

Research article

**Rediscovery of the workerless inquiline ant  
*Pogonomyrmex colei* and additional notes on natural  
history (Hymenoptera: Formicidae)**

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**Key words:** Interspecific trail following, workerless inquiline ant, *Pogonomyrmex colei*, reproductive biology, seed-harvester ants.

**Summary**

*Pogonomyrmex colei* is a workerless inquiline ant known only from nests of *P. rugosus*, its closest relative. Ten of 776 (1.3%) host nests were parasitized at a site in central Arizona, while none of 1499 potential host colonies were parasitized at two other locales. Colonies of *P. colei* are perennial, and host alate females in 9 of 10 colonies demonstrates that host queens survive parasitism. Three of 10 colonies died over 19 colony years of observation, while only 1 of 601 colonies became newly parasitized. Mating occurs in morning for up to 2–3 days following summer and fall rains and in afternoon during cool fall days. Mating is intranidal just outside the nest entrance, with males returning to the natal nest. Male *P. colei* may be flightless because their wing area is reduced compared to host males. Females fly from the nest and locate potential host colonies by following trunk trails. Workers are the largest barrier to nest establishment, as they removed over 90% of *P. colei* females placed in trunk trails or that entered host nests. Males and females of *P. colei* and *P. anergismus*, the only other congeneric inquiline species, are diminutive compared to their hosts, with females 30% lighter than host workers. Fat content is lower and water content is higher in *P. colei* and *P. anergismus* females than in their hosts.

**Introduction**

Social parasitism in ants has received attention because of curiosity regarding evolution and ecology of this syndrome (Rissing, 1983; Buschinger, 1986; Bourke and Franks, 1991; Nonacs and Tobin, 1992). The most derived form of social parasitism is complete inquilinism in which species typically possess a suite of characters including size reduction, loss of the worker caste, intranidal mating, and extreme rarity (Hölldobler and Wilson, 1990).

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*Pogonomyrmex colei* is a workerless inquiline species known from a nest of *P. rugosus* 3.2 km southeast of Boulder City, Nevada, and from one alate female 27.7 km north of Globe, Arizona; *P. rugosus* is its closest relative (Snelling, 1981; Rissing, 1983). This paper reports colony frequency, population dynamics, reproductive biology, colony initiation, and additional locations of *P. colei*.

## Methods

### *Study sites*

Three *P. rugosus* colonies parasitized by *P. colei* were located 3 km south of Signal Peak, Pinal County, Arizona (32°56'30"N, 111°39'30"W), and nine others were located 4 km to the west. One *P. colei* male also was found in a *P. rugosus* colony 1 km west of the McDowell Mountains in North Scottsdale, Maricopa County, Arizona (33°39'50"N, 111°52'W), 79 km north of the Signal Peak colonies. Habitat of both areas was Sonoran Desert.

### *Census technique and population dynamics*

We censused for *P. colei* by observing *P. rugosus* nests for 15 sec on mornings following summer and fall rains, as males typically emerge then. Males were visible immediately at all host colonies in which they were located; males were also observed at parasitized colonies before and after assays. Population dynamics were assessed by surveying parasitized and unparasitized Signal Peak *P. rugosus* colonies over three years. Regional patterns of occurrence were examined by assaying host colonies 2 km northwest of Florence Junction (33°16'N, 111°22'W) and 9 km southeast of Lake Pleasant (33°48'N, 112°12'W), both in Maricopa County, Arizona. All sites were separated by  $\geq 50$  km.

### *Reproductive biology*

Colonies with *P. colei* were examined in 1992–1994 to verify previous observations. Male *P. colei* re-enter their nest after mating with colony-mates (Rissing, 1983), implying a reduced wing size. Accordingly, we measured wing area on 5–10 male and female *P. colei*, *P. rugosus* (host), and *P. barbatus* (host of *P. anergismus* and possible host of *P. colei*). Wing area was regressed against wet mass across sexes in each species.

### *Colony initiation*

Female *P. colei* may initiate nests by entering host nests, co-founding with a *P. rugosus* gyne, or both; we examined invasion of mature nests because this method was supported by initial observations. Field trials used mated, dealate females, which were obtained by placing numerous pairs in a covered container with an overhead

light. This allowed continued mating and elicited wing removal. Dealate females were marked with paint and released in or 1 m from foraging columns of *P. rugosus* and *Messor pergandei*. Upon crossing columns, we recorded behavior of parasite females and host foragers, and fate of females that entered host colonies for  $\geq 75$  min.

Fat content is associated with method of colony founding (Keller and Passera, 1989). Consequently, body mass allocation was assessed by measuring water and total fat content of *P. colei* and *P. anergismus* and their hosts, *P. rugosus* and *P. barbatus*. Individuals were dried for  $\geq 72$  h at 50–55 °C and reweighed. Fat was extracted by placing crushed females in individual vials of petroleum ether (boiling point 30–60 °C) for  $\geq 24$  h. Individuals were rinsed through filter paper, dried, and weighed.

Voucher specimens are deposited at the Los Angeles County Museum of Natural History and the Museum of Comparative Zoology at Harvard University.

## Results

### *Population status*

*Pogonomyrmex colei* occurred at extremely low frequencies; only 10 of 776 (1.29%) *P. rugosus* colonies were parasitized near Signal Peak, while 0 of 688 and 811 colonies were parasitized at the Florence Junction and Lake Pleasant sites, respectively. Host colonies may remain parasitized for multiple years, as one colony was  $\geq 3$  years old and eight others, including the type colony, lived  $\geq 2$  years. Host gynes survive, as evidenced by alate females in 9 of 10 colonies and the type colony; the host gyne was observed in one parasitized colony. Lack of *P. colei* males on occasions when flights occurred at other colonies suggests *P. colei* died in 3 of 10 colonies (host colonies persisted) over 19 colony observation years, for a colony mortality rate of 16% per year. Coupled with this, *P. colei* established in 1 of 601 (0.17%) previously unparasitized colonies.

### *Mating flights and behavior*

Light precipitation triggered emergence of males, which aggregated in and near the nest entrance. Females emerged only after rains that wetted the soil to several centimeters; mating occurred over 2–3 mornings following such rains from mid-August through late October. Colonies typically had multiple mating flights; during 1992, all seven colonies flew at least twice, and two colonies flew  $\geq$  six times.

Mating and subsequent flights began about 8.30 h and lasted 1–3 h. Observations on 22 August, 1992, typify mating and flight behavior and parallel those of Rissing (1983). Few males were visible at 6.30 h, but this number increased to several hundred males by 8–8.30 h. Females emerged subsequently, were grasped immediately, and in copula with male nestmates, even in the nest entrance. The first female flew at 9.23 h (air temperature 27.6 °C at 30 cm above surface, ground temp. 31.4 °C), and the last at 10.40 h (air temp. 36.4 °C, ground temp. 35.5 °C). After mating, females left the aggregation and often climbed a small plant stem from

which they flew; one female flew 60 m before being lost as she continued upward. One mated female re-entered her host nest, with status thereafter undetermined. Males are flightless and returned to the nest. Mating shifted to early afternoon (1200–1530 h) in mid-October 1994, when daytime temperatures were 23–25 °C. During *P. colei* mating, *P. rugosus* workers defended aggressively the nest area as occurs during host flights (Hölldobler, 1976; Rissing, 1983).

As in congeners (Hölldobler, 1976), *P. colei* females are capable of mating with multiple males. Such behavior was determined by placing females that had just mated in a container with several males: most females were in copula within minutes. Females occasionally mated twice during field observations but more often left the aggregation and flew after the first observed copulation.

Alates of *P. rugosus* did not fly on days that *P. colei* flew in 1992; no *P. rugosus* alates were seen at 22 colonies between 10.45–11 h following a *P. colei* flight on 22 August, 1993, and no host foundresses were located. Both hosts and inquillines had a major mating flight on 21 August, with subsequent nest excavations indicating that all host alates had flown. Individuals of *P. colei* flew again one month later but no host alates were seen.

Flightlessness (but not winglessness) in *P. colei* males may be associated with reduced wing size, as indicated by a within-species, across-sex regression slope steeper than that of free-living congeners, especially the host. Indeed, the slope was more steep for *P. colei* ( $b = 12.33 \pm 0.67$ ,  $p < 0.01$ ) than for *P. rugosus* ( $b = 3.32 \pm 0.31$ ) and *P. barbatus* ( $b = 2.54 \pm 0.28$ ) (wing size in mm<sup>2</sup>, mass in g).

#### *Trail following and colony invasion*

Nearly all *P. colei* females followed host trunk trails. While in trunk trails, *P. colei* females frequently reversed direction and sometimes followed the trail away from the nest. If females strayed from foraging columns, they exhibited a circling behavior that almost always resulted in relocating the column. Females appeared strongly geotropic or photophobic, as entrances to host colonies or holes along the foraging column were entered quickly. Females ignored foraging columns of *M. pergandei* in all of 38 trials.

Host workers were often aggressive towards *P. colei* foundresses in trunk trails grasping the female, while the female ran away with the worker close behind, but soon giving up. Five of 14 females were attacked by workers, dragged from the foraging column, and released  $\geq 10$  m from the column; one female was killed by removal of the gaster. Only 2 of 13 *P. colei* females remained in nests  $\geq 75$  min; workers dragged nine females out of the nest and up to 10 m away. Two females left the nest, apparently voluntarily, one after 2 h 15 min.

#### *Body mass allocation*

Like most inquillines, sexuals of *P. colei* and *P. anergismus* are diminutive compared to their hosts, with female dry mass about 30% less than host workers (Table 1). *Pogonomyrmex colei* and *P. anergismus* females had a higher body water content

Table 1. Body mass (mg), percent water content, and total fat content for *Pogonomyrmex* inquilines and hosts

Species	Males		Females		% Fat	Workers	
	body mass	% water	body mass	% water		body mass	% water
<i>P. barbatus</i>	29.19 (0.36)	67.0 (0.2)	48.48 (0.63)	50.1 (0.3)	39.93 (0.76) <sup>a</sup>	15.32 (0.36)	67.4 (0.3)
<i>P. rugosus</i>	29.79 (0.55)	68.2 (0.2)	47.91 (0.68)	49.0 (0.7)	40.46 (0.78) <sup>a</sup>	13.86 (0.42)	64.6 (0.6)
<i>P. anergismus</i>	8.16 (0.15)	ND	9.19 (0.11)	57.2 (0.7)	27.28 (1.94) <sup>b</sup>	NA	NA
<i>P. colei</i>	6.74 (9.11)	67.2 (0.5)	9.15 (0.10)	56.1 (0.3)	25.33 (1.23) <sup>b</sup>	NA	NA

Values are means ( $\pm 1$  SE); N = 40 per caste per species for body mass and water content, except *P. anergismus* (N = 10 for males, N = 20 for females); N = 18–20 for fat content and water content, except for *P. anergismus* females (N = 9). NA = Not applicable as species is workerless; ND = No data. For fat content, significantly different values among congeners are indicated by the superscripts a, b; a > b.

(Table 1; ANOVA followed by an LSD test,  $P < 0.0001$ ) and lower fat content ( $P < 0.0001$ ) than *P. rugosus* and *P. barbatus* females. Body water content of *P. colei* males was similar to that of host males ( $P > 0.10$ , Table 1).

## Discussion

### *Population status*

*Pogonomyrmex colei* is a rare ant species, even in areas where it is known to occur. Such rarity appears related to locating host colonies, short duration over which host colony foraging columns are active, following foraging columns in the correct direction, aggressive behavior by host workers in columns and inside nests, and *P. colei* females leaving host nests, apparently voluntarily. Females of both *P. colei* and *P. anergismus* also exited nests voluntarily during attempted introductions to lab colonies. These departures appeared caused by high levels of worker harassment, as females typically left after extricating themselves from attacking workers. Overall, host workers are the primary defense against invasion by *P. colei* females, as they removed or caused exit of over 90% of the females that followed trunk trails or entered host nests.

Absence of *P. colei* at two locales indicates that distribution of this species is patchy, as apparently occurs for other inquiline species (Hölldobler and Wilson, 1990). The mechanism causing population patchiness may relate to variability in rejection of inquiline females or to unstable population dynamics. Variability in acceptance of new gynes occurs in *Leptothorax curvispinosus*, where colonies accept or reject consistently addition of mated female offspring, while alien colonies always reject these females (Stuart et al., 1993); host colonies could demonstrate similar variability on a geographic scale. High mortality rates and low establishment rates could also cause patchy populations via high levels of local extinction. It is unknown how mortality rates of about 16% per year coupled with low establishment rates affect dynamics and viability of *P. colei* populations, as no comparable data exist. Death of three *P. colei* colonies (but not of host colonies) over 19 colony observation years implies that at least some *P. colei* colonies consist of only one gyne or that gynes are short-lived.

Survival of host gynes, as occurs for *P. colei* and *P. anergismus* (Johnson, 1995), is common for workerless inquiline species (Hölldobler and Wilson, 1990), and insures a continuous worker supply over the years in which a colony may survive. Affect of *P. colei* on production of host workers and alates is unknown. However, it seems likely that host alate production is affected (see Hölldobler and Wilson, 1990) given that several hundred or more *P. colei* alates represent a significant fraction of colonies that average 7000–15000 workers (MacKay, 1981).

### *Mating, trail following, and entry to host colonies*

Observations of mating behavior parallel those of Rissing (1983) in that flights occur early in morning several or more times a year. Like its host and most other species of *Pogonomyrmex*, mating flights are triggered by rain with number of

flights dependent on frequency of rains sufficient to trigger emergence of females. Amount of rain needed to trigger flights is low compared to that required by the host species, as indicated by absence of host mating flights during several *P. colei* flights; similarly, mating flights occurred at only 2 of 58 host colonies during observations of the type colony (Rissing, 1983). Moreover, *P. colei* mating flights occur after rains that are sufficient to trigger foraging by host workers, whose trails the females can then use to locate mature colonies.

Mating with nestmates is common in rare ant species, and presumably evolved to insure mating when probability of locating mates is extremely low (Wilson, 1963). This phenomenon is common among inquiline ants (Hölldobler and Wilson, 1990), and also occurs in the congener *P. anergismus* (Johnson, 1995). Mating with nestmates may be the only alternative for fertilization in *P. colei*, as males are flightless.

Interspecific trail following is rare in ants and is known only from a few xeno- or parabiogenic species (Wilson, 1965; Hölldobler and Wilson, 1990). Our observations are the first demonstration of trail following by an inquiline ant, a behavior that functions for females to locate and enter mature host colonies. The mechanism likely relates to following recruitment pheromones rather than just the ants themselves given that one female followed a foraging trail 2 m to the nest entrance after foragers had returned to the nest. Ability to follow foraging trails may develop from exposure to host pheromones while in the natal colony. Interspecific trail following likely occurs in other inquiline species such as *P. anergismus*, but is probably restricted to host species that have trunk trails or use recruitment trails. Use of multiple host species, as occurs in *P. anergismus* (MacKay and Van Vactor, 1985), may be common in inquiline species where closely related potential host species exist within their range. Multiple hosts could result from females responding to trail substances of non-conspecifics (Blum et al., 1964). This scenario is especially likely in species such as *P. rugosus* and *P. barbatus* because their recruitment pheromones are nearly identical (B. Hölldobler, pers. comm.).

One of us (Rissing, 1983) was unable to introduce newly mated *P. colei* foundresses into adult colonies and speculated that inquilines may gain entry into host colonies during host colony foundation. Our more recent data suggest this is not the case. First, *P. colei* foundresses can enter host colonies by following trunk trails; this experiment was not considered prudent in the earlier study due to small sample sizes. Second, current observations confirm the protracted mating season of the inquiline relative to its host; this seems maladaptive if inquiline foundresses must enter the host colony during the brief window of colony initiation.

Size reduction of *P. colei* and *P. anergismus* is associated with a reduced fat content, the loss of which probably results in an increased water content (Hadley, 1994). The small size of inquilines relative to their hosts likely precludes independent colony founding until workers eclose (Keller and Passera, 1989). Reduction of fat content would likely follow development of dependent colony founding.

This study demonstrates that several factors are involved in rarity of inquiline ants. *Pogonomyrmex colei* has numerous traits in common with other inquiline species including loss of the worker caste, rare and local distribution, reduced size, and intranidal mating with males returning to the natal colony. Interspecific trail following, a lower rain threshold for mating flights, and small body size and low fat

content infer that *P. colei* and probably *P. anergismus* can only initiate colonies by invading mature host colonies, as was observed for one new *P. colei* colony.

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