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The cost of being queen: Investment across *Pogonomyrmex* harvester ant gynes that differ in degree of claustrality

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ABSTRACT

The role of the ant colony worker largely consists of non-reproductive tasks, such as foraging, tending brood, and defense. However, workers are vitally linked to reproduction through their provisioning of sexual offspring, which are produced annually to mate and initiate new colonies. Gynes (future queens) have size-associated variation in colony founding strategy (claustrality), with each strategy requiring different energetic investments from their natal colony. We compared the per capita production cost required for semi-claustral, facultative, and claustral gynes across four species of *Pogonomyrmex* harvester ants. We found that the claustral founding strategy is markedly expensive, costing approximately 70% more energy than that of the semi-claustral strategy. Relative to males, claustral gynes also had the largest differential investment and smallest size variation. We applied these investment costs to a model by Brown and Bonhoeffer (2003) that predicts founding strategy based on investment cost and survivorship of foundresses during the foraging period. This suggested that non-claustral foundresses of the study species have to survive the foraging period with a probability of 30–36% in order for a foraging strategy to be selectively favored. These results highlight the importance of incorporating resource investment at the colony level when investigating the evolution of colony founding strategies in ants.

1. Introduction

Social insects form decentralized systems where a concordance between individual and colonial behavior must translate to fitness gain. Ant colonies are composed of physically independent somatic (worker) and germ (queen and male) components that perform different tasks. However, during annual reproduction collective worker behavior is vitally linked to development of new sexual offspring. Resource investment by workers into gynes (future queens) is likely to affect their success in colony founding. Given the interdependence of both individual and colonial components, cost-benefit analyses at both levels are integral to understanding how reproductive strategies evolve in ants.

Colony founding is an extremely vulnerable period for harvester ant gynes. Individuals of independently founding species first leave their natal colonies during a nuptial flight to mate. They then disperse and initiate new colonies, usually solitarily. The mortality rate during this stage is extremely high (Pfennig, 1995) and may reach roughly 99 percent (Billick et al., 2001; Gordon and Kulig, 1996; Wiernasz and Cole, 1995), but surviving colonies experience high longevity (15 to >30 years, Gordon, 1991; Johnson, 2001). Although survival is often a matter of stochastic good luck of a foundress happening to land in a suitable and unoccupied area, there is, however, likely to be strong selection pressure upon even upon these fortunate females to behave optimally relative to claustrality. Thus, every mature, reproductive colony has been 'lucky' at its initiation, but has also simultaneously survived a strong selective filter.

Several colony founding strategies correlate with gyne morphology and physiology in ants (Johnson et al., 1996; Keller and Passera, 1988, 1989; Peeters and Ito, 2001; Rüppell and Heinze, 1999; Rüppell et al., 1998, 2001; Stille, 1996). One such tactic is the degree of claustrality, which describes the extent to which gynes rely on their internal reserves for raising their first brood of workers (termed nanitics or minims). Claustral (C) gynes depend entirely on their internal body reserves and do not forage (Hölldobler and Wilson, 1990). They have a large body size with sufficient lipid and protein stores (Hahn et al., 2004). Alternatively, semi-claustral (SC) gynes are smaller in size with fewer reserves, necessitating obligate foraging during colony initiation. Finally, some species are facultative foragers (F), meaning that some gynes

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forage while others do not. For these species, foraging variation exists among gynes within colonies (Anderson and Keyel, 2006; Brown and Bonhoeffer, 2003; Enzmann and Nonacs, pers. obs.; Johnson, 2002, 2006), and likely exists across populations and across years due to variation in resource availability (Brown and Bonhoeffer, 2003; Johnson, 2006). Gynes of facultative species are generally intermediate in size and contain higher lipid and storage protein reserves (Hahn et al., 2004; Johnson, 2002, 2006) than obligately semi-claustral species.

Given the disparity of when resources for reproduction are obtained, variation in claustrality has been equated to different breeding strategies in life history theory (Johnson, 2006). Claustral gynes are capital breeders because they use only stored energy for reproduction, while semi-claustral gynes are income breeders because they use energy that is acquired during the reproductive period (Stearns, 1992).

In the harvester ant genus *Pogonomyrmex*, a full range of claustrality (C, F, and SC) is present across species (Brown and Bonhoeffer, 2003; Hahn et al., 2004; Johnson, 2006). This variability is an unusual case in the Myrmicinae, since fully claustral founding is a derived condition and largely predominant in more derived ant subfamilies (Myrmicinae, Formicinae, Dolichoderinae). Although the semi-claustral strategy is a basal trait (Brown and Bonhoeffer, 2003; Peeters, 1997; Peeters and Ito, 2001) and dominant in older subfamilies (Ponerinae, Myrmeciinae, Northomyrmecinae), its secondary reoccurrence in *Pogonomyrmex* and thirteen other more derived ant genera (Brown and Bonhoeffer, 2003) suggests that it has current adaptive value. The full continuum of claustrality within *Pogonomyrmex* makes it an excellent study genus for cost-benefit analysis of this trait.

Given that gynes are almost always larger than workers in ants, their production cost is an expensive investment on the part of the colony (Keller and Passera, 1989). Gynes that vary in degree of claustrality have different resource needs, such that greater individual quality (more lipid and protein) trades off with greater numbers. Workers are vitally linked to the claustrality in that they are responsible for providing adequate nutrition to gynes during the larval (Wheeler, 1986) and post-eclosal (Boomsma and Issaks, 1985; Nielsen et al., 1985) stages of development. While obligately claustral and semi-claustral species have more rigid investment strategies, facultative species must make prudent decisions of resource investment into the gynes they produce.

Different colony founding strategies have likely evolved in response to variability of food resources at the time of colony reproduction (Brown and Bonhoeffer, 2003; Johnson, 2006). Colonies must invest resources into gynes, with the amounts differing according the strategy employed. However, a comprehensive study of gyne investment across different degrees of claustrality has not been conducted. The difference in production cost between claustral, facultative and semi-claustral gynes is unknown, though it is accepted that claustral gynes are more expensive. Even though production cost can be roughly estimated by adult mass, this value is not always accurate because it doesn't account for respiration throughout development. Metabolic costs can be very high a certain developmental stages, such as in *Lasius flavus* where gyne pupal metamorphosis consumes more than a third of the biomass accumulated as larvae (Peakin et al., 1989). Also, while absolute body size of large gynes may render them more costly to produce initially, small gynes have higher mass-specific metabolic rates (Johnson, 1998), such that their developmental costs may in part balance out the investments required by large size. Thus it is important to determine production costs across strategies. Here we investigate the energetic costs of gynes that differ in degree of claustrality in terms of:

(1) The average per capita energetic cost, size, and lipid reserve.
(2) The comparative cost of gynes relative to males.
(3) When each strategy may be selectively advantageous (Brown and Bonhoeffer, 2003).

2. Methods

2.1. Study species

Four species of *Pogonomyrmex* harvester ants that differ in degree of claustrality were collected in California and Florida during their reproductive seasons (spring and summer) over four years (Table 1). Colonies of *Pogonomyrmex californicus* were monogynous in the collection localities. It should be noted that having only one claustral representative, *P. badius* may limit the generality of this study, as this species may turn out to be atypical relative to all other claustral species. However, there is no *a priori* reason as to why the demands of colony founding relative to claustrality would be fundamentally different in *P. badius* and therefore make it inappropriate for comparison. Gynes and males were collected in the following developmental stages: larvae (late instar), early pupae, late pupae, and virgin imagos. Imagos (both sexes) were present approximately a month after larvae and pupae were found in nests of all species, with some overlap of imago and pupae presence. Only imagos whose cuticle was darkened in color were used in measurements, since mature individuals and callows are significantly different in lean mass (dry mass – lipids) (Enzmann pers. obs.; Tschinkel, 1998). Gynes typically accumulate reserves after eclosion up to a limit. Because we could not determine the eclosion dates of the gynes that were collected, so the average lipid and protein reserves may be underestimated.

2.2. Size measurements

For all species, late-instar larvae were grouped as having the largest wet masses out of all larvae collected ($\geqslant$20.0 mg for *P. californicus, P. occidentalis,* and *P. salinus* and $\geqslant$50 mg for *P. badius*). Larvae of this size were not found in *P. occidentalis* colonies, presumably because all the sexual larvae had pupated by the time of collection. Therefore, size and mass measurements for late instar *P. occidentalis* larvae were extrapolated by calculat-

Table 1
Location, degree of claustrality, and dates of collection of the *Pogonomyrmex* study species.

Species	Degree of claustrality	Location	Dates
P. californicus	Semi-claustral[a]	Independence, CA Motte Rimrock Reserve, Perris, CA	June–July 2006, 2007, 2008
P. salinus	Facultative[b,c]	Sierra Nevada Aquatic Research Laboratory, Mammoth Lakes, CA	July–August 2006, 2008
P. occidentalis	Facultative[a,d]	Hallelujah Junction, CA	July–August 2006, 2007, 2008
P. badius	Claustral[e]	Apalachicola National Forest, near Tallahassee, FL	May–June 2009, 2010

[a] Johnson (2002).
[b] Anderson and Keyel (2006).
[c] Enzmann and Nonacs (unpub data).
[d] Billick et al. (2001).
[e] Smith (pers. comm).

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