Robert A. Johnson

Semi-claustral colony founding in the seed-harvester ant *Pogonomyrmex californicus*: a comparative analysis of colony founding strategies

Abstract The evolution of queens that rear their first brood solely using body reserves, i.e. fully claustral, is viewed as a major advance for higher ants because it eliminated the need for queens to leave the nest to forage. In an apparently unusual secondary modification, the seed-harvester ant *Pogonomyrmex californicus* displays obligate queen foraging, i.e. queens must forage to garner the resources necessary to survive and successfully rear their first brood. I examined the potential benefits of queen foraging by comparing ecological and physiological traits between *P. californicus* and several congeners in which the queen can rear brood using only body reserves. The primary advantage of foraging appears to lie in providing the queens of *P. californicus* with the energy to raise significantly more brood than possible by congeners that use only body reserves; the workers reared in the first brood were also heavier in mass than that predicted by their head width. Other correlates of queen foraging in *P. californicus* relative to tested congeners included a significantly lower total fat content for alate queens, a small queen body size, and a low queen to worker body mass ratio. Queens also forage in several other well-studied species of *Pogonomyrmex*, suggesting the possibility that queen foraging may be more common than previously thought in higher ants.

Keywords Brood production · Fat content · Nest founding · *Pogonomyrmex californicus* · Queen body size

Introduction

Nest founding is the most vulnerable stage in the life of an ant colony (Hölldobler and Wilson 1990; Herbers 1993; Johnson 1998), and ants have evolved numerous

R.A. Johnson (✉)
Department of Biology, Arizona State University,
Tempe, AZ 85287–1501, USA
e-mail: atraj@imap1.asu.edu
Tel.: +1-480-8972473, Fax: +1-480-9652519

strategies to survive this stage. The two primary modes of nest founding are dependent colony founding, in which a queen starts a colony with a retinue of workers, and independent colony founding, in which a queen starts a nest without workers. Both founding strategies display several variants (Hölldobler and Wilson 1977). For example, queens that found nests independently can be fully claustral, in which case the queen remains sealed in the nest chamber and uses only body reserves to support herself and raise her first brood. Alternatively, semi-claustral queens leave the nest to forage. Fully claustral nest founding is common in morphologically "advanced" subfamilies of ants (Myrmicinae and Formicinae) and is the derived state, whereas the ancestral state of semi-claustral nest founding is common in morphologically "primitive" subfamilies of ants (Ponerinae and Myrmeciinae; Peeters 1997).

The evolution of fully claustral queens is viewed as a major advance for ants because it eliminated the need for queens to leave the nest to forage, where they are exposed to predation and other sources of mortality (Haskins and Haskins 1950, 1955; Hölldobler and Wilson 1977; Rissing et al. 1989; Peeters 1997). Consequently, the observation that some ant species in the subfamilies Myrmicinae and Formicinae have returned to semi-claustral nest founding, when most of their congeners are fully claustral, requires explanation. Information on semi-claustral nest founding in higher ants is limited to scattered behavioral observations. The only physiological data indicate that queens of *Messor andrei* lack storage proteins (Brown 1999), which comprise a necessary energy source for fully claustral queens to raise their first brood (Wheeler and Buck 1995, 1996).

It has been suggested that queen foraging is associated with the small size of queens relative to the workers (Haskins and Haskins 1950; Stille 1996; Peeters 1997). Correlative evidence for this hypothesis occurs within ponerines, which display a gradation of colony founding methods that range from dependence on queen foraging to ability of the queen to successfully rear her first workers using only body reserves. One of the few species in

the latter group is *Pachycondyla* (= *Brachyponera*) *lutea*, which is exceptional among ponerines because of the unusually large size of queens relative to workers (the maximum known caste dimorphism among ponerines; Haskins and Haskins 1950, 1955; Hölldobler and Wilson 1990; Peeters 1997).

The primary disadvantage for fully claustral queens seems to be that a fixed amount of energy is available to raise the first brood. This requires that the queen allocate her energy to maximize colony success, either by producing many small workers or few large workers. Theory predicts that queens should maximize the initial number of workers produced because some minimum number is needed to perform the gamut of colony tasks that include raising the second brood. Additional brood allow these tasks to be performed more efficiently through division of labor rather than sequentially by the same individual (Oster and Wilson 1978). As predicted, fully claustral ant queens invariably produce many small workers (these small workers from the first brood are called minim workers or minims). Empirical data also demonstrate the adaptive advantage of producing many small workers because the number of workers (not their size) is the primary factor affecting production of the second brood (Porter and Tschinkel 1986).

This study was motivated by observations that queens of the seed-harvester ant *Pogonomyrmex californicus* (subfamily Myrmicinae) forage in the field and laboratory. I assessed the possible benefits of queen foraging by quantifying parameters related to nest founding for *P. californicus* and several congeners. Two hypotheses were tested: first, foraging releases queens from the size versus number tradeoff relative to producing their first brood; second, queen foraging is correlated with body size constraints. I also assessed: (1) if foraging is necessary for queens of *P. californicus* to survive and successfully rear their first minim workers, and (2) if there are additional ecological and physiological correlates of queen foraging in comparison with fully claustral congeners. To this end, I measured several ecological and physiological parameters across several species of *Pogonomyrmex*.

Materials and methods

Queen survival and brood production in *P. californicus*

I examined survival and brood production for queens of *P. californicus* using two experimental setups. The first setup used glass "ant farms" (16×10×1.5 cm) that facilitated observing queen status (live or dead), presence of eggs, and the time course of brood development. The second treatment group was reared in bottles and provided the quantitative data. Both the ant farms and the bottles were filled with soil that had been passed through a 2-mm sieve and mixed into a composite sample. Queens were collected at the Salt River Recreation Area, Maricopa County, Arizona, within 2 h of their mating flight (Table 1). Each queen was maintained for several hours in an Eppendorf tube containing a small piece of moist paper towel, then weighed.

Data on queen status and time course of brood development were collected in each of 2 years by placing single queens in glass ant farms. Ant farms were maintained in darkness at about 25°C, and water was added, as necessary, to keep the soil moist. Ant farms were observed for several days to determine if the queens laid eggs prior to obtaining food. Kentucky blue grass (KBG) seeds were provided ad libitum to a subset of queens after 12 days in 1999 and after 10 days in 2000; other queens remained unfed. Thereafter, I recorded queen status and stage of brood development every 2–3 days until all queens had produced workers or died; this was for 54 days in 1999 and 64 days in 2000. I compared survival curves of fed and unfed queens in each year using the Kaplan-Meier survival analysis log-rank test for censored data (PROC SURVIVAL of SPSS; SPSS 1990); the comparison ran from the day on which seeds were first provided through to the last day of observation.

The quantitative comparison of survival and brood production for single queens used a one-factor (two food levels) laboratory experiment; each treatment contained 85 bottles for a total of 170 bottles. The experiment used 8-ounce glass bottles that contained 250 ml soil and 35 ml water. A plastic petri dish containing several holes covered each bottle. The bottles were randomly positioned in a darkened room maintained at 25–30°C. KBG seeds were provided ad libitum to one-half of the queens beginning on day 7, and 10–15 ml water were added to all bottles every 10 days beginning on day 20. Bottles were emptied after 53 days to determine queen status and number of brood (larvae, pupae, and workers). This interval was about 10 days after observing the first worker, thus allowing time for most queens to successfully rear workers, but not so long as to deplete queen energy reserves (see Johnson 1998). Survival of fed and unfed queens was compared by a Chi-square test, and number of brood was compared by a *t*-test. All of the above experiments were set up so that the initial wet mass of fed and unfed queens was similar (*t*-test, $P > 0.50$), thus eliminating effects due to queen mass.

Comparative data with other species of *Pogonomyrmex*

Comparative data for fully claustral congeners provide insight into the evolution of foraging by queens of *P. californicus*. Ecological and physiological variables that were measured included time to emergence of the first minim worker, number of brood (larvae, pupae, and workers) produced by each queen, dry mass and head width of minim workers, dry mass of queens and workers from mature colonies, the ratio of queen to worker mass, and fat content of alate queens; sample size for each variable is given in Table 1. Congeners that were examined included *P. barbatus* and *P. rugosus* from the *P. barbatus* complex, *P. occidentalis* and *P. salinus* from the *P. occidentalis* complex, and *P. maricopa* from the *P. californicus* complex; the latter species is closely related to *P. californicus* (Cole 1968; Taber 1990).

Data related to colony establishment were obtained for all species by placing single queens in glass ant farms filled with moistened soil (see above). Nests were placed in a darkened incubator at 30°C, and water was added as necessary to maintain moist nest conditions. Queens of *P. californicus* were provided KBG seeds ad libitum; queens of the other species remained unfed to verify the assumption that they were fully claustral. Queens were monitored every 2–3 days until the first minim worker emerged. At a standard time after emergence of the first minim, each nest was opened, and the brood were counted. For each nest, this standard time was calculated as the interval at which the first minim emerged plus 0.25× this interval, i.e. if the first minim emerged after 28 days, then brood were counted at 35 days. Two to three minims that had developed mature coloration were removed from several ant farms per species at this time, dried at 55°C for >72 h, and weighed. Head width of these minims was measured by projecting a 10× image from a binocular microscope to a video monitor; the image on the monitor was measured to 0.01 mm using NIH Image (available at http://rsb.info.nih.gov/nih-image/). Time to emergence of the first minim worker, number of brood produced, and dry mass and head width of minim workers were compared across species by a one-way ANOVA followed by a Duncan's multiple range test.

Dry mass of queens and workers from mature colonies, and the ratio of queen to worker mass were measured for *P. californicus*

Table 1 Collection locales (state: county, locale) and sample size for species of *Pogonomyrmex* that were used in this study. Taxonomy follows Bolton (1995). Voucher specimens are deposited in the Robert A. Johnson collection, Tempe, Arizona

Species	Latitude	Longitude	Elevation (m)	Queens[a]	Minim workers[b]	Queen-worker mass ratio[c]	Fat content[d]
P. californicus complex							
P. californicus (Buckley)							
AZ: Maricopa, Salt River Rec. Area, Coon Bluff	33°33′N	111°39′W	460			24	22 (4)[e] 20 (6)[f] 23 (14)[g]
AZ: Maricopa, Salt River Rec. Area, Blue Point Bridge	33°33′N	111°34′W	425	16	20	16	
P. maricopa Wheeler							
AZ: Pinal, 2.0 km N Superior	33°18′N	111°08′W	825			5	17 (4)
AZ: Gila, Hwy 288 at 23.7 km N Salt River	33°47′N	110°58′W	1,370	22	25	4	
P. occidentalis complex							
P. occidentalis (Cresson)							
AZ: Yavapai, Chino Valley	34°47′N	112°27′W	1,410			2	21 (4)
AZ: Yavapai, Ash Fork	35°13′N	112°30′W	1,555	23	29	8	
AZ: Navajo, Hwy 60 at 1.5 km N Cibicue turnoff	33°58′N	110°19′W	1,630			6	
NV: Nye, 8 km SW Belmont	38°32′N	116°56′W	2,010				19 (4)
P. salinus Olsen							
NV: Clark, N side Dry Lake	35°54′N	115°56′W	520			4	19 (4)
P. barbatus complex							
P. barbatus (F. Smith)							
NM: Hidalgo, Hwy 80 at 6.9 km N Rodeo	31°54′N	109°02′W	1,260			4	18 (4)
AZ: Yavapai, Chino Valley	34°46′N	112°27′W	1,410	21	22	8	
AZ: Yavapai, 1.5 km E Cornville	34°43′N	111°54′W	1,040			2	
P. rugosus Emery							
NM: Hidalgo, Hwy 80 at 9.4 km N Rodeo	31°55′N	109°02′W	1,260			4	
AZ: Pinal, 1.8 km SW Jct. McCartney Rd and I-10	32°56′N	111°42′W	430			16	
AZ: Pinal, Hwy 60 at 1.5 km NW Florence Junction	33°16′N	111°21′W	270	28	45	7	19 (4)

[a] Number of queens used to measure time to emergence of the first minim worker and number of brood produced (see Fig. 2)
[b] Number of minim workers used to measure dry mass and head width (see Fig. 3)
[c] Number of colonies used to measure dry mass of queens and workers and the queen to worker mass ratio (see Fig. 4)

[d] Number of alate queens (number of colonies) used to measure fat content (see Fig. 5)
[e] 1997
[f] 1998
[g] 2001

and all five congeners. For each species, I collected from five to ten alate queens and workers from several colonies (Table 1). Individuals were placed in an oven at 50–55°C for >72 h, then weighed. Dry mass of queens and workers was averaged within each colony, and these mean colony values were used to calculate the grand mean for each species. Likewise, the queen to worker mass ratio (queen mass/worker mass) was calculated for each colony, then averaged across conspecific colonies. Queen mass, worker mass, and the ratio of queen to worker mass were compared across species using a one-way ANOVA followed by a Duncan's multiple range test. I also examined spatial and temporal variation in body mass of queens and workers and queen to worker mass ratios in *P. californicus*. This was accomplished by collecting colonies over 2 years (1998 and 2001) at the Coon Bluff site and at a second site about 8 km away in 2001 (Blue Point Bridge; Table 1). The three collections of *P. californicus* were treated as separate groups in the ANOVAs.

Total fat content was determined for mature alate queens of all six species. Additionally, colonies of *P. californicus* were sampled over 3 years at one site and colonies of *P. occidentalis* were sampled at two sites. Individuals from at least four colonies per species were collected, dried at 55°C for >72 h, weighed, and then each individual was placed in a vial of petroleum ether (boiling point 30–60°C). Individuals were crushed to expose fat bodies and remained in ether for >24 h. The contents of each vial were rinsed through filter paper, dried, and weighed to 0.01 mg. Percent total fat content was calculated using the formula: $100 \times (DM - FFDM)/DM$, where DM is dry mass and FFDM is fat free dry mass. Fat content was compared among species using a nested one-way ANOVA (individuals nested within colony); the multiple samples for *P. californicus* and *P. occidentalis* were treated as separate groups. For all statistical tests, data were transformed, as necessary, to meet the normal distribution and homogeneity of variance assumptions.

Results

The role of food in queen survival and brood production

Survival of *P. californicus* queens varied with food level. In both years, survival was significantly higher for
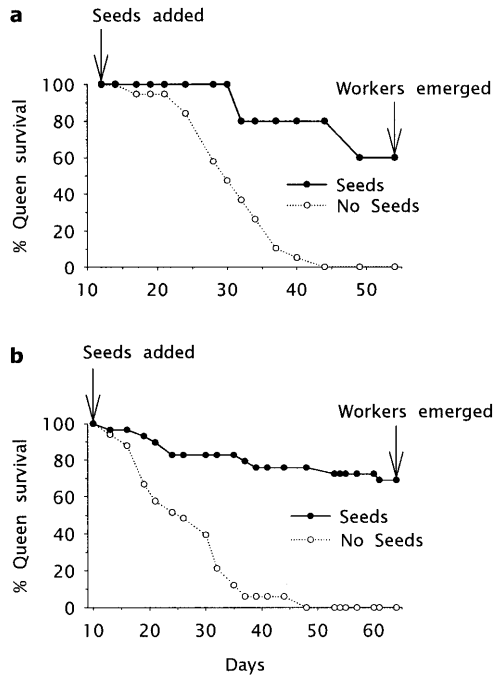
Fig. 1a, b Survival curve for single queens of *Pogonomyrmex californicus* in a one-factor experiment (two food levels) using observation ant farms in 1999 (**a**) and 2000 (**b**). The two food levels were Kentucky blue grass seeds provided ad libitum and without seeds. Sample size: n =5 with seeds, n =19 without seeds in 1999 (**a**); n =29 with seeds, n =33 without seeds in 2000 (**b**)
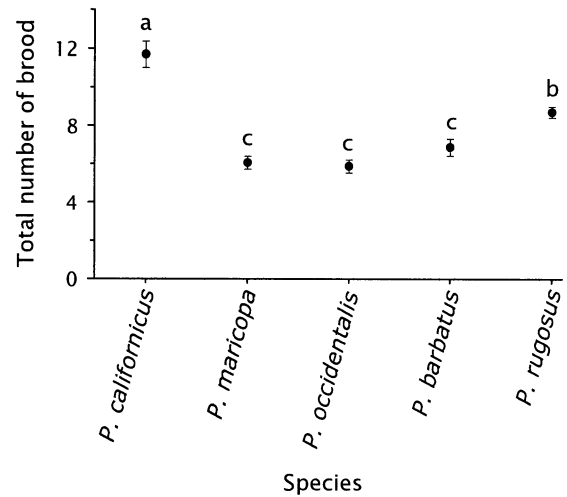

Fig. 2 Number of brood (workers, pupae, and larvae) produced by queens for several species of *Pogonomyrmex* (mean ± SE) at a standard time following emergence of the first minim worker. Significant differences among species are indicated by the letters *a–c*: a > b > c. Groupings are based on a one-way ANOVA followed by a Duncan's multiple range test. Sample size ranged from 16–28 queens per species (see Table 1)

fed queens compared to unfed queens (Kaplan-Meier log-rank test, LR_{1999}=12.3, n=24, 1 df, P=0.0005; LR_{2000}=39.6, n =62, 1 df, P <0.0001; Fig. 1). At the end of the 1999 observations, 3 of the 5 fed queens were alive and had successfully reared a worker, but all 19 unfed queens had died (Fig. 1). This pattern was repeated in 2000, as 20 of the 29 fed queens survived and reared a worker, while all 33 unfed queens had died (Fig. 1). In both years, all of the unfed queens had died several days before any of the fed queens had reared a worker. Survival rates in the bottles were also significantly higher for fed queens than for unfed queens: 34 of 85 fed queens survived compared with 1 of 85 unfed queens (χ^2=31.1, 1 df, n=170, P <0.001).

Fed and unfed queens of *P. californicus* also displayed different patterns of brood development. All 86 queens (24 in 1999 and 62 in 2000) in the ant farms laid eggs within 1–2 days of digging their nest chamber, and before seeds had been added to the nests. Subsequently, the brood of unfed queens developed to the stage of approximately 2nd instar larvae. Soon thereafter, these brood disappeared, and the queens died. The one surviving unfed queen in the bottle experiment also lacked brood. In contrast, fed queens successfully reared workers in the observation ant farms and bottles. In the bottles, fed queens produced an average of 4.8±0.3 brood; 29 of the 34 surviving queens produced minim workers (mean±SE=2.2±0.2), and the other five queens produced at least one pupa.
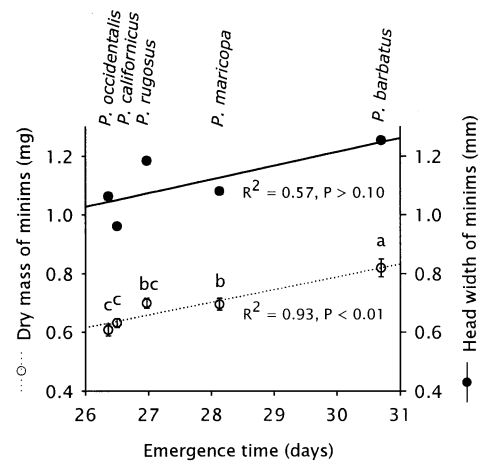
Fig. 3 Number of days to emergence of the first minim worker (mean ± SE) at 30°C as a function of minim dry mass and head width across species of *Pogonomyrmex*. *Lines* represent the regression lines for comparing emergence time relative to minim dry mass (*dotted line*) and head width (*solid line*). Significant differences across species in time to emergence of the first minim worker are indicated above the lower regression line by the letters *a–c*: a > b > c. Groupings are based on a one-way ANOVA followed by a Duncan's multiple range test. Sample size for each species is given in Table 1

Interspecific variation in brood production

Queens of the four tested congeners (*P. barbatus*, *P. rugosus*, *P. occidentalis*, *P. maricopa*) were fully claustral because they successfully reared minim workers without food. Thus, these four species provide data for comparing the potential costs and benefits of semi-claustral nest founding in *P. californicus*.
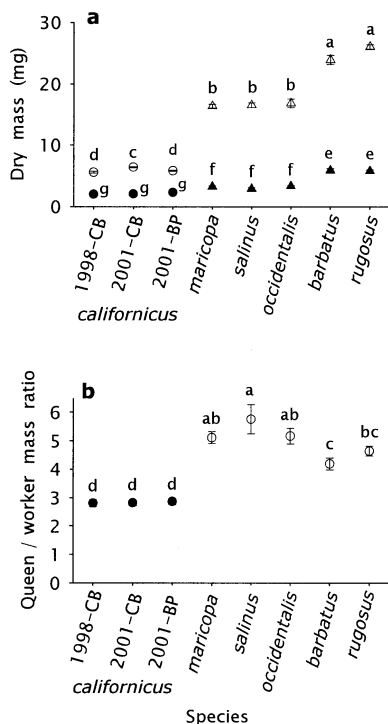
Fig. 4 Dry mass (mean ± SE) of queens and workers (**a**), and queen to worker mass ratios (**b**) for six species of *Pogonomyrmex*. **a** *Open symbols* depict queens, *solid symbols* depict workers, *circles* depict *P. californicus*, *triangles* depict congeners. **b** *Solid circles* depict *P. californicus*, *open circles* depict congeners. Individuals of *P. californicus* were collected at Coons Bluff (*CB*) in 1998 and 2001 and at Blue Point Bridge (*BP*) in 2001 (see Table 1). For each caste, significant differences among species are indicated by the letters *a–d*: a > b > c > d for queens; and *e–g*: e > f > g for workers. Groupings are based on a one-way ANOVA followed by a Duncan's multiple range test. Sample size (number of colonies) for each species is given in Table 1

Queens of the five species displayed significant differences in number of brood produced and time to emergence of the first minim worker. Most importantly, the number of brood produced by new queens varied across the five species (one-way ANOVA, $F_{4,105}$=25.9, P<0.001) and was significantly higher in *P. californicus* than for any of the tested congeners (Duncan's multiple range test, P<0.05; Fig. 2). Time to emergence of the first minim worker also varied significantly among the five species (one-way ANOVA, $F_{4,128}$=14.7, P<0.001; Fig. 3); this time was the shortest for *P. occidentalis* and *P. californicus*, intermediate for *P. maricopa* and *P. rugosus*, and longest for *P. barbatus* (Fig. 3). I assessed potential correlates of emergence time by regressing emergence time against the mean dry mass and head width for minims of each species. Time to emergence of the first minim was correlated with dry mass (r=0.97, P<0.01, n=5), but not head width (r=0.75, P>0.10; Fig. 3). Relative to *P. californicus*, dry mass of minim workers was also higher than expected based on comparisons with congeners; *P. californicus* minims had the smallest head width (Duncan's multiple range test, P<0.001), but their dry mass was similar to that of *P. occidentalis* minims (P>0.40; Fig. 3).
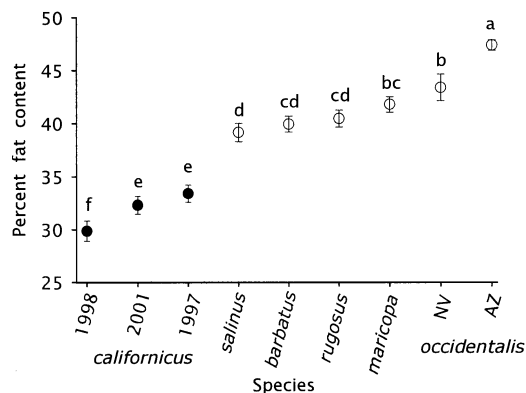

Fig. 5 Percent fat content (mean ± SE) for alate queens in the genus *Pogonomyrmex*; n =17–25 queens per species/population. *P. californicus* are depicted by *solid circles*; congeners are depicted by *open circles*. Significant differences among the species/populations are indicated by the letters *a–f*: a > b > c > d > e > f. Groupings are based on a one-way ANOVA followed by a Duncan's multiple range test. Sample size for each species is given in Table 1

Body size and queen-worker dimorphism

Dry mass of queens and workers varied significantly across the six species of *Pogonomyrmex* [one-way ANOVA, $F_{7,102(queens)}$=344.7, P<0.001: $F_{7,102(workers)}$=82.4, P<0.001], with queens and workers of *P. californicus* being significantly smaller than those of the five congeners (Duncan's multiple range test, P<0.05; Fig. 4). The queen-worker dimorphism (the ratio of queen to worker dry mass) varied across species [$F_{7,102(queens/workers)}$=35.3, P<0.001] and was significantly lower (P <0.05) for *P. californicus* than for the five fully claustral congeners (Fig. 4).

Fat content

Percent total fat content of alate queens varied significantly among the six species of *Pogonomyrmex* [one-way ANOVA, $F_{8,130(species)}$=46.2, P<0.001] and for the nested factor [$F_{39,130(colony within species)}$=1.8, P<0.01; Fig. 5]. An a posteriori test divided the species into six groups (Duncan's multiple range test, P <0.05). The four groups with the highest fat content included the five fully claustral congeners, while the two groups with the lowest fat content included queens of *P. californicus* that had been collected over 3 years (Fig. 5).

Discussion

Evolutionary patterns

The evolution of semi-claustral nest founding in advanced subfamilies of ants is poorly understood. While this behavior is common in the morphologically primitive subfamilies Ponerinae and Myrmeciinae, it is rare in the more advanced subfamilies. In the subfamily Formic-

inae, this behavior is only known for *Cataglyphis bicolor* (Fridman and Avital 1983), *Polyrachis laboriosa* and *P. militaris* (Lenoir and Dejean 1994); in the subfamily Myrmicinae, queen foraging is known for *Manica rubida* (Le Masne and Bonavita 1969), *Messor andrei* (Brown 1999), and several species of dacetines (DeJean 1987) and attines (Weber 1972; Rissing et al. 1989; Ulrich Mueller, personal communication). Congeners of these semi-claustral species typically exhibit fully claustral nest founding, suggesting that semi-claustral nest founding is a secondary modification that has presumably evolved in response to local ecological conditions (Peeters 1997). Similarly, semi-claustral nest founding appears to be a secondary modification in *P. californicus* because several congeners, including its close relative *P. maricopa*, are fully claustral.

Benefits and costs of queen foraging

This study demonstrates obligate semi-claustral nest founding in the seed-harvester ant *P. californicus* because single queens cannot survive and successfully rear their first brood without an external food source. In contrast, survival rates were high for single, fed queens, and all of these queens reared at least one worker or pupa.

The primary advantage of foraging appears to lie in providing the queen with sufficient energy to raise significantly more brood than is possible by fully claustral congeners. Note, however, that this study compares the number of brood produced between *P. californicus* queens fed seeds ad libitum and congeners that were not provided with food. Consequently, these data likely reflect optimal conditions for nest founding and brood production by *P. californicus*. Number of brood produced by *P. californicus* queens probably decreases when food availability is low. Comparative data from several congeners indicate that the minim workers of *P. californicus* are also heavier in mass than that expected from their head width. Moreover, queens of fully claustral species allocate a fixed amount of energy to brood, which results in a tradeoff between producing a high number of small minims or a few large minims (Hölldobler and Wilson 1990). In *P. californicus*, this tradeoff has been uncoupled because queen foraging facilitates producing both more and larger brood. A companion bottle experiment, similar to that described here, documented that foraging also has positive effects on queen mass. This experiment used queens from a southern California population of *P. californicus* in which multiple queens co-found a colony (see Rissing et al. 2000). To explore the additional effect of queen number, I conducted a two-factor experiment that varied number of queens per bottle (one, two, or five) and food level (fed and unfed). Across all three group sizes of queens, those queens that were provided seeds ad libitum lost a significantly lower percentage of their body mass from the beginning to the end of the experiment than did unfed queens (R. Johnson, unpub-

lished data). Thus, queens that forage have higher energy reserves at the time of worker emergence.

These benefits are thought to be offset by the mortality costs associated with the queen leaving the nest to forage. Unfortunately, no data quantify mortality for foraging queens, but rather this cost is assumed as a corollary of high mortality for workers while foraging outside the nest (see Hölldobler and Wilson 1990; Peeters 1997). For queens, this presumed cost appears to decrease through time, however, because queens of *M. andrei* cease foraging partway through nest founding (Brown 1999), and queens of *P. californicus* forage less frequently as the seed cache grows (R. Johnson, personal observation).

Relative to queen mortality, it is known that queens and incipient colonies of fully claustral species experience extremely high mortality (>99%; see Johnson 2001). Moreover, if mortality is extremely high for fully claustral queens, then the low increment of additional mortality incurred while foraging might be offset by the advantage of producing additional brood, especially given that the number of first brood correlates with early colony success (Oster and Wilson 1978; Porter and Tschinkel 1986; Hölldobler and Wilson 1990). Thus, it is interesting that queens of more higher ant species do not forage given the potentially low additional mortality cost relative to the possible gain. An alternative possibility is that queen foraging may be relatively common, but just rarely observed. For example, queen foraging occurs in at least three other species of *Pogonomyrmex*, *P. occidentalis* (Billick et al. 2001), *P. desertorum* (Blaine Cole, personal communication), and *P. salinus* (Sanford Porter, personal communication). I reaffirmed this observation for *P. occidentalis* by placing seeds in five of the ant farms; all five queens came to the surface and harvested seeds. Thus, *P. occidentalis* queens are facultatively semi-claustral, that is, they forage even though they can successfully rear workers in the absence of food. Overall, it is assumed that many morphologically advanced ants are fully claustral, but this picture may change as the natural history of additional species is detailed. This possibility is supported in that queen foraging is only starting to be discovered and understood in *Pogonomyrmex*, which is probably the most well-studied genus of ants in North America (see also Hölldobler and Wilson 1990; Johnson 2000, 2001).

Correlates of semi-claustral nest founding in *Pogonomyrmex*

For queens to survive beyond the founding stage requires that their first workers perform the entire suite of colony tasks including raising the second brood. Performing these tasks requires some minimum number of workers; colony growth, and hence success, is maximized by producing a large number of small workers rather than few large workers (Oster and Wilson 1978; Porter and Tschinkel 1986). The disadvantage of this strategy is that

minim workers have high metabolic rates and short longevities, and thus are energetically more expensive to produce and maintain per unit mass (Porter and Tschinkel 1985, 1986). In contrast to this strategy, queens of *P. californicus* produce a larger number of minim workers whose mass is also significantly heavier than that expected from their head width (Fig. 3). The best hypothesis to explain both effects relates to queen foraging and presence of food in the nest. This study demonstrates that queen foraging facilitates producing more first brood than that possible by fully claustral congeners. Support for the hypothesis that queen foraging increases mass of these minims comes from this study, and also from a companion experiment that quantified brood production for queens from the southern California population of *P. californicus* in which multiple queens co-found a colony. This population provides the advantage that multiple unfed queens survive and produce minim workers, unlike the single unfed queens used in this study. In this experiment, the effect of food was evidenced by a dry mass that was significantly heavier for minim workers produced by fed queens compared with unfed queens at group sizes of both three queens and five queens. Head width, however, did not differ for minims produced by fed and unfed queens in either group size of queens (R. Johnson, unpublished data).

The most conspicuous ecological or physiological difference among the examined species of *Pogonomyrmex* is the small size of *P. californicus*, as mass of *P. californicus* queens and workers averaged approximately 40% and 55%, respectively, of the next smallest congener (*P. maricopa*). The queen/worker size ratio was also lowest in *P. californicus* (Fig. 4), thus mimicking the body-size ratio patterns displayed by ponerine and myrmeciine ants (Peeters 1997). Overall, queens of *P. californicus* are among the smallest in the genus, and queens of *P. occidentalis* and *P. salinus* are also small, indicating that queen foraging may be associated with small queen size. For *P. californicus*, this hypothesis is supported by experimental data on queens from the southern California population, because the percentage of nests that produce workers is low for single unfed queens, but increases to a high percentage for nests of multiple unfed queens (R. Johnson, unpublished data). A similar body size pattern occurs among the three ecologically equivalent species of *Messor*, *M. andrei*, *M. julianus*, and *M. pergandei* (see Johnson 2000). Among these species, only the queens of *M. andrei* are known to forage, and their dry mass (around 8 mg) is much lower than that for queens of *M. julianus* (around 10.9 mg) and *M. pergandei* (around 14.9 mg; R. Johnson, unpublished data). Moreover, if queen foraging is associated with small queen size, then it likely that this behavior occurs in other small-bodied species of *Pogonomyrmex* and *Messor*.

Small queen size likely has evolutionary implications relative to possible energy constraints during nest founding, and begs the question of why *P. californicus* queens are so small. Possibilities include that foraging allows the queens to produce workers without possessing significant reserves, thus they could evolve a smaller size. This possibility confers the advantage that queens are cheaper to produce and colonies could thus produce more of them. Alternatively, some unknown selective force drove the evolution of small body size and the inadequacy of the associated lower reserves necessitated queen foraging.

Relative to the energetics of nest founding, a strong relationship has also been shown between fat reserves and founding strategy. Queens of species, or forms within a species (e.g. *Solenopsis invicta*), that exhibit independent colony founding possess significantly greater fat reserves than queens that exhibit dependent founding (Keller and Passera 1989; Keller and Ross 1993). As might be expected, queens of *P. californicus* contain proportionally less fat reserves than their fully claustral congeners. Storage proteins are also necessary for fully claustral queens to rear their first brood (Martinez and Wheeler 1994; Wheeler and Buck 1995, 1996). It is expected that, like fat reserves, storage protein reserves would be highest in fully claustral species. Accordingly, these proteins occur in a diverse taxonomic array of ant species, but are lacking in queens of the semi-claustral myrmicine ant *Messor andrei* (Brown 1999). Storage proteins are also lacking in *P. californicus*, whereas substantial quantities occur in alate queens of *P. maricopa, P. barbatus, P. rugosus*, and *P. occidentalis* (D. Hahn and D. Wheeler, unpublished data). Interestingly, among the four latter species, storage proteins are significantly less abundant in the facultatively semi-claustral queens of *P. occidentalis*.

Other types of nutritional constraints might also necessitate queen foraging. For example, leafcutter ants (tribe Attini) have a highly specialized life history in which the foragers harvest a substrate to culture their fungus garden, upon which the colony survives. Sustaining such a fungus garden likely requires distinctive nutrients that the queens may not have evolved to synthesize, thus requiring the queens to forage for these nutrients even if they possess high levels of other reserves. Indeed, queen foraging appears to be somewhat common in the leafcutter ants, where it apparently occurs in all genera except *Atta* (Weber 1972; Ulrich Mueller, personal communication). Other ecological conditions might also pre-dispose queen foraging. For example, the ability to store food, such as occurs in seed-harvester ants, might facilitate queen foraging and may explain its occurrence in several species of *Pogonomyrmex* and *M. andrei*.

Overall, this study demonstrates that the importance of queen foraging lies in gathering energy that is not accessible to fully claustral queens. Additional experimental comparisons, especially using facultatively semi-claustral species, would prove valuable in generalizing these results. Lastly, observations suggest that queen foraging may be somewhat common in some groups of higher ants. Understanding the evolution of this behav-

ior requires surveying a broader array of taxa, along with collecting the relevant ecological and physiological data.

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