

## Research article

# Capital and income breeding and the evolution of colony founding strategies in ants

R.A. Johnson

School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA, e-mail: atraj@imap1.asu.edu

Received 16 November 2005; revised 1 March 2006; accepted 29 March 2006.  
Published Online First 30 June 2006

**Abstract.** Ability to store resources that will be used for reproduction represents a potential life history adaptation because storage permits feeding and reproduction to be decoupled spatially and/or temporally. The two ends of a continuum involve acquiring all resources prior to reproduction (capital breeding) or acquiring all resources during the reproductive period (income breeding). Traditional life history theory examines tradeoffs between costs and benefits of such strategies, but this theory has not been integrated into life history studies of ants, even though founding queens have the analogous strategies of fully claustral (capital breeding) and semi-claustral (income breeding). This study demonstrates that facultatively semi-claustral queens of the seed-harvester ant *Pogonomyrmex desertorum* exhibit phenotypic plasticity during colony founding because unfed queens produced few, small minims, whereas ad libitum fed queens produced larger, heavier minims and additional brood. Fed queens also lost less mass than unfed queens despite their producing more brood. Overall, foraging provides queens with a suite of benefits that likely offset potential negative effects of foraging risk.

Life history studies across a diverse array of taxa show that capital breeding is consistently associated with low availability and/or unpredictability of food, i.e., environmental conditions that favor prepackaging of reproductive resources. Such a broad and consistent pattern suggests that similar factors favored the evolution of fully claustral (capital breeding) colony founding in ants. Overall, these data suggest that ant researchers should revise their conventional view that fully claustral colony founding evolved because it eliminated the need for queens to leave the nest to forage. Instead, colony founding strategies should be examined from the perspective of environmental variation, i.e., availability and predictability of food. I also provide a functional scenario that could explain the evolution of colony founding strategies in ants.

**Keywords:** Brood production, capital breeding, income breeding, life history, colony founding strategies.

## Introduction

A key life history trait is the time at which organisms acquire resources that are used for reproduction. These resources can be acquired prior to the reproductive period (capital breeders), during the reproductive period (income breeders), or during both periods (mixed capital/income breeders) (Bonnet et al., 1998, 2002; Gauthier et al., 2003; Jönsson, 1997; Tammaru and Haukioja, 1996). Capital breeding is probably the most common reproductive strategy in ectothermic vertebrates (Bonnet et al., 1998), and in numerous groups of insects, including those in which the adults lack mouthparts (Tammaru and Haukioja, 1996; Wheeler, 1996). However, capital breeding is rare in endothermic vertebrates, possibly because of the higher cost of energy storage associated with endothermy (Bonnet et al., 1998).

Capital breeding and income breeding have striking parallels with the continuum of reproductive strategies exhibited by queen ants. Fully claustral queens store their reproductive energy prior to mating flights and rear their first brood solely using body reserves (capital breeders). Alternatively, semi-claustral queens forage for reproductive resources during colony founding, and such foraging can be obligate (income breeders) or facultative (mixed capital/income breeder). Obligate semi-claustral queens lack the resources to produce minim workers without an external food source, whereas facultative semi-claustral queens can produce at least some minim workers in the absence of external food (Anderson et al., 2006; Hahn et al., 2004; Hölldobler and Wilson, 1990; Johnson, 2002).

The evolution of fully claustral colony founding is viewed as a major evolutionary advance for ants because it eliminated the need for queens to leave the nest to forage, where individuals are exposed to predation and other sources of mortality (Hölldobler and Wilson, 1990). However, one potential disadvantage for fully claustral (capital) colony founding is that reproductive resources are fixed, necessitating a tradeoff between number and size of offspring (Jönsson,

1997; Oster and Wilson, 1978; Porter and Tschinkel, 1986; Stearns, 1976). In contrast, queen foraging provides a flexible strategy that decouples this tradeoff, such that number and/or size of brood can be matched to environmental resources. Under ideal conditions, brood production can exceed that of fully claustral species (Johnson, 2002).

Fully claustral colony founding is largely restricted to higher ants (subfamilies Dolichoderinae, Formicinae, Myrmicinae), where it is viewed as the typical mode of colony founding (Hölldobler and Wilson, 1990). However, queen foraging is now known to occur in several genera of higher ants, and it seems likely that this behavior is moderately common in these ants (Brown and Bonhoeffer, 2003; Johnson, 2002). The few comparative data on the evolution of colony founding strategies indicate that fully claustral colony founding is positively associated with queen body size (Johnson, 2002), queen to worker size dimorphism (Haskins and Haskins, 1950; Johnson, 2002; Peeters, 1997; Stille, 1996), amount of storage proteins (Hahn et al., 2004), and fat content (Keller and Passera, 1989). Understanding the patterns and processes underlying this variation in colony founding strategies necessitates detailed data on costs and benefits in additional ant species, along with integrating these studies with traditional life history theory that social insect researchers have largely neglected (but see Bourke and Franks, 1995; Heinze and Tsuji, 1995).

Comprehensive analysis of the various modes of colony founding requires data across species that exhibit the range of strategies. The prominent gap in data is the near absence of studies on facultatively semi-claustral species (but see Anderson et al., 2006). This study bridges that gap by examining how food affects queen survival, queen mass, and brood production in the facultatively semi-claustral seed-harvester ant *Pogonomyrmex desertorum* Wheeler. I also provide a functional scenario to explain the evolution of various colony founding strategies.

## Methods

I examined survival and brood production by queens of *P. desertorum* using glass "ant farms" (16 × 12 × 0.75 cm of soil) that facilitated observing queen status (live or dead) and the time course of brood development. The ant farms were filled with soil that had been passed through a 2-mm sieve and mixed into a composite sample. Dealate queens were collected in San Simon Valley, Cochise County, Arizona (31° 57' N, 109° 08' W; elevation 1380 m), immediately after a mating flight in early August 2005. Each queen was placed into an Eppendorf tube containing a small piece of moistened paper towel, then transported to the laboratory. One queen was placed into each ant farm, and the farms were placed in a darkened incubator at about 32° C. Queens were randomly divided into fed and unfed treatments (n = 26 queens per treatment); fed queens were provided ad libitum Kentucky blue grass seeds beginning on day 8. Water was added to nests, as necessary, to keep the soil moist.

Queen status was monitored every several days until a minim worker emerged in one colony. From that time onward, I monitored nests for minim workers every one to two days. At a standard time after emergence of the first minim, each nest was opened, brood (larvae, pupae, and workers) were counted, and the queen was weighed. For each nest, this standard time was calculated as the interval at which the first minim emerged plus 0.25x this interval, i.e., if the first minim emerged after 28

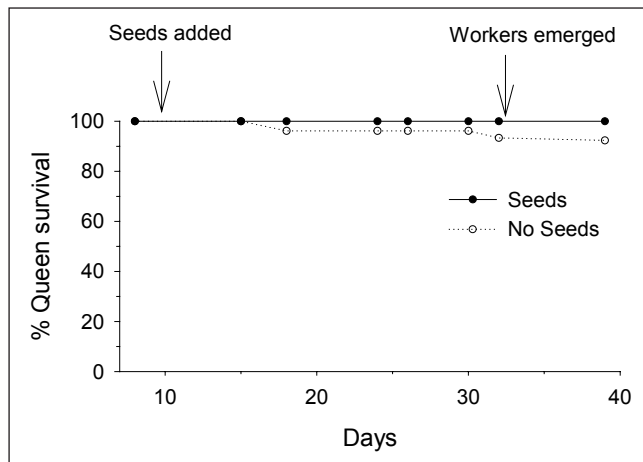
days, then brood were counted at 35 days. Nests were opened at this interval for two reasons: (1) to provide time for the first minims to acquire mature coloration and mass, and (2) to estimate the number and type of brood that unfed queens could produce using their initial body reserves. One to two minims that had developed mature coloration were removed from each nest, dried at 50–55 °C for >72 h, and weighed. I measured head width of minims by projecting a 63x image from a binocular microscope to a video monitor; the image on the monitor was measured to 0.01 mm using Image-Pro Express.

I compared survival curves of fed and unfed queens using the Kaplan-Meier survival analysis log-rank test for censored data (PROC SURVIVAL in SPSS (SPSS, 1990); the comparison ran from the day on which seeds were first provided through the day that nests were emptied. No fed queens died during observations, and the model will not run with all censored events. I dealt with this problem by adding one queen mortality event to each treatment on the day that nests were emptied. Number of days to emergence of the first minim worker, dry mass and head width of minim workers, and wet mass of queens were compared between fed and unfed treatments using a t-test; *P* values were adjusted using the sequential Bonferroni technique. Number of workers, pupae, and larvae were analyzed using a MANOVA followed by t-tests for variables that differed significantly. Data were square-root or log-transformed, as necessary, to equalize variances. Nests that lacked workers and pupae at the end of the experiment were excluded from analyses of brood production and queen mass.

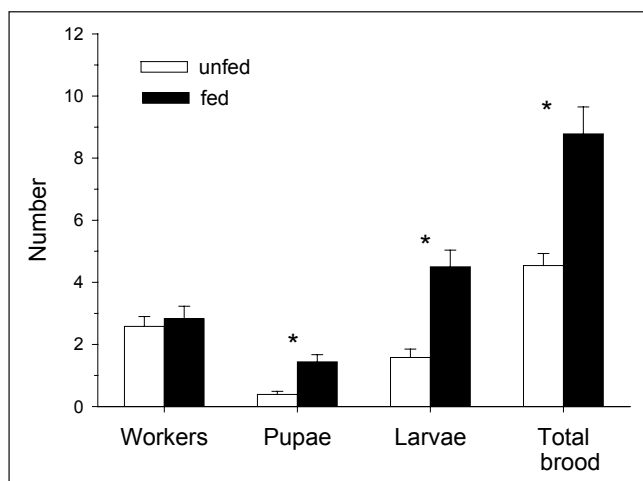
Queens were not weighed prior to the experiment. Therefore, I estimated initial wet mass using alate queens that were collected from the same population immediately before the mating flight. I collected 5–10 alate queens from 12 colonies, which were later dried at 50–55 °C for 72 h, then weighed. Dry mass was averaged within each colony. These mean colony values were used to calculate the grand mean, then doubled because alate queens contain approximately 50% water mass (R.A. Johnson, unpubl. data). I used this estimate of initial wet mass to calculate percent mass loss by fed and unfed queens.

## Results

Survival of *P. desertorum* queens did not vary with food level (Kaplan-Meier log-rank test, LR = 1.1, *n* = 52, 1 *df*, *P* = 0.29; Fig. 1). Fed queens harvested seeds (as indicated by seed caches in their nest chambers), and these seeds conferred a suite of benefits during colony founding. Number of days to emergence of the first minim worker did not differ by food level (*t* = 1.5, *P* > 0.10, 41 *df*; fed = 32.7 ± 0.5; unfed = 32.0 ± 0.0). Number of brood produced by fed and unfed queens differed significantly (Wilks' lambda = 0.51, *F*<sub>(3, 38)</sub> = 12.50, *P* < 0.001). Fed queens produced significantly more larvae (*F* = 25.2, *P* < 0.001) and pupae (*F* = 21.4, *P* < 0.001) than did unfed queens, but number of workers did not differ between the two treatments (*F* = 0.25, *P* = 0.62; Fig. 2). Fed queens also produced minim workers that were larger, both in head width (*t* = 2.7, *P* = 0.01, 37 *df*; *X*<sub>(fed)</sub> = 1.15 ± 0.01 mm, *X*<sub>(unfed)</sub> = 1.12 ± 0.01 mm) and dry mass (*t* = 10.5, *P* < 0.001, 38 *df*; *X*<sub>(fed)</sub> = 0.80 ± 0.01 mg, *X*<sub>(unfed)</sub> = 0.58 ± 0.02 mg) than those produced by unfed queens. Fed queens also weighed about 2.8 mg more than did unfed queens (*t* = 4.3, *P* < 0.001, 36 *df*). All variables remained significant after adjusting *P* values using the sequential Bonferroni technique. Relative to alate queens (24.4 ± 0.2 mg), fed queens (17.4 ± 0.5 mg) lost 28.7% of their initial wet mass, and unfed queens (14.6 ± 0.4 mg) lost 40.2% of their initial wet mass (Fig. 3).



**Figure 1.** Survival curves for single queens of *Pogonomyrmex desertorum* in a one-factor experiment (two food levels) using observation ant farms. The two food levels were Kentucky blue grass seeds provided ad libitum and without seeds. Sample size:  $n = 26$  with seeds,  $n = 26$  without seeds.

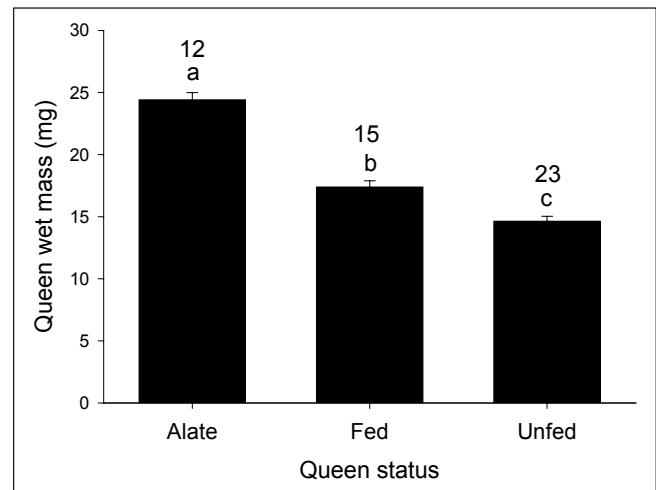


**Figure 2.** Number of workers, pupae, and larvae produced by fed and unfed queens of *Pogonomyrmex desertorum*. Significant differences were determined using a MANOVA followed by a t-test for variables that differed significantly. Significant differences are denoted by asterisks:  $* = P < 0.001$ . Sample size:  $n = 18$  with seeds,  $n = 24$  without seeds.

## Discussion

### *Benefits of queen foraging in Pogonomyrmex desertorum*

Queens of *P. desertorum* employed a mixed capital/income breeding strategy because they were able to produce workers solely using body reserves, but they also foraged for additional food resources. Food provided a suite of benefits that included ability to produce a larger number of brood (especially pupae and larvae) and larger minim workers compared to those produced by unfed queens. Despite their increased reproductive output, fed queens lost less mass than did the



**Figure 3.** Comparison of wet mass (mg) for alate queens, fed queens, and unfed queens of *Pogonomyrmex desertorum*. Significant differences were determined using a one-way ANOVA followed by a Duncan's multiple range test and are denoted by a–c:  $a > b > c$ . Sample size is given above each bar.

less productive unfed queens. These benefits parallel those demonstrated by the facultatively semi-claustral congener *Pogonomyrmex salinus* (Anderson et al., 2006), suggesting that a mixed capital/income breeding strategy provides a generalized suite of benefits during colony founding (see also Johnson, 2002; 2004). Moreover, queens of *P. desertorum* and *P. salinus* exhibit phenotypic plasticity in regard to food availability that results in unfed queens producing small minims and few brood to ad libitum fed queens producing larger minims and additional brood. It seems probable that a range of food levels would result in a graded response in terms of minim size and number of brood produced; this prediction should be tested in further studies.

### *Comparing costs and benefits of queen foraging*

The evolution of life history traits, such as the various modes of nest founding, consists of tradeoffs between costs and benefits. High mortality to foraging queens has been considered the primary cost driving the evolution of fully claustral colony founding in ants (Hölldobler and Wilson, 1990). However, this view conveys an incomplete picture because mortality costs have not been measured and potential benefits have not been considered.

The primary cost of queen foraging is considered to be mortality risk (for a vertebrate example see Lima and Valone, 1986), but the only data on such risk are extrapolated from mortality rates of foraging workers (Hölldobler and Wilson, 1990). This extrapolation is tenuous, however, because foraging risk is undoubtedly lower for queens than for workers. For example, horned lizards (*Phrynosoma* spp.) are the most significant predator to species of *Pogonomyrmex* (Rissing, 1981; Whitford and Bryant, 1979) because they often remain

near the nest entrance, where they can capture numerous workers from one colony. Such a behavior would be less effective on isolated foraging queens, suggesting that predation rates on queens would be lower than for workers. Similar considerations apply to spiders that prey upon *Pogonomyrmex*, especially those that construct a web over the nest entrance (Hölldobler, 1970; MacKay, 1984). Predators of other ant genera probably also focus their activities near mature nests. A last consideration is that workers forage on a mostly continual basis, whereas queens appear to forage in response to nest conditions. Queens of *Messor andrei* cease foraging partway through colony founding (Brown, 1999), and queens of *Pogonomyrmex californicus* foraged less frequently as the seed cache grew in laboratory colonies (R.A. Johnson, pers. obs.). Moreover, queens probably spend much less time outside the nest than conspecific workers because they travel shorter distances and take fewer foraging trips, and hence experience less exposure to predators. Most importantly, future studies should compare potential sources of mortality and mortality rates between foraging queens and workers.

Until recently, queen foraging was considered to be detrimental because no data existed on possible benefits conveyed by this behavior. That fed queens can produce both more and larger workers increases the probability of long-term colony survival, and may balance foraging risk to the queen. Ability to produce larger first brood minim workers is advantageous because larger minims have lower metabolic rates and higher longevities than regular-sized minim workers, such that they are less expensive to produce and maintain per unit mass (Porter and Tschinkel, 1985; 1986). Another consideration is that first brood workers also face a foraging risk. Given that fully claustral queens produce fewer first brood workers than well fed semi-claustral queens (Johnson, 2002), then the death of one minim worker is a substantially higher loss for a fully claustral queen. Lastly, fully claustral queens typically lose >50% of their initial body mass to produce the first worker cohort (Johnson, 1998; Tschinkel, 1993; 2002), leaving them nearly depleted of energy by the time the first workers begin to forage. Queen foraging reduces this cost because well-fed semi-claustral queens retain more energy reserves at the end of the nest founding period. For example, fed queens of *P. desertorum* lost significantly less mass than did unfed queens (28.7% versus 40.2%), and similar benefits occurred in *P. salinus* and the obligate queen foraging species *P. californicus* (Anderson et al., 2006; Johnson, 2004). One potential advantage of queen foraging that has not been explored is the time at which minim workers begin to forage. Given that minims from fed queens are better provisioned and that queen collected food may remain in the nest, then it seems possible that these minims could delay their first foraging trip by several days. Consequently, minims of semi-claustral queens could help rear the second brood for several additional days rather than expose themselves to external sources of mortality. Overall, a suite of costs and benefits need to be considered when comparing various modes of colony founding, and models that consider only costs or only benefits are incomplete. The only paper

that has modeled aspects of nest founding concluded that fully-claustral colony founding becomes more favored as foraging risk increases or as queen provisioning becomes less expensive (Brown and Bonhoeffer, 2003). One of the most important points relative to the model was their suggestion that environmental variability, i.e., year to year variation in resource availability, might affect mortality risk for foraging queens.

The magnitude of costs and benefits to foraging queens is directly affected by food availability. High food availability would be most beneficial to semi-claustral queens because of their phenotypic plasticity in regard to number and size of first brood workers that are produced. Semi-claustral queens will also end the founding period with substantial body reserves under conditions of high food availability, whereas fully claustral queens would end the founding period nearly depleted of reserves. Conversely, semi-claustral queens will do poorly under conditions of low food availability because they will produce fewer brood than fully claustral queens, and they will still end the founding period extremely low on body reserves. Thus, availability of food should be associated with the evolution of various modes of colony founding.

#### *Conditions that select for capital breeding*

Ability to store resources represents a potential life history adaptation because storage permits feeding and reproduction to be decoupled spatially and temporally, i.e., reproductive resources can be sequestered at a time when they may be more plentiful than during reproduction (Jönsson, 1997; Reznick and Yang, 1993). Jönsson (1997) listed five conditions during the breeding period that would favor capital breeding: (1) food is absent or scarce, (2) food demands are very high, (3) foraging success or food demands are variable, (4) high cost of obtaining food due to risk of predation, and (5) time available to forage is limited. Examples that illustrate the link between capital breeding and resource availability include phocid seals (Costa, 1993), migratory birds that breed in polar areas (Gauthier et al., 2003; Meijer and Drent, 1999), poeciliid fish (Thibault and Schultz, 1978; Trexler and DeAngelis, 2003), ectothermic vertebrates (Bonnet et al., 1998) Lepidoptera (Jervis et al., 2005), and parasitoid wasps (Jervis et al., 2001). In all of these examples, capital breeding is viewed as an adaptive trait for organisms that inhabit environments in which food is low in abundance and/or unpredictable in occurrence.

Capital breeding also shows a correlation with body size in several taxa. Capital or near capital breeding appears to occur in only the largest of the migratory bird species that breed in polar regions, while small passerine species are almost exclusively income breeders (Meijer and Drent, 1999). Similarly, body size is consistently much larger for phocid seals (capital breeders) than for species in their sister family Otariidae (income breeders) (Costa, 1993). In contrast, body size is smaller for capital breeding than for related income breeding species of parasitoid wasps (Jervis et al., 2003).



Capital breeding in parasitoid wasps was also negatively correlated with lifespan, apparently because short-lived species must lay their lifetime complement of eggs over their several-hour to several-day lifespan. Extrinsic mortality was suggested as a condition that could cause this correlation because higher mortality rates for smaller species should select for a shift to earlier maturation of eggs. Jervis et al. (2003) suggested desiccation as the likely causal factor because of its much higher impact on smaller species.

One additional cost for capital breeders is that storing large amounts of reproductive resources can reduce immediate survival of an organism, i.e., demographic costs in Jönsson (1997). Stored mass can decrease locomotion, flight, and maneuverability with the effect of increasing risk of predation (Bonnet et al., 1998; Hedenström, 1992; Jönsson et al., 1998). Ectothermic vertebrates incur a storage cost because they often increase basking frequency following mating, which exposes females to predation (Bonnet et al., 2002).

#### *Capital and income breeding in ants*

The above theoretical and empirical studies indicate that capital breeding is associated with low availability and/or unpredictability of food across a diverse array of taxa. Such a broad and consistent pattern suggests that similar factors favor the evolution of fully claustral colony founding (capital breeding) in ants. Determining costs and benefits of founding strategies for additional species is straightforward and valuable, and can be accomplished using experiments such as performed in this study (see also Johnson, 2002), whereas it is much more difficult to evaluate factors that drive the evolution of these strategies. Understanding the evolutionary context of various colony founding strategies requires detailed information on numerous congeners that vary in method of colony founding, combined with mapping these traits onto a phylogeny such as has been done for fish species in the genus *Poeciliopsis* (Reznick et al., 2002). Species that display secondarily derived queen foraging (e.g., *P. californicus*) (Johnson, 2002) provide the best cases in which to link colony founding strategy with habitat and/or food availability. In addition, suites of life history traits are often linked, which suggests that traits such as body size, colony size, fecundity (ovariole number), and foraging method should also be assessed (Jervis et al., 2005; Tschinkel, 1991).

It is also important to note that ants provide a unique system in which to examine the evolution of capital and income breeding. In almost all non-ant species, resources that will be allocated to reproduction are collected by the individual that will reproduce. In contrast, ants (and some other social insects) have sterile workers that collect (and store in some genera) the food used to provision reproductive sexuals. Consequently, acquisition and storage of reproductive resources exerts a negligible demographic cost to the reproductive queen of the colony, regardless of the method of colony founding. Likewise, storage costs to well-provisioned

pre-reproductive queens are probably also negligible given that these individuals are only exposed to environmental vagaries during their short-lived mating flight. Overall, the largest difference among provisioning strategies appears to be that producing poorly provisioned semi-claustral queens allows a proportionate increase in number of sexuals produced.

Queen foraging is correlated with body size across species of *Pogonomyrmex*; species with the smallest queens are obligate foragers, those with intermediate sized queens are facultative foragers, and those with the largest queens are fully claustral (R.A. Johnson, unpubl. data). Queens are also relatively small in most genera that Brown and Bonhoeffer (2003) list as having queen foraging. Interestingly, the full range of colony founding methods can occur across sympatric species of *Pogonomyrmex*. For example, the obligate foraging *P. pima*, the facultative foraging *P. desertorum*, and the fully claustral *P. rugosus* often co-occur at sites in the Sonoran Desert (Johnson, 1998; 2000). All three species have mating flights that are triggered by summer rains, often on the same days, such that founding queens of all three species experience similar soil conditions and food levels. This similarity begs the question of why these three species use a spectrum of colony founding strategies under similar environmental conditions, or alternatively, in what way does the evolutionary history of these species differ such that they experience this similar environment in very different ways (for a similar example in birds, see Martin, 2004)?

One possible functional scenario to explain this pattern results from extrinsic mortality that is correlated with body size (see also Jervis et al., 2003). The most obvious difference among the above three species is body size, which averages about 1.5 mg dry mass for queens of *P. pima*, 12.2 mg for *P. desertorum*, and 26.5 mg for *P. rugosus* (R.A. Johnson, unpubl. data). Desiccation is a common and significant source of mortality for founding queens of desert ants (Johnson, 1998; 2000a), and also for ants that inhabit relatively moist habitats (Green, 1962; Talbot, 1934). Desiccation should impact survival of smaller species most strongly because of their higher surface to volume ratio (Johnson, 2000a), similar to the pattern proposed for parasitoid wasps (Jervis et al., 2003). Large queens should survive over a broader range of moisture regimes than do small queens, e.g., somewhat moist to moist for large queens but only moist for small queens. Under this scenario, queens of larger capital breeding species would experience more variable environments, and hence more variation in food availability across years.

The scenario proposed for ants also explains how desiccation can promote opposing patterns of body size and allocation strategy for ants and parasitoid wasps. The exceedingly short lifespan of very small capital breeding parasitoid wasps necessitates that all eggs are laid within several days (semelparity). In contrast, both small and large founding queens must survive an extended juvenile period that lasts up to several years. At that point, the mature colony begins to produce reproductive sexuals, and continues to do so over most of its adult years (iteroparity).

## Conclusions

Colony founding is the most vulnerable and critical period in the life of an ant colony, and founding queen behaviors such as foraging have been traditionally viewed as increasing mortality (Hölldobler and Wilson, 1990). Phenotypic plasticity in brood production and potential benefits of queen foraging have not been considered until recently, and their occurrence suggests that queen foraging involves a complex suite of costs and benefits. Based on these data, I propose that our view of queen foraging and queen reproductive strategies should be revised and incorporated into the broader evolutionary framework provided by traditional life history theory. This requires studies that examine queen reproductive strategies at both the proximate and ultimate level.

## Acknowledgments

I thank T.E. Martin for pointing out key literature on life history, and J. Oettler and C. Smith for helping to collect queens. The manuscript benefited from comments by K.E. Anderson, J. Gadau, C.T. Holbrook, O. Niehues, J. Oettler, R. Overson, C. Smith, and two anonymous reviewers. I dedicate this paper to Jake, my long-term companion, who provided continual entertainment in the field, and enjoyed the desert even more than me.

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