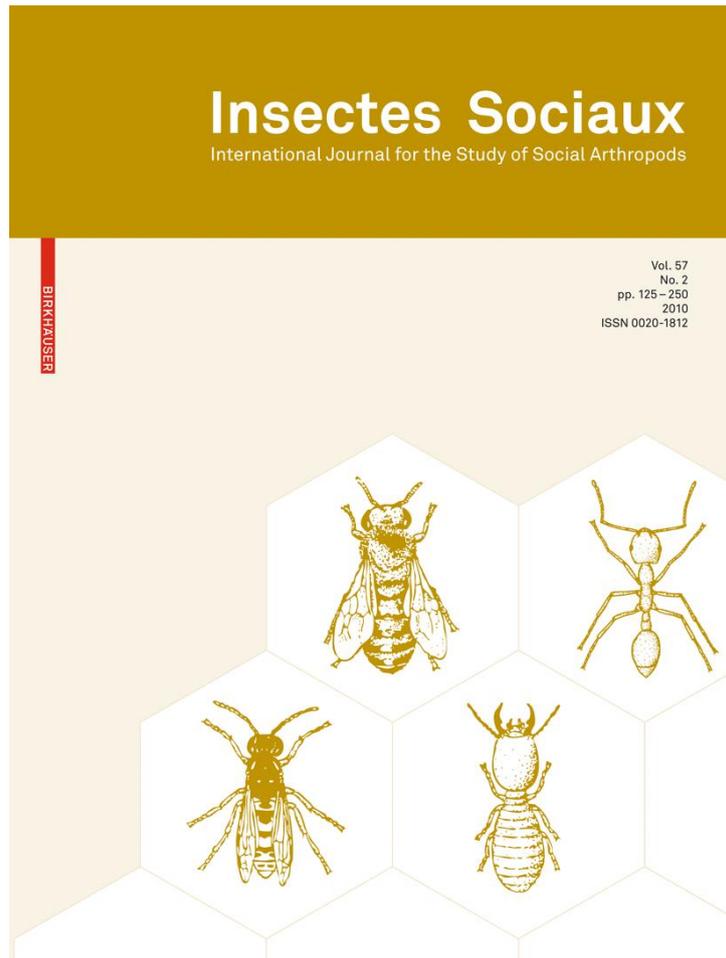


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Independent colony founding by ergatoid queens in the ant genus *Pogonomyrmex*: queen foraging provides an alternative to dependent colony founding

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Abstract Ant queens exhibit two primary strategies to initiate nests, independent colony founding (ICF) by solitary queens and dependent colony founding (DCF) when the queen starts a nest with a group of workers that disperse on foot from the parent nest. Numerous ant species have wingless (ergatoid) queens, and it is generally assumed that these species exhibit obligate DCF because their lack of wing musculature provides them with few resources to divert towards producing their first brood of workers. Thus, ICF by ergatoid queens is viewed as maladaptive because these queens need to take additional dangerous foraging trips to garner sufficient food to rear their first brood of workers. Contrary to this prediction, I document ICF by ergatoid queens for three species of harvester ants in the genus *Pogonomyrmex* (subfamily Myrmicinae), *P. cunicularius cunicularius*, *P. cunicularius pencosensis*, and *P. huachucanus*. Queens of *P. huachucanus* were obligate foragers, i.e., no minim workers could be produced without external food, and one queen of *P. cunicularius pencosensis* was observed foraging in the field. Abundant and/or predictable food resources likely select for the evolution of semi-claustral nest founding and ICF by these ergatoid queens. Under these conditions, foraging time would be minimized and the number and size of minim workers would be maximized. These benefits should increase founding success, which could compensate for loss of long-range dispersal. Overall, this study demonstrates that care should be taken before concluding that ant colonies employ DCF based solely on queen morphology.

Keywords Brachypterous queen · Ergatoid queen · Independent colony founding · Queen foraging · Wingless queens

Introduction

The evolution of flight has promoted the enormous diversity and evolutionary success of insects by allowing them to disperse over long distances to find food and mates and to colonize new habitats (Roff, 1990; Wagner and Liebherr, 1992). Despite the numerous benefits of flight, many insect species have lost the ability to fly, and this loss is typically associated with low dispersal distance and a reallocation of body tissue that results in increased fecundity relative to the flight capable morph. At the ultimate level, loss of flight is viewed as an adaptation to promote survival in homogeneous or persistent habitats, whereas flight promotes dispersal from heterogeneous or temporary habitats (Heinze and Tsuji, 1995; Roff, 1986, 1990; Zera and Denno, 1997).

Like other insects, ant queens have a wide array of wing phenotypes (Buschinger and Heinze, 1992; Heinze and Keller, 2000; Heinze and Tsuji, 1995). The vast majority of ant species have winged queens that engage in a mating flight, after which they remove their wings and start a new nest solitarily or with other queens, i.e., independent colony founding (ICF). These queens can be fully claustral in which case they rear their first brood of workers using solely body reserves, or they can be semi-claustral in which case they leave the nest to forage for resources to rear their first brood of workers (Johnson, 2002, 2006; Peeters and Molet, 2009). In either case, the dealate queens histolyze their bulky wing muscles, which then provide a substantial amount of energy toward rearing their first workers

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(Marden, 2000). Flightlessness has also evolved numerous times in ant queens, and these wingless (ergatoid) queens are relatively cheap to produce because they lack the wings and wing muscles that are present in fully winged volant queens. Thus, ergatoid queens have relatively few reserves to divert towards producing their first workers, which has led ant biologists to generally assume that ergatoid queens cannot start a nest solitarily using ICF, but rather that these queens display obligate dependent colony founding (DCF) in which the queen starts a nest with workers from the maternal colony (Peeters and Ito, 2001; Peeters and Molet, 2009). Moreover, ICF by ergatoid queens is viewed as maladaptive because these queens would require additional dangerous foraging trips to successfully garner sufficient food to rear their first workers (Liebig et al., 1998; Peeters and Molet, 2009).

The tradeoffs between ICF and DCF involve differences in dispersal distance and queen survival. The cheaper ergatoid queens employ DCF and consequently have high rates of survival, but they can only disperse locally on foot, whereas the well-provisioned ICF queens have low rates of survival, but they can disperse over much longer distances. Ecological conditions that substantially decrease the survival probability of ICF queens are thought to favor the evolution of ergatoid queens. For example, ergatoid queens and DCF appear to be favored in cold climates, harsh or patchy habitats, or when nest sites are unstable or limited (Heinze and Tsuji, 1995; Liebig et al., 1998; Roff, 1986; Zera and Denno, 1997). Several studies also suggest that food limitation favors the evolution of ergatoid queens—high food availability would provide abundant resources to produce the more expensive alate queens, while low food availability would only provide sufficient resources to produce the cheaper ergatoid queens that have a higher probability of survival (Briese, 1983; Forder and Marsh, 1986; Molet et al., 2008; Tinaut and Heinze, 1992).

The amazing diversity of colony founding strategies that occur within ants is largely paralleled within the seed-harvester ant genus *Pogonomyrmex* (subfamily Myrmecinae). ICF occurs via single or multiple queens, and these queens run the gamut of founding strategies from obligate foragers to fully claustral (Johnson, 2002, 2004, 2006). Alternatively, queens of the two social parasite species, *P. anergismus* and *P. colei*, employ DCF in which founding queens invade a congeneric host colony (Johnson, 1994; Johnson et al., 1996), and two species (*P. pima* and *P. imberbiculus*) produce dimorphic queens (i.e., winged and ergatoid), and in both species the polygynous, ergatoid queen colonies are presumed to form new colonies via DCF (Heinze et al., 1992; Johnson et al., 2007). However, no information exists on colony founding strategies for any of the nine species (all in South America) that are thus far known to have only ergatoid queens (Buschinger and

Heinze, 1992; Heinze and Tsuji, 1995; Kusnezov, 1951; R.A. Johnson, unpubl. data), plus the only known functionally ergatoid queen species in North America (*P. huachucanus*). This paper documents ICF in three of these ergatoid queen species, *P. cunicularius cunicularius* Mayr, *P. cunicularius pencosensis* Forel, and *P. huachucanus* Wheeler. The only previous reports of ICF by ergatoid queens are observations for a limited number of queens from three species of poneroid ants, *Myrmecia regularis* (subfamily Myrmeciinae) (Haskins and Haskins, 1955), *Plectroctena mandibularis* (subfamily Ponerinae) (Villet, 1991, 1999), and the brachypterous (having rudimentary or abnormally short wings) queen of *Nothomyrmecia macrops* (subfamily Myrmeciinae) (Taylor, 1978).

Methods

Queen morphology and wing structure

Queen morphology and wing structure are undescribed or poorly known for *P. cunicularius pencosensis*, *P. cunicularius cunicularius*, and *P. huachucanus*. Workers and the undescribed queens of *P. cunicularius pencosensis* display a high degree of morphological similarity, with the only apparent external differences between the two castes being presence of ocelli and the slightly larger size of queens. This high degree of morphological similarity between queens and workers has also been noted in other species, where queens are distinguishable only in the anatomy of their ovaries, size, or presence of feebly impressed thoracic sutures and vestigial ocelli (see Heinze and Tsuji, 1995). Consequently, I measured and dissected individuals to verify caste. Head width was measured for individuals of each caste by projecting a 25× image from a binocular microscope to a video monitor; the image was captured, then measured to 0.01 mm using NIH Image (available at <http://rsb.info.nih.gov/nih-image/>). I also dissected individuals of both castes under a binocular microscope to document presence or absence of a spermatheca and to count ovarioles. The queen of *P. cunicularius cunicularius* is also ergatoid (Santschi, 1931), but individuals were not available to measure or dissect.

Queens of *P. huachucanus* were described as brachypterous (Cole, 1968). Cole (1968) also noted finding both brachypterous and dealate queens in nests, and presumed that *P. huachucanus* had intranidal mating and that the mated dealate queens returned to their natal nest. I also found both brachypterous and dealate queens in several nests, but my observations occurred prior to mating flights, whereas those of Cole occurred after mating flights. Laboratory observations indicated that the wings fell off of these brachypterous queens by the time they had acquired

their adult coloration. I further examined this phenomenon by following queen development via: (1) rearing field-collected sexual brood (larvae, pupae, and callow queens) in the laboratory, and (2) rearing queens from queenright laboratory colonies.

Nest founding

Incipient nests of three ergatoid queen species were excavated to determine queen number. Nests of *P. cunicularius cunicularius* were excavated along Ruta 14 at 8.2 km north of Gualeguychú, Entre Ríos province, Argentina, those of *P. cunicularius pencosensis* were excavated along Ruta 73 at 83.8 km northeast of Chamental, La Rioja province, Argentina, and those of *P. huachucanus* were excavated at 1.3 km north of the junction of Highway 60 and Little Mormon Lake Road, Navajo County, AZ, USA. Numerous founding queens were only available for *P. huachucanus*, such that this was the only species on which I conducted laboratory experiments to determine method of colony founding (i.e., obligate forager, facultative forager, or fully claustral). Data on survival and brood production were collected by placing single mated queens of *P. huachucanus* in glass “ant farms” (16 × 10 × 1.5 cm) that were filled with sieved soil (Johnson, 2002). Ant farms were then placed in a darkened incubator at 30°C, and water was added, as necessary, to keep the soil moist. Kentucky blue grass seeds were provided ad libitum to a random subset of queens, while other queens remained unfed. Thereafter, I monitored queen status (live or dead) every 2–3 days until all queens had died or produced at least one worker. Survival of fed and unfed queens was compared using a χ^2 test.

Results

Queen morphology

Dissections corroborated that external morphology separated workers and queens of *P. cunicularius pencosensis* because reproductive queens contained: (1) a spermatheca ($n = 18$), which was lacking in workers ($n = 5$), and (2) a higher number of ovarioles (queen mean 10.4, range 8–13, $n = 30$; worker mean 4, $n = 5$; t -test, $t = 12.8$, $P < 0.001$). Queens were also significantly larger than workers (queen head width in mm: 2.16 ± 0.02 , range 1.99–2.26; worker head width: 1.77 ± 0.04 , range 1.57–1.95; $t = 9.1$, $P < 0.001$, $n = 12$ per caste), they lacked all morphological structures associated with wings, and the mesosomal sclerites were completely fused (Fig. 1). Queens of *P. cunicularius cunicularius* also possess ocelli and they lack wings along with all morphological structures associated with wings, but their mesosoma is slightly

more enlarged and queenlike than that of *P. cunicularius pencosensis* (Fig. 2).

All queens of *P. huachucanus* eclosed with wings that extended about one-third the length of the gaster regardless of the rearing method (Fig. 3), whereas the wings of volant congeners reach well beyond the apex of the gaster (see also Cole, 1968). Continued observations demonstrated that all of these queens became apterous (wingless) because all of their wings fell off by the time they had acquired adult coloration.

Nest founding

Incipient nests of all three species contained one queen. A total of 80 single founding queens of *P. huachucanus* were excavated, and Cole (1954) also noted finding solitary foundresses under stones. In two other cases, I found two foundresses under a stone; these occurrences were presumably a haphazard event rather than pleometrosis. I also excavated one haplometrotic queen of *P. cunicularius cunicularius* and one haplometrotic queen of *P. cunicularius pencosensis*. No brood was found in either of the latter two nests. Prior to excavation, the queen of *P. cunicularius pencosensis* had been observed harvesting cookie crumbs over several foraging trips.

Laboratory experiments documented that dealate queens of *P. huachucanus* are obligate foragers, i.e., no workers could be produced without queen foraging. Eight of 14 fed queens survived and produced at least one worker, while all of 14 unfed queens had died by the time that all surviving fed queens had produced a worker ($\chi^2 = 11.2$, 1 df , $n = 28$, $P < 0.0015$). Seed caches were observed in all laboratory nests of the fed queens indicating that they harvested seeds.

Discussion

ICF by ergatoid queens

This study reports the first cases of ICF by ergatoid queens in formicoid ants (subfamily Myrmicinae), and it adds to the meager existing data that DCF is not an obligate reproductive strategy for ergatoid ant queens (see also Haskins and Haskins, 1955; Villet, 1991, 1999). Queens of *P. huachucanus* were demonstrated to be obligate foragers, i.e., income breeders (Johnson, 2006), that cannot produce any minim workers without an external food source. This result is also supported by physiological data indicating that these queens lack the storage proteins (R.A. Johnson, unpubl. data) that are necessary to produce minim workers (Hahn et al., 2004; Wheeler and Martinez, 1995). Additional data need to be collected to further document

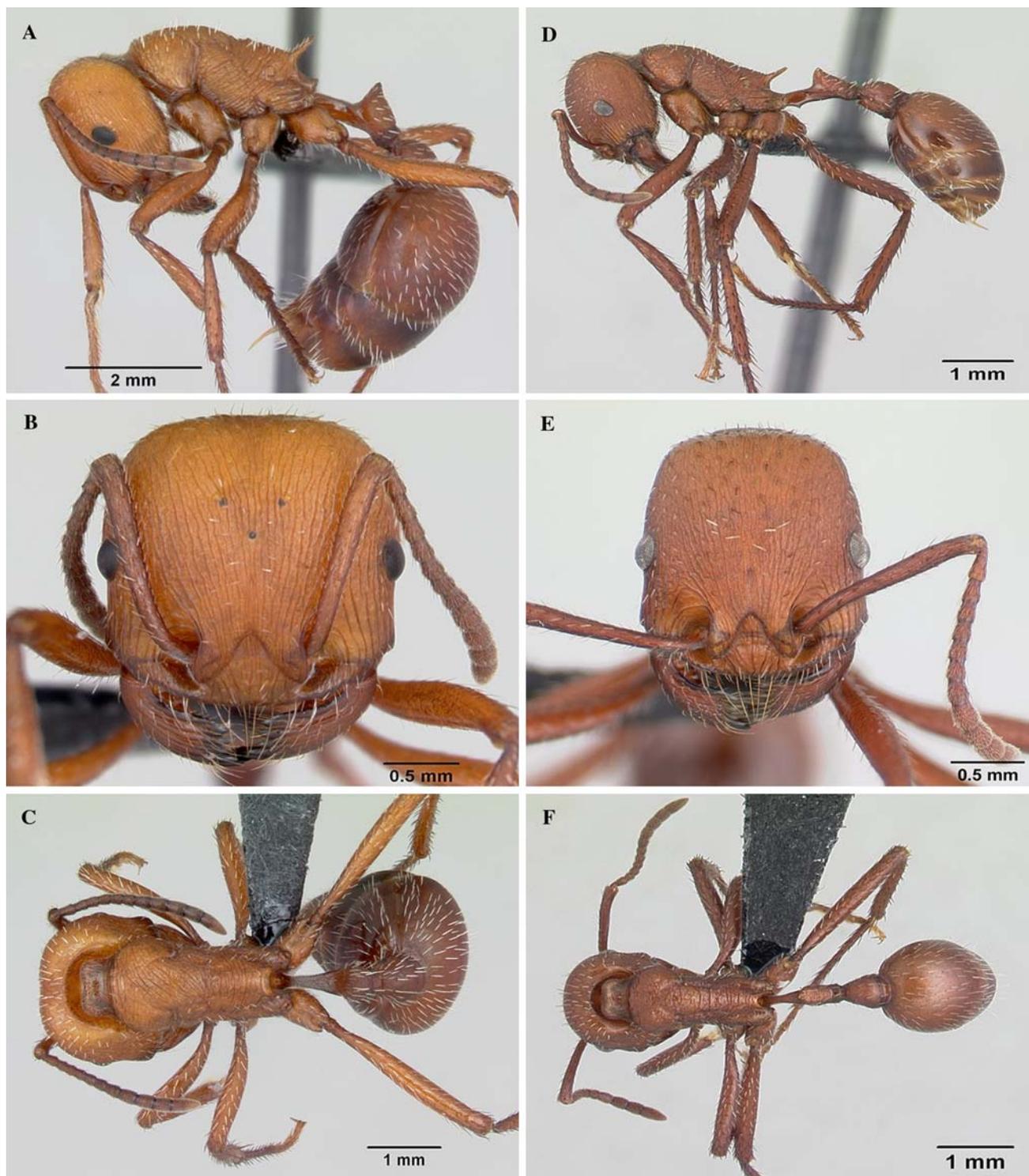


Fig. 1 Photograph of *Pogonomyrmex cunicularius pencosensis* Forel ergatoid queen and worker: **a** lateral view of ergatoid queen body, **b** frontal view of ergatoid queen head, **c** dorsal view of ergatoid queen

body, **d** lateral view of worker body, **e** frontal view of worker head, and **f** dorsal view of worker body

the meager observations of ICF by *P. cunicularius cunicularius* and *P. cunicularius pencosensis*; queens of the latter species appear to be semi-claustral based on observa-

tions of one queen foraging in the field (R.A. Johnson, pers. obs.). Overall, ICF by ergatoid queens is likely related to specialized ecological conditions (see below), such that this



Fig. 2 Photograph of *Pogonomyrmex cunicularius cunicularius* Mayr ergatoid queen and worker: **a** lateral view of ergatoid queen body, **b** frontal view of ergatoid queen head, **c** dorsal view of ergatoid

queen body, **d** lateral view of worker body, **e** frontal view of worker head, and **f** dorsal view of worker body

founding strategy probably occurs in few species compared to the number of ergatoid queen species that employ DCF.

Observations do not exclude the possibility that newly mated ergatoid queens of these three species might also return to their natal nest, which would then become



Fig. 3 Photograph of *Pogonomyrmex huachucanus* Wheeler brachypterous callow queen in dorsal view. The forewing (which has already fallen off) extends approximately the same length as the hindwing. For comparison, the wings of fully winged volant congeners extend beyond the tip of the gaster

polygynous, or that they could subsequently leave with a group of workers to form a new colony (DCF). Thus far, no nests have been found in any of these three species that would suggest DCF, i.e., with a queen, few workers, and no brood.

It should be noted that *P. huachucanus* and *Mymecia regularis* are similar in that queens of both species are brachypterous, but the wings soon fall off in both species (this study, Haskins and Haskins, 1955). The brachypterous queens of *Nothomyrmecia macrops* also display ICF and disperse short distances from the nest on foot (see Peeters and Molet, 2009; Taylor, 1978). Moreover, from an ecological and investment point of view, brachypterous queens are equivalent to ergatoid queens because they cannot fly and thus have the same colony founding options as ergatoid queens, they probably lack developed wing muscles (Schrempf and Heinze, 2007; Zera and Denno, 1997), and they are cheaper to produce than winged queens.

Costs and benefits of ICF by ergatoid queens

Semi-claustral colony founding is being documented for an increasing number of formicoid ants suggesting that this behavior is much more common than previously thought (Brown and Bonhoeffer, 2003; Johnson, 2002). Congeners of semi-claustral species typically exhibit fully claustral colony founding, suggesting that semi-claustral colony founding is a secondary modification that has presumably evolved in response to local ecological conditions (Johnson, 2002; Peeters, 1997). Wing loss by ant queens also seems to be a secondary modification that is favored by ecological conditions. Moreover, the evolution of semi-claustral nest founding and of wingless queens may or may not occur independently, suggesting that ICF by ergatoid

queens should be examined as two questions: (1) what ecological conditions favor semi-claustral colony founding, and (2) what factors favor the loss of long-distance dispersal by ant queens?

What ecological conditions favor the evolution of semi-claustral colony founding? Queen foraging has traditionally been considered to be a risky and detrimental behavior because of mortality risk to the queen while outside the nest (Hölldobler and Wilson, 1990). Mortality risk for foraging queens has not been measured, but a model that examined conditions under which claustral colony founding might occur suggested that this behavior becomes more advantageous as the risk of mortality increases (Brown and Bonhoeffer, 2003). It has also been argued that method of colony founding is a life history trait that is related to the time at which queens acquire the resources that are used to produce their first brood of workers (Johnson, 2006). Fully claustral queens acquire their reproductive energy prior to mating flights and rear their first brood solely using body reserves, which results in a tradeoff between number and size of workers. Alternatively, semi-claustral queens forage for reproductive resources during colony founding such that they can adjust brood production to environmental conditions; queens produce fewer and smaller minimum workers when food resources are low, while more and larger workers are produced when conditions are exceptional (Johnson, 2002, 2006). Under the latter conditions, semi-claustral queens produce more workers than fully claustral queens that have fixed energy reserves. Thus, queen foraging is adaptive for taxa that inhabit environments in which food is high in abundance and/or predictable in occurrence (see Johnson, 2006 and references therein). Many arid and semi-arid habitats, such as those occupied by species of *Pogonomyrmex*, experience relatively predictable pulses of seed production that result from seasonal rainfall. These seeds can remain dormant in the seed bank for several or more years (Lopez, 2003; Reichman, 1984; Tevis, 1958), and have the additional advantage that they can be stored by the ants for extended periods.

Factors that favor the loss of long-distance dispersal by ant queens involve tradeoffs associated with both dispersal distance and probability of survival. ICF queens have long-distance dispersal combined with very low rates of survival, whereas DCF queens disperse locally on foot but have much higher rates of survival. Ecological conditions that substantially decrease survival by ICF queens are thought to favor a shift to ergatoid queens and DCF (Heinze and Tsuji, 1995). Support for this hypothesis includes a shift from ICF to DCF along a gradient of environmental harshness within the *Rhytidoponera impressa* group (Molet et al., 2008; Ward, 1983), and by the disproportionate number of ergatoid queen species that occur in harsh arid habitats (Bolton,

1986; Briese, 1983; Forder and Marsh, 1986; Tinaut and Heinze, 1992; Ward, 1983). In all of these cases, environmental harshness was associated with limited food availability. Thus, fewer resources would be available to rear sexual brood, such that producing fewer ergatoid queens that have high survival rates is favored over producing numerous, more expensive alate queens that have very low survival rates (see Bolton, 1986; Buschinger and Heinze, 1992; Tinaut and Heinze, 1992).

That ergatoid queens for three species of *Pogonomyrmex* employ ICF suggests that seed resources are relatively predictable in most years. Similarly, Villet (1999) argued that *Plectroctena mandibularis* employed ICF because the ergatoid queens utilized an abundant prey of millipedes that did not appear dangerous or difficult to harvest. Moreover, abundant and/or predictable food should increase success by ICF queens because it would minimize foraging time and maximize the number and size of minims that are produced. These potential advantages should increase founding success, which could compensate for loss of long-range dispersal, especially in homogeneous or persistent habitats where long-distance dispersal is less advantageous.

Overall, it seems that occurrence of ICF versus DCF by ergatoid queens should relate to survival probability in a manner similar to explanations for the occurrence of pleometrosis (nest founding by multiple unrelated queens). For pleometrosis to persist in the presence of queen reduction requires that the survival probability for a queen in an association of n queens is more than n times greater than that of a solitary queen (see Adams and Tschinkel, 1995). Similarly, ICF by ergatoid queens should only occur when survival for x grams of ergatoid queens is higher than survival by x grams of ergatoid queens plus workers that initiate a nest(s) via DCF.

Conclusions

In conclusion, this study supports the growing body of data indicating that ant reproductive strategies are extremely diversified. Evidence for ICF by the three ergatoid species in this study also demonstrate that care should be taken before concluding that ant colonies reproduce via DCF based solely on queen morphology. Queen foraging is especially important in this regard because it provides a wide range of benefits to ICF queens, and it can enable ICF for species that have small and/or wingless queens (see also Heinze et al., 2002; Johnson, 2006). That a range of ICF strategies occur for sympatric congeners of *Pogonomyrmex* in both North and South America makes this system ideal for examining the evolution of colony founding strategies (see also Johnson, 2006).

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