given that feeding and cleaning are sources of stress, a weekly disturbed but unfed group was also set up as a control. Each queen and young colony in this group received a three-dimensional printed plastic particle (2 mm × 2 mm × 3 mm) of a similar size to the crickets, imitating feeding and disturbance. In each case, the residue of the food or the plastic particles was removed on the day after feeding. Finally, there was a control group that was not given any treatment (neither fed nor disturbed).

The experiment started on the day after collection (7 July 2021) and lasted for 7 weeks (49 days; a week after the first workers appeared with some queens), when the numbers of pupae and workers (P&W) were counted (25 August 2021).

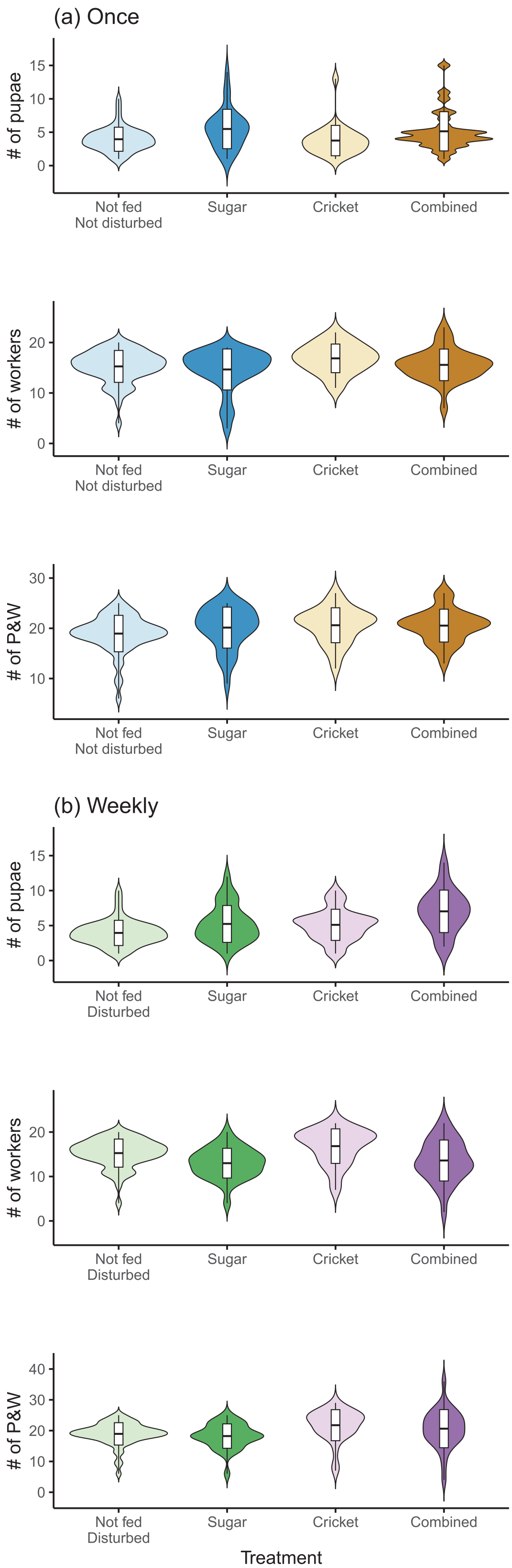

Figure 1. Descriptives of *Lasius niger* queen groups submitted to different treatments on the basis of their pupae and worker production in 49 days. Abbreviation: P&W, pupae and workers.

Statistical analysis

All statistical analyses were performed using R v.4.2.2 (R Core Team 2020). We applied linear regression models (LMs) to evaluate the effects of sugar, cricket, and combined diet on the number of P&W in separate models for treatments once or weekly. We checked the normality of the response variables by visual investigation of histograms and quantile–quantile plots, and we excluded outlier cases to reach approximately normally distributed variables (N = 220 colonies). We ln-transformed the number of pupae before executing LMs. The predictors were centred and scaled before entering them into the models. To keep our work simple, we have provided additional analyses of our multifactor experimental design, including group comparisons, in the Supporting Information (Appendix S2).

RESULTS

For ant queens fed once at the beginning of the experiment (Fig. 1A), we found that the number of pupae increased when they were treated with sugar ($\beta = 0.120$, $t_{131} = 2.936$, $P = .004$), but feeding the cricket diet ($\beta = -0.034$, $t_{131} = -0.836$, $P = .405$) or the combined diet ($\beta = 0.079$, $t_{131} = 1.945$, $P = .054$) resulted in statistically similar numbers. Queens fed with crickets produced more workers ($\beta = 0.507$, $t_{134} = 2.044$, $P = .043$), but those fed with sugar ($\beta = 0.066$, $t_{134} = 0.268$, $P = .789$) or with the combined diet ($\beta = 0.107$, $t_{134} = 0.431$, $P = .667$) were similar.

In contrast, production of pupae by weekly fed ant queens (Fig. 1B) was significantly greater when treated with sugar ($\beta = 0.089$, $t_{136} = 2.184$, $P = .031$) or crickets ($\beta = 0.104$, $t_{136} = 2.557$, $P = .012$). However, the largest effect was produced by feeding the combined diet ($\beta = 0.197$, $t_{136} = 4.798$, $P < .001$). Interestingly, the number of workers was lower for queens fed with sugar ($\beta = -0.850$, $t_{133} = -3.061$, $P = .003$) but higher for queens fed with crickets ($\beta = 0.769$, $t_{133} = 2.769$, $P = .006$). The combined diet had no significant effect on the number of workers ($\beta = -0.327$, $t_{133} = -1.181$, $P = .240$).

We summed the number of P&W and found that ant queens fed once produced a similar number of P&W regardless of the diet (sugar: $\beta = 0.405$, $t_{136} = 1.415$, $P = .159$; cricket: $\beta = 0.554$, $t_{136} = 1.939$, $P = .055$; combined: $\beta = 0.414$, $t_{136} = 1.444$, $P = 0.151$), whereas weekly feeding with crickets ($\beta = 1.194$, $t_{133} = 3.976$, $P < .001$) had a highly significant effect on the total number of P&W, but sugar ($\beta = -0.358$, $t_{133} = -1.187$, $P = .237$) and the combined diet did not ($\beta = 0.504$, $t_{133} = 1.681$, $P = .095$).

DISCUSSION

The results show the positive influence of feeding on colony-founding success of *L. niger* queens in the laboratory. However, different feeding frequencies and different diets influenced this success on varying levels.

According to our experiment, the cricket-based diet and the combined diet exerted the strongest influence on the number of P&W, because the colonies that were fed with one of these diets had more P&W than the colonies that were given a sugar-based diet. Altogether, the least effective way of feeding was the regular sugar-based diet, because these colonies had fewer workers. Consequently, the best way to reach the highest number of P&W is the cricket diet (see also Supporting Information, Appendix S2). It is interesting to note that the primarily semi-claustral ant species are basically hunters and typically feed more on protein than on carbohydrates (Hölldobler and Wilson 1990).

Given that proteins are the basic nutritional component of the body of an ant (Sorensen and Vinson 1981, Cassill and Tschinkel 1999, Dussutour and Simpson 2008b, 2009, Csata and Dussutour 2019), it seems obvious that a protein-rich diet should yield the highest number of P&W, but Dussutour and Simpson (2012) found that *L. niger* workers can die young from a high-protein diet.

At first glance, it seems that our results confirmed that a sugar-based diet alone is not sufficient for developing ant workers (Dussutour and Simpson 2009, Kay *et al.* 2014, Madsen *et al.* 2017). However, we found that the number of pupae was higher when feeding only once with the sugar-based diet (Fig. 1B), which can be interpreted as a developmental delay. It is worth noting here that a carbohydrate-based diet increases social immunity in ants (Kay *et al.* 2014).

Interestingly, in the case of feeding with a combined diet, independently of the feeding frequency, fewer P&W were present in the colonies than in the case of feeding with only crickets, except for the number of the pupae in the case of weekly feeding. At first, this seemed puzzling, but during the feeding procedure we usually observed that if crickets and sugar solution were provided together, the queens attacked the dead crickets immediately and then started drinking the sugar solution. On the day after feeding, food residues were removed, and at that time the crickets were usually intact. Presumably, this way the larvae did not get the extra protein we offered to the queen. This might indicate that queens were engaged primarily with feeding themselves rather than their larvae.

Although claustral queens have adapted not to eat during colony foundation (Brown and Bonhoeffer 2003, Matte and Billen 2021), starvation is a stressor for them (Matte and Billen 2021). Based on our results (Fig. 1; Supporting Information, Appendix S2), starvation seems more stressful for queens than disturbance, because queens that were fed crickets weekly produced significantly more P&W than queens that were not fed and not disturbed.

Although the queens that were not fed and were disturbed produced fewer P&W than the queens that were not fed and were not disturbed, there was no statistically significant difference between them. This was an unexpected finding that does not clearly support the notion that the optimal habitat for ant queens to found new ant colonies is a calm place (Andrasfalvy 1961, Brown and Bonhoeffer 2003).

After the number of P&W had been summed, only one statistically significant different group combination remained. We explain these results with the suggestion that there might be differences in the hatching days of workers from pupae in the case of the different groups, which is worth testing further. These findings summarize the main results clearly: the group of ant queens that was fed with crickets weekly (and therefore also disturbed) produced more P&W than the group of ant queens that was not fed and not disturbed.

Consequently, weekly feeding with crickets is an effective treatment to increase the number of the P&W of *L. niger* queens. According to these findings and the experiences of hobby ant keepers with numerous claustral ant species (https://www.facebook.com/groups/hangyaszat), a cricket diet and perhaps a combined diet might help claustral ant queens during colony foundation. However, our results also show that claustral ant queens usually raise a great number of workers without any food supply. Nonetheless, it would be worth considering the possible risks mentioned in the Introduction.

Some characteristics of the semi-claustral strategy can reappear to a certain extent during the colony-founding period among claustral ant queens (Brown and Bonhoeffer 2003). Such features can make an evolutionary transition path from claustral to semi-claustral colony founding (Peeters and Molet 2009). Our results confirm that the claustral colony-founding strategy is a forced response to selective pressures, e.g. predation (Hölldobler and Wilson 1990, Brown and Bonhoeffer 2003), and thus, limited brood size is a cost. However, artificial feeding helps claustral ant queens during the colony-foundation period and, consequently, they can raise more nanitic workers than during starvation. Thus, our results confirm that the claustral colony-founding strategy is affected by the reserved nutrients available, in addition to body size and dispersal ability, under selective pressures (Hölldobler and Wilson 1990, Johnson 2002, 2006, Brown and Bonhoeffer 2003).

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The data on which this article is based are available in the Supporting Information (Appendix S1).

AUTHOR CONTRIBUTION

A.T. and N.S. contributed to the study conception and design. A.T. and N.S. contributed to the purchase of materials. The experimental works, data preparation and data collection was performed by S.N. and A.T. Data analyses were performed by J.N. The first draft of the manuscript was written by S.N., A.T. and J.N. All authors commented on revised versions of the manuscript. All authors read and approved the final manuscript.

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