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

By Steven W. Rissing Department of Zoology Arizona State University Tempe, Arizona 85287

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

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).

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

²Temperature determined as above with thermistor 30 cm above ground and shaded.

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	Myrmecia		Douglas and Brown 1959				
inquilina	vindex	survives	Haskins and Haskins 1964				
MYRMICINAE							
Myrmica	Myrmica						
hirsuta	sabuleti	survives	Elmes 1974a, 1978				
Sifolinia	Myrmica		Brian 1972				
laurae	sabuleti	survive	Brian 1772				
	sucur	5411110					
Pogonomyrmex	Pogonomyrmex						
colei	rugosus	survive*	this study				
Anergates atratulus	Tetramorium caespitum	apparently killed by host	Wheeler 1910, Crawley 1912, Donisthorpe 1915, Creighton				
arrararas	cuespnum	workers	1950				
Teleutomyrmex	Tetramorium		Stumper 1950+,				
schneideri	caespitum	survives	Kutter 1969				
T	T 4 . 4						
Leptothorax kutteri	Leptothorax acervorum	survive	Buschinger 1965				
Kulleri	acervorum	Survive	Buschinger 1903				
Leptothorax	Leptothorax		Smith 1942,				
minutissimus	curvispinosus	survive	Buschinger 1981				
Epimyrma	Leptothorax	killed by	Vandel 1927				
vandeli	nigriceps	inquiline	Stumper and Kutter 1951				
	,,,g,,ceps		Bramper and Russer 170.				
Doronomyrmex	Leptothorax		Kutter 1945+, 1969+				
pacis	acervorum	survive					
Monomorium	Monomorium						
pergandei	minimum	survive*	Creighton 1950				
Doronomyrmex	Leptothorax						
pocahontas	muscorum	survive*	Buschinger 1979				
Monomorium	Monomorium	killed by	Wheeler 1910				
adulatrix	salomonis	host workers	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	Plagiolepsis		Le Masne 1956;			
xene	pygmaea	survive	Passera 1964, 1966, 1972			
Aporomyrmex ampeloni	Plagiolepis vindobonensis	survives	Faber 1969+			

^{*}Presence of host queen(s) determined by presence of host reproductives

(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 inquilinerich 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

⁺Cited in Wilson (1971)

related Epimyrma inquiline species, themselves degenerate slavemakers (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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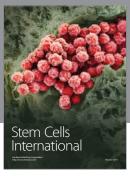
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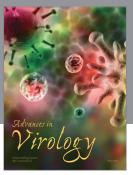
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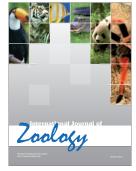
















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