

On the evolution of claustral colony founding in ants

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ABSTRACT

The dispersal and survival of offspring is a key step in an organism's life history. In ants, the main strategy used to complete this step is known as independent colony-founding. Here, individual young queens leave their natal nest, find a suitable area to dig a new nest and found their own colony. There are two versions of this strategy. First, in the primitive version, queens forage for food on which to raise their brood; such queens are semi-claustral. Second, in the derived version, queens do not forage but seal their nest and raise their brood by metabolizing specially laid-down body reserves; this is the claustral (meaning 'cloistered') strategy. Claustral queens exhibit a suite of traits that have evolved to favour this derived colony founding strategy. Mortality during foraging has been suggested as the main selective pressure behind the evolution of claustral colony founding. This shift, from semi-claustral to claustral founding, is an essential step in the evolution of ants. However, the explicit conditions under which it might occur have not been examined. Furthermore, in some derived species the primitive semi-claustral founding strategy has re-appeared. We review the occurrence of semi-claustral founding and develop a simple model to determine when foraging mortality might favour claustral colony founding. Claustral founding is favoured when mortality is high or costs of provisioning claustral queens are low. Surprisingly, our model shows that semi-claustral colony founding may be favoured under biologically realistic parameter values. This may explain the increasing number of reports of semi-claustral founding in derived ant taxa. However, in the general absence of data on foraging and provisioning costs, it remains unclear how frequently semi-claustral founding will be the preferred strategy.

Keywords: ants, colony founding, evolution, Formicidae, mortality, semi-claustral.

INTRODUCTION

In many organisms, reproduction involves the immediate dispersal of offspring (e.g. seeds or aquatic larvae) away from the sessile parent into new areas. Such dispersal may reduce competition between parents and offspring (Lambin *et al.*, 2001), while enabling colonization of new habitats. Thus, successful reproduction requires both survival of the dispersal

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phase and successful establishment by the dispersed offspring. High mortality during this period of life history has led to numerous adaptations, including the production and release of vast numbers of offspring and offspring defences (Crawley, 1983, 1992).

Ants, eusocial Hymenoptera, live in colonies that act as single reproductive units. Although colonies can relocate (e.g. Brown, 1999a), they can usefully be considered as sessile organisms (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). Reproductive strategies are diverse in ants, but the main mode of reproduction involves the release of new queens (reproductive females) from the parental colony (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). These queens then disperse, excavate a nest site and attempt to found a new colony. The ancestral strategy, which is still prevalent among the socially and morphologically more primitive ants (e.g. the sub-families Ponerinae, Myrmeciinae and Nothomyrmecinae), is known as semi- or partially claustral founding (e.g. Haskins, 1941; Haskins and Haskins, 1950a,b, 1955). Here, after nest-digging and egg-laying (Johnson, 2002), foundress queens continue to leave their new nest and forage for food with which to provision their brood. A derived strategy, known as claustral colony founding, is usually accepted to be the general mode of colony founding in the socially and morphologically more advanced ants [especially the sub-families Formicinae and Myrmicinae (Hölldobler and Wilson, 1990)]. In this strategy, after excavating their nest, new queens seal it up and raise their first brood by metabolizing nutritional reserves without going outside to forage. Such fully claustral colony founding is associated with a suite of derived characters, including ingluvial feeding [the ability to feed larvae on metabolized body reserves (Hölldobler and Wilson, 1990)], the storage of large quantities of fat (Keller and Passera, 1989), the ability to produce, store and later metabolize special storage proteins (Wheeler and Buck, 1995, 1996; Wheeler and Martinez, 1995), and, obviously, a change in behaviour post-mating flight (Haskins and Haskins, 1950b). Although the ability to break down and metabolize flight muscles is generally thought of as an adaptation for claustral colony founding, evidence from semi-claustral ponerine (morphologically primitive) species suggests that this may have been a precursor to the evolution of claustral founding (Haskins, 1941).

Given the intricate suite of adaptations that make claustral founding possible, what selection pressures might have led to its evolution? Hölldobler and Wilson (1990) suggested that the mortality risk during foraging, which has been found to be high for workers in some species of ants (Porter and Jorgensen, 1981; Schmid-Hempel and Schmid-Hempel, 1984), may have selected for a founding strategy that reduces this risk. That is, claustral founding was favoured because the chance of dying during foraging for semi-claustral queens was too high.

In this paper, we have three main aims. First, we review the literature to determine the occurrence and nature of semi-claustral foundation among the so-called 'higher' ants. Hölldobler and Wilson (1990) briefly reviewed reports of semi-claustral founding and suggested that it was infrequent in such taxa. If obligatorily semi-claustral species are present within taxa where claustral founding has evolved, then models for the evolution of claustral founding must also explain the re-appearance of semi-claustral foundation in 'higher' taxa. Second, we develop a simple model to determine the conditions under which mortality might select for claustral colony founding. Third, we discuss the results of our model with reference to the distribution of semi-claustral founding strategies and recent experimental data, and make suggestions for future research.

SEMI-CLAUSTRAL FOUNDING AS A STRATEGY IN 'HIGHER' ANTS

Overall occurrence

Hölldobler and Wilson (1990: 145) stated that semi-claustral foundation had been observed in the myrmicine genera *Acromyrmex*, *Manica* and *Pogonomyrmex* and in the formicine genus *Cataglyphis*. We conducted a thorough review of the literature for reports of semi-claustral founding in higher ants, using Hölldobler and Wilson (1990), Bourke and Franks (1995), Seifert (1996), Weber (1972), Web of Science[®] and the specialist journals *Insectes Sociaux* and *Psyche* as starting points. We found that semi-claustral founding has been observed in 12 genera of myrmicines and two genera of formicine ants, for a total of 28 species (Table 1). Given the recent upsurge in reports (10 of the 28 species reports were published in the last 10 years) and the low probability of observing foraging in semi-claustral species, we suggest that the true occurrence of this phylogenetically primitive trait in 'higher' ant species may be much higher (see also Johnson, 2002).

Obligate versus facultative semi-claustral founding

The simple observation of semi-claustral founding behaviour does not automatically imply that it is the obligate strategy of a species. Observations of foraging queens may simply reflect the occurrence of queens that failed to get sufficiently provisioned to raise their first brood claustally. In contrast, most queens may be fully provisioned and thus not observed. Alternatively, a species might employ a mixed founding strategy, with the production of both claustral and semi-claustral queens. Only a few of the reports listed in Table 1 shed light on this matter. Foraging, and thus semi-claustral founding, is obligatory for *Acromyrmex* and *Atta* foundresses, as without fresh leaves their fungus gardens would die and they would lose their source of nourishment. Semi-claustral founding also appears to be obligatory for *Messor andrei*, as female alates lack the storage proteins (Brown, 1999b) essential for claustral founding (Wheeler and Buck, 1995, 1996; Wheeler and Martinez, 1995). Laboratory experiments have shown that semi-claustral founding is obligatory in *Pogonomyrmex californicus*, but facultative in *P. maricopa* and *P. occidentalis* (Johnson, 2002). Currently, the obligatory or facultative nature of semi-claustral founding for the other species listed in Table 1 remains unknown.

The distribution of semi-claustral founding in the higher ants described above suggests that this founding strategy may have re-evolved several times in groups in which claustral founding is otherwise the rule [e.g. *Messor* and *Pogonomyrmex* (Johnson, 2002)]. Consequently, understanding if and when mortality may select for claustral founding should also shed light on the re-emergence of the primitive semi-claustral founding strategy.

THE MODEL

We assume a population in which colonies (the reproductive units) have two options: (i) the resources available for queen production are used to make semi-claustral (i.e. unprovisioned) foundresses, or (ii) the resources are allocated to the production of claustral (i.e. provisioned) foundresses. We further assume that the cost of making unprovisioned semi-claustral and claustral queens (i.e. prior to provisioning) is equal, and that the fitness

Table 1. The occurrence of semi-claustral founding in morphologically derived ant taxa

Subfamily	Species	Type	Reference
Formicinae	<i>Polyrachis laboriosa</i>	?	Lenoir and Dejean (1994)
	<i>P. militaris</i>	?	Lenoir and Dejean (1994)
	<i>Cataglyphis niger</i>	?	Fridman and Avital (1983)
Myrmicinae	<i>Acromyrmex balzani</i>	O	Fowler (1992)
	<i>A. lundi</i>	O	Weber (1972)
	<i>A. niger</i>	O	Fowler (1992)
	<i>A. octospinosa</i>	O	Cordero (1963)
	<i>A. striatus</i>	O	Diehl Fleig and De Araujo (1996)
	<i>A. versicolor</i>	O	Rissing <i>et al.</i> (1986)
	<i>Atta cephalotes</i>	O	Weber (1972)
	<i>Cyphomyrmex colombianus</i>	O	Weber (1940)
	<i>C. costatus</i>	O	Weber (1972)
	<i>Trachymyrmex septentrionalis</i>	O	Weber (1972)
	<i>Serrastruma serrula</i>	?	Dejean (1987)
	<i>Smithistruma emarginata</i>	?	Dejean (1987)
	<i>Strumigenys rufobrunea</i>	?	Dejean (1987)
	<i>Leptothorax nylanderii</i>	?	Buschinger (1969) and L. Plateaux (personal communication) in Keller and Passera (1989)
	<i>Manica rubida</i>	?	Le Masne and Bonavita (1967) in Hölldobler and Wilson (1990), M. Brown (personal observation)
	<i>Myrmica</i> spp.		Buschinger (1990)
	<i>M. laevinodis</i>	?	Hölldobler (1938) in Dumpert (1978)
	<i>M. lobicornis</i>	?	Hölldobler (1938) in Dejean (1987)
	<i>M. rubra</i>	?	Hölldobler (1938) in Dejean (1987)
	<i>M. rugulosa</i>	?	G. Elmes (personal communication) in Keller and Passera (1989)
	<i>M. scabrinodis</i>	?	G. Elmes (personal communication) in Keller and Passera (1989)
	<i>Pogonomyrmex californicus</i>	O	Johnson (2002)
	<i>P. desertorum</i>	?	B. Hölldobler (personal communication), Johnson (2002)
	<i>P. maricopa</i>	F	B. Hölldobler (personal communication), Johnson (2002)
	<i>P. occidentalis</i>	F	I. Billick (personal communication), Johnson (2002)
	<i>Messor andrei</i>	O	Brown (1999b)

Note: The table lists the subfamily and species where semi-claustral founding has been observed. The third column states whether semi-claustral founding is obligatory (O), facultative (F) or of unknown status (?) for each species. The references for the data are given in column four.

of all queens that survive the threat of mortality is equal. First, we define the parameters of the model. Let:

- F = total resources available to a colony for queen production
- C_q = the cost of constructing one new queen
- f_q = the additional resource cost of provisioning a queen to be a claustral foundress
- P_n = the probability of surviving the nuptial flight until the excavation of the new nest
- P_f = the probability of surviving the foraging stage for semi-claustal foundresses

Note that we separate mortality into two parts: P_n = mortality faced by all queens and P_f = mortality faced only by semi-claustal queens.

To determine the conditions under which the claustral strategy is favoured, we calculate the total number of offspring colonies produced by both strategies:

$$N_{\text{claustral}} = P_n F / (C_q + f_q)$$

$$N_{\text{semi-claustal}} = P_n P_f F / C_q$$

Claustral founding is selected for when $N_{\text{claustral}} > N_{\text{semi-claustal}}$. So,

$$P_n F / (C_q + f_q) > P_n P_f F / C_q$$

which simplifies to $1 / (1 + f_q / C_q) > P_f$.

Interestingly, this inequality is independent of F and P_n . Thus, whether a claustral or a semi-claustal reproductive strategy is favoured is independent of the total resources available for producing new queens and their probability of surviving until the excavation of a new nest. The only quantities of interest are the ratio f_q / C_q (i.e. the relative cost of provisioning a claustral queen compared with the construction cost) and P_f (i.e. the probability of surviving through the foraging stage).

Figure 1 shows this relationship for relative provisioning costs from 0 to 3, and for the full range of probabilities of surviving the foraging stage. The basic message of the figure is that, as mortality increases or the relative cost of provisioning claustral queens decreases, the claustral founding strategy is favoured. More simply, as foraging gets more dangerous or provisioning gets less expensive, the more likely it is that a claustral founding strategy will be favoured by natural selection. The central line ('Equal fitness') represents the relationship given our assumptions about (i) the equal cost of constructing claustral and semi-claustal queens and (ii) the equal fitness of colonies produced by all surviving queens. However, these assumptions may not be valid. In the only study of its kind, Johnson (2002) showed that semi-claustal queens may be up to half the size of claustral congeners, and that incipient colonies of semi-claustal queens may have twice as many members. Work on the fire ant *Solenopsis invicta* has shown that the production of a larger initial worker force leads to positive feedback, with such colonies growing faster and producing sexuals earlier (and thus, presumably, having higher fitness) (Vargo, 1988).

The lower line in Fig. 1 ('Claustral fitness = 0.5') represents a relaxation of our assumptions. The relationship shown is for the case when semi-claustal queens are twice as fit, on average, either because they cost less to construct or because they produce fitter incipient colonies (as described above). The parameter space within which claustral founding is favoured is considerably smaller. The upper line in Fig. 1 represents the relationship when claustral queens are twice as fit, perhaps because resources are scarce for foraging queens (reducing their ability to rear offspring successfully) or because queen lifespan is reduced

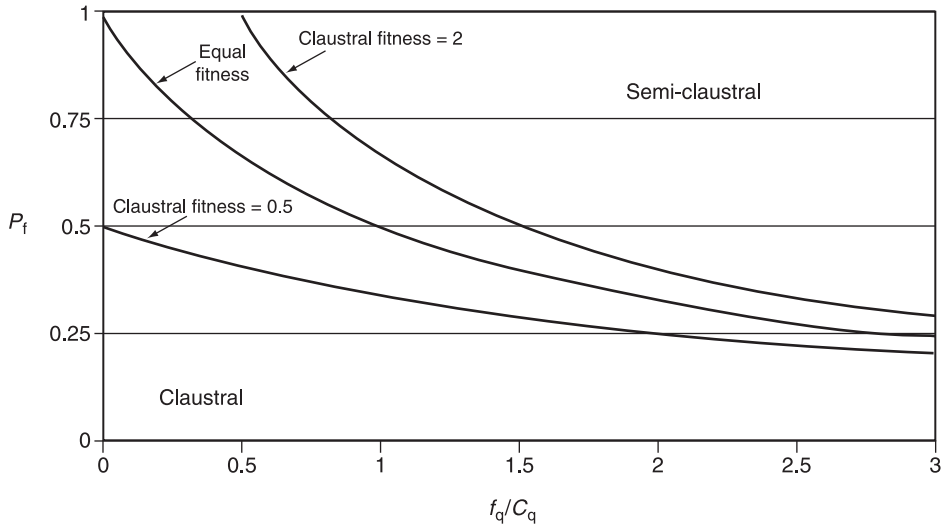


Fig. 1. The relationship between the relative cost of provisioning new queens (f_q/C_q ; on the x-axis), the probability of surviving foraging for semi-claustral queens (P_f ; on the y-axis) and whether semi-claustral or claustral founding will be favoured by selection through foraging mortality. As f_q/C_q and P_f increase, semi-claustral founding is increasingly favoured. The lines represent three different fitness ratios between claustral and semi-claustral queens. For further explanation, see text.

due to wear and tear during foraging. In this case, the parameter space in which claustral founding is favoured increases.

DISCUSSION

Mortality has been suggested to explain the evolution of claustral founding in ants, a strategy often presumed to be almost universal in the derived ant taxa (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). However, semi-claustral founding is more frequent in these taxa than was supposed, and appears to have re-evolved several times (this study; Johnson, 2002). Using a simple but explicit model, we have shown that while mortality during foraging may indeed favour claustral colony founding, in a significant proportion of the parameter space semi-claustral colony founding may be the favoured strategy. Consequently, we should not be surprised either by the presence of semi-claustral founding in derived ant taxa, or its apparently increasing ubiquity (this study; Johnson, 2002).

Clearly, the frequency of semi-claustral founding (or, conversely, claustral founding) in derived ant taxa should be related to the biologically realistic range of the parameter space. Unfortunately, there appear to be no data available on mortality rates during foraging for semi-claustral queens. However, observational evidence suggests that there may have been selection to reduce mortality rates and thus favour semi-claustral founding. In *Messor andrei*, foraging queens run away from and escape encounters with conspecific workers (M.J.F. Brown, unpublished data) – such encounters may be the major source of mortality in ant populations (Hölldobler and Wilson, 1990). Similarly, queens of *Polyrachis* spp. show aposematic coloration and physical traits, including hooks on the thorax and petiole, that

have been interpreted as adaptations to reduce mortality during foraging (Lenoir and Dejean, 1994).

In contrast, there are some data on the relative cost of provisioning claustral queens. Keller and Passera (1989) showed that in *Manica rubida*, semi-claustral queens increased their dry weight between emergence and nuptial flight by approximately 73%, whereas the mean increase for three species of claustral queens was 172%. Assuming equal initial construction costs, this gives a relative provisioning cost for claustral queens of 0.57. If we assume equal fitness of surviving queens, Fig. 1 shows that under such a provisioning cost claustral founding is favoured under most foraging mortality rates. Clearly, we need more information on both mortality rates and provisioning costs before we can determine how likely semi-claustral or claustral founding strategies are to be favoured.

The existence of semi-claustral founding in the derived ant taxa provides an opportunity to examine whether our model provides a good explanation for the evolution of claustral founding strategies. A first test of our model would be to determine the foraging mortality rate of semi-claustral queens and the relative costs of constructing and provisioning queens in semi-claustral and related claustral species. If our model is correct, we would expect data points from semi-claustral taxa to fall above the relevant line on Fig. 1. Such data should be relatively straightforward to collect, and Table 1 provides a number of taxa that would be suitable for such an analysis. An alternative approach would be to examine mortality risk and investment in semi-claustral and claustral queens in a facultatively semi-claustral species (e.g. *Pogonomyrmex occidentalis*). We would expect the position of such a species either to be on the line (if the two strategies are equivalent in this species) or, more likely, to vary from year to year depending upon variation in mortality risks and the amount of resources available to foraging queens.

Can our model explain the existence of facultative semi-claustral founding? As suggested above, such a population strategy may reflect annual fluctuations in mortality risks [perhaps due to changes in conspecific population density (e.g. Gordon and Kulig (1996)] or the availability of resources (Brown and Gordon, 2000). Such fluctuations could alternately favour claustral and semi-claustral founding, and in variable environments the presence of facultative semi-claustral founding may represent a form of reproductive bet-hedging. An alternative and non-adaptive explanation is that the occurrence of facultative semi-claustral founding is the result of behavioural stochasticity in provisioning queens (i.e. some queens simply never get provisioned enough) or due to a sudden reduction in resource availability during the provisioning of queens. Such hypotheses could be tested by manipulating the provisioning of young queens to determine whether this alters their subsequent founding strategy.

As a final point, note that in our model we separate the effects of mortality during the nuptial flight, nest-digging and incipient colony life from those due to foraging behaviour. Although mortality costs may be extremely high for these first three life stages (Gordon and Kulig, 1996; Johnson, 2001), our model suggests that such costs should be irrelevant for an understanding of the evolution of claustral and semi-claustral founding strategies.

Mortality, as suggested by Hölldobler and Wilson (1990), may indeed select for claustral founding in ants. By explicitly stating which parameters should be important, our model enables this statement to be tested empirically. Furthermore, our model provides an explanation for the re-appearance of the primitive state – that is, semi-claustral founding – in otherwise derived ant taxa. This approach, and subsequent tests of this and future

models, are essential if we are to understand the reproductive strategies of one of the most ecologically dominant groups of terrestrial organisms (Hölldobler and Wilson, 1990).

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