NATURAL HISTORY OF THE WORKERLESS INQUILINE ANT *POGONOMYRMEX COLEI* (HYMENOPTERA: FORMICIDAE)*

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At least 10 workerless inquiline ant species are known from North America (Francoeur 1968, 1981; Wilson 1971, 1976; Talbot 1976; Buschinger 1979; DuBois 1981; Snelling 1981), most only from original collections. In this paper I present field and laboratory observations of *Pogonomyrmex colei* Snelling a new, apparently workerless, inquiline ant inhabiting a colony of *Pogonomyrmex rugosus.*

P. colei appears to be a very rare species: extensive searching of the type locality for 4 yr has resulted in discovery of only a single colony. Nonetheless, observations on this colony provide insight into several important aspects of inquiline ant biology. *P. colei* is also of interest since it is the second apparently workerless congeneric inquiline inhabiting colonies of *P. rugosus*. Cole discovered the first inquiline species, *Pogonomyrmex anergismus,* near Silver City, New Mexico apparently prior to any major flight since he exposed "more than one hundred" inquiline reproductives upon opening the host nest (Cole 1954, 1968). Since host species mating flights occur soon after rain during mid to late summer (Hölldobler 1976; Rissing personal observation), it seemed reasonable to suspect *P. anergismus* responds to the same environmental cues for mating as does its host. Accordingly, in an effort to rediscover *P. anergismus*, I routinely checked most *P. rugosus* nests on a 25 ha study area in Boulder City, Nevada for flight activities and possible presence of inquilines during late summer 1978 and 1979 (study area described in Rissing 1981). *P. colei* was discovered during this effort.

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Observations

Mating Activities and Season. Five *P. colei* males were collected at a single *P. rugosus* nest during the morning of 13 August 1978; a series of thunderstorms and rain had occurred 12 hr earlier. Frenzied host worker activity suggested a mating flight or similar activity occurred immediately prior to my arrival. No flights of either species occurred at any nearby *P. rugosus* nests observed simultaneously.

I observed a complete inquiline and host flight at this same nest on 15 September 1978 following an extensive rain storm the preceding day. Flights were occurring at 2 of 23 nearby *P. rugosus* nests; *P. colei* was not found at any other nest. Mating activities began with accumulation of several hundred host workers in and around the nest crater. These workers pugnaciously defended the area throughout both flights as is typical during *P. rugosus* flights (Rissing, personal observation). As ground and air temperatures increased male *P. colei* climbed to the crater and were soon joined by much larger females. While both sexes of *P. colei* are winged, mating occurred at the nest entrance followed by females flying from the area and males re-entering the nest. Such *in situ* mating is common in rare ant species apparently due to very low probability of reproductives finding individuals from other nests with which to mate (Wilson 1963). Following copulation and departure of *P. colei* females, male and female *P. rugosus* flew from the crater as the temperature continued to climb. Reproductive forms of *P. rugosus* fly to a site away from the nest and copulate there (Hölldobler 1976). Mating activities of host and inquiline were separated by at least 30 min and, perhaps more importantly, 3° C ground temperature (Table 1). Reproductive forms of each species were seen occasionally in the nest entrance during the mating activity of the other. On at least one occasion, *P. colei* males tried unsuccessfully to mount a *P. rugosus* female. During this flight I observed no differences in behavior of host workers to host or inquiline reproductives. *P. rugosus* workers frequently encircled copulating pairs of *P. colei* and frantically ran around them, although they never interfered.

During 1979 routine observations were begun at the study area on 18 September. A complete *P. colei* flight was observed at the host nest during the afternoon of 30 September immediately following a trace of rain. No flights of either species were observed at 35 nearby *P. rugosus* nests during this time. On 8 October 1979 I poured approximately 7.5 l of water directly onto the host nest crater resulting in an immediate flight of *P. colei*. This procedure was repeated unsuccessfully on 17 and 18 September 1982. Viability of the host nest (as determined by worker activity, size of crater and refuse pile, and absence of plants growing in the crater) has remained constant and similar to that of nearby *P. rugosus* colonies from 1978 to 1982. I have never observed any forms that might be considered *P. colei* workers.

Colony foundation. Ten newly mated *P. colei* females from the 15 September 1978 flight were placed into a 7.5 m high flight enclosure made of plastic sheeting and permitted to fly. Subsequent to this all females removed their wings but did not dig burrows when placed into laboratory nest boxes containing moist sand. Five of these dealate inquilines were transferred to 5 laboratory nests containing only newly mated *P. rugosus* queens. These *P. rugosus* queens had been collected one week earlier at a mating site 3.2 km from the host nest making it unlikely that they were related to the host colony. Four of these laboratory nests contained a single, mated dealate *P. rogusus* queen; the fifth contained two *P. rugosus* queens. The *P. colei* queen added to the nest with two *P. rugosus* queens was immediately attacked and removed from the glass tube occupied by the *P. rugosus* queens. Of the *P. colei* queens added to the single queen *P. rugosus* colonies, one was found dead within several hours (decapitated), and the other was found dead (entire) 5 d later. The other two *P. colei* queens lived peacefully along side the *P. rugosus* queens for at least a month. During this time I frequently observed the *P. colei* queens grooming the *P. rugosus* queens; *P. rugosus* queens did not reciprocate. These last two colonies ultimately failed during (or possibly in response to) transportation from Boulder City to Seattle.

Five other newly mated, dealate *P. colei* queens were released in the field at the entrance of large, active *P. rugosus* colonies near the host nest. Inquilines were always removed immediately from the nest by one or more workers and dropped several meters from the crater. The *P. colei* queens made no attempt to re-enter these nests following removal.

Discussion

Repeated (and continuing) attempts to find *P. colei* or *P. anergismus* around Boulder City, NV, or Globe, AZ, where a single *P. colei* male has been collected (Snelling 1981) have yet to be successful. Nonetheless, observations of *P. colei* from the type nest in Boulder City provide insight into several questions of general inquiline biology including possible method of inquiline entry into host colonies and fate of host queen.

Inquiline entry into host colonies. Newly mated *P. colei* queens are accepted into 1 week old workerless host nests in the laboratory, while they appear incapable of entering established host nests in the field (see above). Similar observations have been made in laboratory experiments with the inquiline *Plagiolepis xene* and its host, *Plagiolepis pygmaea* (Passera 1964). This suggests that at least some inquiline species enter a host colony at the founding stage prior to production of any workers. That this may occur in the field is supported by discovery of a workerless inquiline queen (*Strumigenys xenos*) in an incipient host colony containing one queen, brood and a single worker of *Strumigenys perplexa* (Brown 1955).

If entry into host colony commonly occurs at host colony foundation in some species of inquilines, overlap with host species flight season would be advantageous. Since all nests of a given species in a locality tend to have a longer "flight season" than any single nest (e.g. for *P. rugosus* see Hölldobler 1976), the inquiline might further be expected to lengthen its flight season relative to that of its host colony to take advantage of the entire flight season and availability of founding nests in its locality. The extended flight season of *P. colei* relative to that of *P. rugosus* may occur for these reasons. Similarly, occurrence of *P. anergismus* reproductives during mid September in the type nest reported by Cole (1954, 1968) may also indicate inquiline-host reproductive overlap.

Fate of host queens. Simultaneous production of host and inquiline reproductives during the 1978 flight (Table 1) strongly suggests coexistence of host and inquiline queen(s) at that time. Continuing existence of the host colony until at least September 1982 further substantiates this. Estimates of maximum longevity of worker ants is 1-2 yr (Rosengren 1971, Brian 1972, Nielsen 1972). Further, there has never been a reported case of queen adoption in any *Pogonomyrmex* species. For the host colony to have a normal foraging

Table 1. Summary of mating activities of *P. colei* and *P. rugosus* in Boulder City, Nevada, 15 September 1978.

Time	Ground Temp. °C[1]	Air Temp. °C[2]	Activity
08:55			Reproductives of both species in nest entrance
09:10	20.5	20.5	*P. colei* reproductives on crater
09:37	21.0	21.5	Number of *P. colei* increases
10:03			First *P. colei* copulation
10:45	26.0	23.8	First *P. colei* female flies
12:15	29.2	25.5	Last *P. colei* female flies
12:47	32.6	26.4	First *P. rugosus* male and female fly
13:15	33.4	30.8	Last *P. rugosus* flies

[1]Temperature as determined by holding tip of a Yellow Springs Instruments direct read thermistor (YSI #405) on ground surface; temperature read on a Yellow Springs Instruments telethermometer (YSI #43TA).
[2]Temperature determined as above with thermistor 30 cm above ground and shaded.

group size in 1982, the host queen must have been alive during the 1978 and 1979 inquiline flights. Although inquiline-host coexistence has been regarded as a "primitive" inquiline trait (Wheeler 1933, Haskins and Haskins 1964), it offers the obviously adaptive advantage of a continuously renewed host worker force for the inquiline. Coexistence occurred in the type nest of *P. colei* and appears common in other workerless inquiline species where information regarding fate of host queen(s) is available (Table 2).

Host queen elimination does occur in at least two well documented cases (Table 2). Wilson (1971) suggests such behavior may develop in short-lived inquiline species; inquiline longevity, however, may be more of an effect than a cause of this behavior. Host queen elimination may be adaptive only when inquiline entry is gained by a queen after development of a host worker force. Host workers appear to be the primary defense against inquiline entry in many colonies. In order to be accepted by host workers, it may be necessary for the prospective inquiline queen to first render the prospective host colony queenless. In those cases where host queens are known or highly suspected of being eliminated (Table 2), the inquiline queen enters an established colony containing workers. In at least one of these cases, *Epimyrma vandeli*, the inquiline must fight with host workers until she is able to kill the host queen. Recent discovery that *E. vandeli* is a degenerate slave-maker

Table 2. Fate of host queen(s) for workerless inquilines. Only those species whose host queen(s) fate is known are listed.

Inquiline species	Host species	Fate of host queen(s)	Reference
MYRMECIINAE			
Myrmecia inquilina	*Myrmecia vindex*	survives	Douglas and Brown 1959 Haskins and Haskins 1964
MYRMICINAE			
Myrmica hirsuta	*Myrmica sabuleti*	survives	Elmes 1974a, 1978
Sifolinia laurae	*Myrmica sabuleti*	survive	Brian 1972
Pogonomyrmex colei	*Pogonomyrmex rugosus*	survive*	this study
Anergates atratulus	*Tetramorium caespitum*	apparently killed by host workers	Wheeler 1910, Crawley 1912, Donisthorpe 1915, Creighton 1950
Teleutomyrmex schneideri	*Tetramorium caespitum*	survives	Stumper 1950+, Kutter 1969
Leptothorax kutteri	*Leptothorax acervorum*	survive	Buschinger 1965
Leptothorax minutissimus	*Leptothorax curvispinosus*	survive	Smith 1942, Buschinger 1981
Epimyrma vandeli	*Leptothorax nigriceps*	killed by inquiline	Vandel 1927 Stumper and Kutter 1951
Doronomyrmex pacis	*Leptothorax acervorum*	survive	Kutter 1945+, 1969+
Monomorium pergandei	*Monomorium minimum*	survive*	Creighton 1950
Doronomyrmex pocahontas	*Leptothorax muscorum*	survive*	Buschinger 1979
Monomorium adulatrix	*Monomorium salomonis*	killed by host workers	Wheeler 1910 Forel 1930

Table 2. Continued.

Inquiline species	Host species	Fate of host queen(s)	Reference
Monomorium talbotae	*Monomorium minimum*	survives	Talbot 1979
Strumigenys xenos	*Strumigenys perplexa*	survive	Brown 1955, Taylor 1967
FORMICINAE			
Plagiolepsis xene	*Plagiolepsis pygmaea*	survive	Le Masne 1956; Passera 1964, 1966, 1972
Aporomyrmex ampeloni	*Plagiolepis vindobonensis*	survives	Faber 1969+

*Presence of host queen(s) determined by presence of host reproductives
+Cited in Wilson (1971)

(Buschinger 1981, Buschinger and Winter 1982) may explain this behavior which is rather unusual among most other inquilines (Table 2). Only the extreme inquiline *Teleutomyrmex schneideri* is known to enter established host nests without having to eliminate host queens; these inquilines may produce a substance highly attractive to host workers (reviewed in Wilson 1971).

Comparison with P. anergismus and other workerless inquilines. P. colei may represent an intermediate form between its host *P. rugosus* and the closely related workerless inquiline *P. anergismus* (for a complete discussion of morphological differences see Snelling 1981). Discovery of *P. colei* adds the genus *Pogonomyrmex* to a growing list of ant genera with more than one workerless inquiline species (Table 2). Such "concentration" of inquilines into a few genera may occur either due to non-random search by myrmecologists (*P. colei* was discovered during an intentional search for *Pogonomyrmex* inquilines) or because certain genera are more likely to give rise to inquilines. The basic biology of the inquiline-rich genera, however, is quite variable suggesting several evolutionary routes may lead to workerless inquilinism. The genus *Leptothorax*, for example, has small, ephemeral colonies subject to slave raids from numerous species and has given rise to several closely related *Epimyrma* inquiline species, themselves degenerate slave-makers (Buschinger 1981, Buschinger and Winter 1982). *Myrmica,* on the other hand, has larger colonies and many species that are highly polygynous (Brian 1972; Elmes 1974a,b); this genus has given rise to at least 7 workerless inquiline species: *Myrmica faniensis* (van Boven 1970), *Myrmica hirsuta* (Elmes 1974a, 1978), *Myrmica lampra* (Francoeur 1968, 1981), *Myrmica myrmecophila* (Bernard 1968), *Myrmica quebecensis* (Francoeur 1981), *Sifolinia karavajevi* (Kutter 1969) and *Sifolinia laurae* (Brian 1972), the *Sifolinia* species likely being congeneric with the other *Myrmica* species (Elmes 1978). *Monomorium* is similar with polygynous species (Dennis 1938, Cole 1940, Gregg 1945) and a number of congeneric inquilines (reviewed in Wilson 1971, see also Talbot 1979 and DuBois 1981). These inquiline species may have evolved through a process of some polygynous host queens acquiring the trait of laying only reproductive eggs (Buschinger 1970, Elmes 1978). To this list must be added the genus *Pogonomyrmex* whose basic biology is unlike any of the above three host genera. Colonies are substantially larger than *Leptothorax, Myrmica* or *Monomorium* (Lavigne 1969, Rogers et al. 1972, Whitford et al. 1976, MacKay 1981), strictly monogynous (Lavigne 1969, Hölldobler and Wilson 1977, MacKay 1981), with no slave-making or similar behavior in any species. Evolutionary processes giving rise to *P. colei* and *P. anergismus* are likely different from those that have given rise to the *Leptothorax, Myrmica* or *Monomorium* inquilines. Certainly, the idea of multiple evolutionary pathways leading to workerless inquilinism is not new (see Wheeler 1919, Buschinger 1970, Wilson 1971). Continued study and search for workerless inquilines can only serve to clarify this challenging evolutionary process.

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