COLONY FOUNDING, QUEEN CONTROL AND
WORKER REPRODUCTION IN THE ANT
APHAENOGASTER (= *NOVOMESSOR*) *COCKERELLI*
(HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

The closely related species *Aphaenogaster cockerelli* and *A. albisetosus* are common ants of the southwestern United States and northern Mexico (Creighton 1950, 1955). Originally described as members of *Aphaenogaster*, until recently these species together with *A. manni* constituted the genus *Novomessor*. However, Brown (1974) suggested returning them to *Aphaenogaster*, which treatment is followed here. The foraging and communication behavior of these ants has been studied intensively by several authors (Hölldobler et al. 1976, Whitford 1976, Davidson 1977, Hölldobler et al. 1978, Markl and Hölldobler 1978). Recently, McDonald and Topoff (1985) and Beshers and Traniello (1987) investigated division of labor in *A. albisetosus*. In the course of analyzing the communication system of *A. cockerelli*, we made a series of observations concerning its social organization which are assembled in the present paper. These include colony foundation and queen number, queen control of oviposition by workers, worker reproduction and tem-

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poral polyethism, and aggression toward ovipositing workers. Some of our findings on *A. cockerelli* are complementary to those reported for *A. albisetosus*.

METHODS

Field studies were conducted during the summer months between 1974 and 1988 in the Chihuahuan desert near Portal, Arizona and Rodeo, New Mexico. For laboratory studies, colonies were excavated and cultured in artificial nests and provided ant diet (Bhatkar and Whitcomb 1970) and chopped insects. One colony, already mature when collected, was maintained in the laboratory for more than 9 years. In addition, several colonies were raised from founding queens. Colonies subjected to detailed behavioral observation were housed in glass test tubes (2.2 cm diameter $\times$ 15 cm), containing water trapped at the end behind a cotton plug. The test tubes were placed in plastic nest boxes of different sizes, connected to foraging arenas in a variety of configurations depending on the size of the colony and on the experiment.

For dissections of their ovaries and fat bodies, ants were killed by placing them in a freezer for a few minutes, and their gasters were opened under distilled water. Numbers of large and small oocytes were counted, and the size of the fat body was scored on an arbitrary scale from 0 (almost absent) to 3 (strongly developed). Further methodological details are given with the descriptions of particular experiments.

RESULTS

Colony Founding and Queen Number

Field and laboratory observations indicate that *A. cockerelli* colonies are monogynous, with queens founding claustrally and independently. Nuptial flights occur in the Chihuahuan desert in the month of July, at dusk (four flights observed, in 1973, 1974, 1984 and 1986). Males emerge from nest entrances between 1800 and 1900 hours, and dealated queens can be found wandering on the ground half an hour later, and sometimes also the following morning. We observed workers attacking dealated queens that entered the nest areas of established colonies, indicating that queens are not ordinarily re-admitted to nests. Sympatric *A. albisetosus* workers

also exhibited aggression toward conspecific dealated queens (Figure 1). Fourteen incipient nests of *A. cockerelli* were excavated in the field following nuptial flights, and each contained only one queen. Of seven mature colonies that were excavated, one queen each was found in four. The other three contained worker brood, but we did not succeed in finding queens.

In the laboratory, 12 single queens and 8 pairs of queens were housed in test tube nests. None of the queens left their test tubes to forage. In 7 of the 8 pairs, the queens exhibited mutual antagonism, sometimes escalating to full fighting resulting in injuries. One queen in each of two pairs died within the first week. The other 5 antagonistic pairs continued to coexist, but kept separate egg piles. Paired queens did not raise more workers or produce them sooner than single queens. On the contrary, though brood was not censused, it was qualitatively apparent that paired queens had smaller egg piles, perhaps due to reduced oviposition or to egg eating.

After eclosion of the first workers, one queen began to consistently dominate the other in the surviving antagonistic pairs. The queen situated near the cotton plug, where all eggs were now piled together, threatened and sometimes charged at the other queen. Workers occasionally nibbled or pulled on the appendages of the subordinate queen; this behavior was never directed toward the dominant. Within a year of initial worker eclosion, the subordinate queens were expelled from four nests and soon died. The subordinate queen of the fifth nest was expelled after 28.5 months, though it was not clear whether she was still ovipositing by that time. In the final pair, in which no antagonistic interactions were ever observed, one of the queens was found dead, with injuries on her antennae and foreleg indicating that she had been attacked, 16 months after the first workers eclosed.

Trophic Egg Production by Workers

Workers produce only trophic eggs in the presence of the queen, which appear to be her major source of nutrition, since food exchange by regurgitation does not occur in this species. (We occasionally observed mouth-to-mouth contacts among adults, but as these were brief and no transfer of liquid could be seen, they most probably represented only licking of the mouthparts. When two workers from a group of 20 that had been starved for 8 days were removed, allowed to gorge on honey water and then returned to

Figure 1. Newly-mated queens of *Aphaenogaster albisetosus*, a sympatric congener of *A. cockerelli*, are attacked by workers on entering the nest area of an established colony.

their group, no regurgitation was observed. Dissection of the workers confirmed that no exchange of crop contents took place.) Trophic eggs are usually round, milky and liquid-appearing, are laid within 5–20 seconds and are fed directly to the queen larvae, or sometimes to workers. Workers sometimes produce clear droplets of fluid which are also eaten by larvae. In addition, larvae are fed prey objects, and may receive (or donate) oral glandular secretions, as mouth-to-mouth contacts occur between larvae and workers. Not surprisingly, workers have considerably smaller ovaries (with 5.3 ± 0.9 ovarioles each, range 4–8; $N = 248$) than those of queens (33.3 ± 5.3 ovarioles, range 28–46; $N = 13$).

The spatial distribution of laying workers within colonies is not random. In three laboratory colonies, workers taken from the nest tube containing the queen, eggs and larvae (Figure 2) contained significantly more large and small oocytes and more developed fat bodies than workers taken from the foraging arenas (Table 1, Figure 3). In addition, most workers in foraging arenas had yellow bodies in their ovaries, evidence of previous activity. Dissection of workers collected from a field colony confirmed that brood chamber workers had significantly more large and small oocytes and stronger fat bodies than foragers (Table 1, Figure 4). The latter were presumably older, since both highly developed ovaries and remaining inside the nest are typical of recently eclosed ant workers (Otto 1958, Hohorst 1972, MacDonald and Topoff 1985; see also ethogram data, below). Workers engaged in construction activity at the nest entrance were intermediate in ovarian development and probably in age; they did not differ from either inside workers or foragers in numbers of large oocytes, though they had significantly more small oocytes and more developed fat bodies than foragers (Table 1, Figure 4). Though these data suggest a typical pattern of temporal division of labor, foragers had a distinctly bimodal distribution of oocyte numbers, with some individuals in both field and laboratory retaining highly active ovaries (Figures 3, 4).

Most mature colonies of *A. cockerelli* are polydomous, with 2–5 nest mounds. We frequently observed workers transporting other workers, larvae and pupae from one nest to another in both field and laboratory, usually during late afternoon or evening. In one laboratory colony, housed in three connected compartments containing nest tubes and more than 500 workers each, workers were

Figure 2. An *A. cockerelli* queen in the central brood chamber of her nest.

Figure 3. Frequency distributions of oocyte numbers (top) and fat body scores (bottom) of foragers and workers in brood chambers, from 3 laboratory colonies. Both are significantly greater in brood chamber workers (χ^2 test, $p < 0.005$, d.f. = 13 for oocytes, $p < 0.0001$, d.f. = 3 for fat bodies).

Table 1. Numbers of oocytes in the ovaries of queenright and queenless *A. cockerelli* workers in laboratory and field nests, under different experimental treatments described in text. Number dissected is the number of individual workers; the number of colonies from which workers were collected is given in parentheses. Data in category 7 (queenright laboratory workers) is pooled from categories 4 + 5. Significance determined by 2-sample t test; * indicates $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, other comparisons not significant.

Category of workers	Number dissected	Number of Large Oocytes	Number of Small Oocytes
In a field nest—			
1. In brood chambers	20 (1)	0.9±0.9 **	4.5±3.1 *
2. Foraging	20 (1)	0.2±0.4	2.3±2.6 *
3. Digging at entrance	20 (1)	0.5±0.7	4.7±3.0
(Categories 1 and 3 not significantly different for either oocyte size)			
In laboratory nests—			
4. In nest tubes	25 (3)	1.6±1.4 ***	6.4±2.6 ***
5. Foraging	34 (3)	0.3±0.6 **	2.4±2.5 ***
6. Being carried	18 (1)	1.6±1.4	5.2±1.7
7. Queenright	59 (3)	0.8±1.2	4.1±3.2
8. Queenless	71 (4)	0.4±0.8	5.8±4.7
Reunited after 7 months of separation—			
9. Attacked	5 (1)	2.2±0.8 **	6.4±1.1 ***
10. Not attacked	15 (1)	0.7±0.8	3.3±2.2

usually, though not exclusively, carried in the direction of the queen (who always remained in the same compartment). A total of 36 workers being carried into the queen's compartment were marked in two experiments; some of these subsequently appeared in other compartments, indicating that not all transported workers remain near the queen. The ovaries of transported workers contained significantly greater numbers of oocytes than those of most workers found outside the nest (Table 1). Laying workers may be actively transported into the queen's vicinity to provide trophic eggs for her. It is also possible that older workers carry young ones to the queen in order to expose them to her control and prevent their laying viable eggs.

Figure 4. Frequency distributions of oocyte numbers (top) and fat body scores (bottom) of foragers, workers digging at the nest entrance and workers in brood chambers, from 1 field colony. No two distributions differ significantly in total numbers of oocytes (χ^2 test, $p > 0.05$), though foragers contain significantly fewer large and small oocytes than brood chamber workers when these are treated separately (χ^2 , $p = 0.02$, d.f. = 3 for large oocytes, $p = 0.02$, d.f. = 8 for small oocytes; see also Table 1). Fat bodies of foragers are significantly weaker than those of both brood chamber workers ($p < 0.0005$, d.f. = 3) and entrance workers ($p < 0.005$, d.f. = 3), but fat bodies of entrance and brood chamber workers do not differ ($p > 0.05$, d.f. = 3).

Queen Control and Worker Reproduction

In queenright colonies, workers produced large numbers of trophic eggs (which were quickly eaten), but were never observed laying viable eggs. However, 17 to 41 days after separation from their queen ($N = 17$ groups varying in size from 9 to over 500 workers, some also containing queen-produced brood), workers began to lay viable eggs. Viable eggs differ in appearance from trophic eggs, being oval, firm and white, and are collected into piles and tended rather than eaten (Figure 5). Oviposition of a viable egg takes longer than that of a trophic egg, 1–3 minutes as opposed to 5–20 seconds. No queenless group failed to produce some viable eggs, and all groups also continued producing trophic eggs, some of which were eaten by workers. In 11 groups, the complete development of worker-laid brood was observed, and only males emerged. Unexpectedly, dissection of all workers from 4 male-producing queenless groups revealed no consistent enhancement of their ovaries. They contained significantly more small oocytes than queenright workers, but significantly fewer large oocytes and weaker fat bodies (Table 1, Figure 6). However, as in queenright colonies, the distribution of oocyte numbers was bimodal, with some individuals having strongly developed ovaries (Figure 6). These individuals were probably the principal egg layers, and may have functioned as “pseudoqueens.” (See also results on aggressive behavior.)

Two four-year-old colonies, reared in the laboratory from founding queens, were divided into two moieties of about 500 workers and 30 pupae each, one of which also contained the queen and her cluster of eggs. After 18 days, the queenless moieties of both colonies contained egg piles, and after two months both had many male pupae and adults, while the queenright moieties contained only worker pupae. Queenless workers reared the remaining queen-produced worker pupae along with their own male brood, then gradually declined in number. However, they continued producing males for 13 months; one group reared its last male when only 16 workers survived. The queenright moieties flourished and grew into large colonies, but produced no males within the next two years, demonstrating that workers do not reproduce in a queen's presence.

Among honey bees, workers can act as “messengers” for queen control, contacting the queen and distributing her inhibitory pheromones (Seeley 1979). To test this possibility in *A. cockerelli*, a third colony of several hundred workers was partitioned into

Figure 5. Worker-laid viable eggs are collected into an egg pile and tended.

queenless and queenright moieties, and 20 individuals on each side were marked with fluorescent paint. Beginning immediately after partitioning, 10 marked workers were transferred from each side to the other every 2–3 days. These exchanges did not inhibit viable egg production on the queenless side, which began 3 weeks after separation. Observations of another colony (while recording the workers' behavioral repertory; see below) indicated little physical contact between workers and their queen. Though surrounded by a loose retinue of callow and adult workers (Figure 2), she was licked fewer than five times per hour. Grooming was not directed particularly toward any body region that might provide a pheromone source. The queen did leave her nest tube fairly often, walking around the colony and perhaps spreading inhibitory substances.

Behavioral Repertories of Queenright and Queenless Workers

The behavioral repertories of workers were examined in a four-year-old colony, raised in the laboratory from a founding queen, divided into queenright and queenless moieties with larvae, pupae and approximately 200 workers distributed equally on both sides. Twenty-one days after separation, the first viable eggs appeared on the queenless side, and a pile of about 75 eggs accumulated over two weeks. Ethograms were constructed from a total of 56 hours of observation (28 hours per moiety), recorded in four half-hour sessions daily (Table 2). Adult and callow workers were distinguished by the pale pigmentation of the latter. Some behaviors such as assisting eclosion and attacking or handling prey were frequently performed cooperatively by groups of 3–5 workers; each individual participating in a collective act is counted separately in Table 2.

Workers of the queenright and queenless moieties differed little in most behaviors. Variation in the care of different brood stages may be ascribed to the differing age distributions of brood in the two moieties, as the queen's large egg pile remained on her side of the partition. On the queenright side, most trophic eggs were produced by callows (116 vs. 51 by adults, $p < 0.001$, χ^2), confirming the influence of age on ovarian activity indicated by dissection data, above. As expected, on the queenless side callow workers began to lay viable eggs, while older workers did not. Having switched to viable egg production, queenless callows concomitantly laid and fed to larvae fewer trophic eggs (69 vs. 116, $p < 0.005$ for oviposition; 58 vs. 101, $p < 0.005$ for feeding). On the queenless side, worker

Figure 6. Frequency distributions of oocyte numbers (top) and fat body scores (bottom) of workers in 4 queenless and 3 queenright laboratory groups (the latter consisting of combined foragers and brood chamber workers from Figure 3). Oocyte numbers do not differ significantly (χ^2 , $p > 0.05$, d.f. = 15). Fat bodies of queenless workers are significantly weaker than those of queenright workers ($p < 0.0005$, d.f. = 3).

Table 2. Behavioral repertoires of workers in a partitioned colony of *A. cockerelli*, with larvae, pupae and approximately 200 workers on each side, and ovipositing workers in the queenless half, based on 56 hours of observation. Adult and callow workers were distinguished by pigmentation.

Acts	Queenright		Queenless	
	Callow	Adult	Callow	Adult
Lay trophic egg	116	51	69	49
Lay viable egg	0	0	12	0
Feed trophic egg to				
larva	101	37	58	34
worker	8	9	6	8
Groom or handle egg	106	19	72	13
Groom or handle larva	1422	526	1166	529
Groom or handle pupa	486	251	497	356
Assist eclosion	67	16	61	26
Groom adult	294	379	248	260
Carry adult	0	2	7	0
Groom callow	484	363	525	271
Carry callow	3	3	2	14
Self-groom	820	864	963	1029
Groom or carry dead ant	26	58	17	36
Dig or manipulate				
nest material	439	780	337	647
Attack or handle prey	76	151	82	111

transport increased in frequency (23 vs. 8 on the queen's side, $p < 0.01$), and only callows were carried by adults, which may relate to the differential transportation of laying workers described above. Though workers on both sides handled and groomed eggs with similar frequency, some queenless workers carried clusters of between 1 and 20 eggs for prolonged periods. Such behavior, which occurred only occasionally in the queenright moiety, may represent guarding of the eggs, though no worker was ever seen eating or damaging a viable egg.

Egg carrying was examined further in 6 queenless groups of 69 ± 38 ($\bar{x} \pm s.d.$) workers each, collected from two field colonies. Following the onset of worker oviposition, workers noted carrying or holding eggs were given individual-specific marks with loops of colored wire tied around the petiole, to a total of 3.7 ± 1.8 marked workers per group. In subsequent observations, made sporadically

Table 3. Carrying or holding eggs by marked and unmarked workers in 6 queenless groups. $N = 77 \pm 34$ ($\bar{x} \pm s.d.$) workers per group at start of observations, 44 ± 23 at end, with a total of 3.4 ± 1.8 marked individuals per group; due to changing proportions of marked and unmarked workers, the number of acts observed is compared to that expected from the proportion present at each observation, by 1-sided Fisher's exact test.

Colony	Total number of acts	Number of acts by marked workers		Difference significant?
		Observed	Expected	
1	14	0	1.2	n.s.
2	20	1	0.3	n.s.
3	15	3	0.5	$p < 0.02$
4	32	10	3.4	$p < 0.002$
5	27	11	2.0	$p < 0.001$
6	11	11	2.4	$p < 0.001$

over 3.5 months (usually between 1700 and 2000 hours), all marked and unmarked workers performing these acts were counted. Mortality reduced the sample to 39 ± 25 workers per group by the end of the experiment, and required marking of additional egg holders to replace the dead. Observed acts were therefore compared to expectation from the ratio of marked to unmarked workers present at each observation, by 1-sided Fisher's exact test (Kendall and Stuart 1979). Eggs were carried or held significantly more frequently by marked individuals in 4 of 6 groups (Table 3). When the surviving 12 members of the sixth group were dissected, the 3 marked workers' ovaries contained 12.3 ± 6.4 oocytes, compared to only 0.8 ± 1.6 oocytes for 9 unmarked workers. Though this difference is not significant due to the small sample ($p = 0.085$, t test), the trend suggests that workers which hold eggs may be the same individuals that oviposit.

Aggression Toward Laying Workers

The partition dividing the ethogram colony was removed after 5 weeks of separation. Workers from the queenright moiety quickly moved into the queenless side and responded very aggressively to the males and certain individual workers (Figure 7), while ignoring most of the queenless workers. Six workers were pinned down, their legs and antennae seized by up to 10 of their queenright former nestmates; none were killed, but injuries resulted. The six attacked individuals were dissected; all had fully developed ovaries with at least one mature oocyte, and were probably able to lay viable eggs.

Approximately 4 weeks after being reunited, the colony ceased to produce males, suggesting that the queen was again exerting a suppressive influence on her formerly separated workers. The same result was obtained when the two moieties of the colony used for the messenger experiment were reunited after 7 months' separation. Five workers were singled out for attack by former nestmates; they and 15 randomly chosen workers were dissected. All of the workers being attacked had fully developed ovaries, containing significantly more large and small oocytes than those of controls (Table 1). Only 3 of the 15 control workers appeared potentially capable of producing viable eggs. Four others had watery oocytes and were probably laying trophic eggs, while the remaining 8 had reduced ovaries.

Antagonistic behavior was also occasionally observed within some, but not all, of the queenless worker groups used in the above experiments. Careful examination revealed no evidence of aggression within the queenless moiety of the ethogram colony. However, sporadic fighting among nestmates occurred in 5 of the 6 groups used to study egg holding and in the queenless moiety of the messenger experiment. Hostility among nestmates was usually limited to mandible-mandible nibbling, seizing and holding or tugging on antennae and limbs (Figure 8). The victim sometimes responded by crouching with folded limbs, and on occasion was lifted and briefly carried by its attacker in a pupal posture. Less frequently workers bit nestmates on the gaster, or dragged them by the head or appendages. This stronger aggression was exhibited by fully-pigmented workers, directed only toward callows and males (particularly toward the wings of the latter), resulting in the deaths of several.

DISCUSSION

Our observations indicate that solitary colony founding and monogyny are characteristic of *Aphaenogaster cockerelli*. Pleometrosis can be induced in the laboratory and may occur on occasion in the field, but does not lead to permanent polygyny since supernumary queens are eliminated before colonies mature. The single queen appears to exercise strong control over her workers: in queen-right laboratory colonies, workers lay many trophic eggs, but no reproductive eggs. By contrast, workers in queenless groups lay viable eggs that produce males, even with queen-produced larvae still present. This indicates that the queen alone regulates the repro-

Figure 7. When a partitioned colony is reunited, workers from the queenright side attack certain individuals among their former nestmates on the queenless side.

ductive activity of her worker offspring, although we do not yet know by what mechanism queen control is achieved. Worker reproduction occurs relatively soon after queen removal, perhaps because the regular production of trophic eggs primes their ovaries for the switch to viable egg production when inhibition ceases.

Figure 8. Antagonistic behavior between two nestmates in a queenless group. Above: A worker seizes and pulls on the head of a nestmate. Below: The attacked worker exhibits a crouching response.

The queens of advanced eusocial insects are generally attractive to workers, and the source of attraction is typically one or more pheromones produced by exocrine glands (reviewed by Fletcher and Ross 1985). Some of these attractants also function as queen substances, by which the queen chemically suppresses worker reproduction. Such queens are usually surrounded by a dense retinue of workers, and "messenger" workers appear to distribute the queen substance throughout the colony (Seeley 1979). It is surprising that an *A. cockerelli* queen is infrequently licked and is not closely surrounded by workers, but nevertheless exerts strong control over them. One possible means by which the queen could spread her inhibitory pheromones, without actively distributing them herself, would be to imbue her eggs with them. Indeed, egg clusters appear more attractive than the queen and are often handled and licked by workers. Brian and Rigby (1977) found that in *Myrmica rubra*, egg clusters alone were sufficient to inhibit worker ovarian development, though they were not as effective as the queen herself.

Overall, this ant exhibits a typical temporal polyethism, with most young workers engaged in activities in the brood chambers of the inner nest while older workers forage and defend the nest territory. Most trophic eggs are laid by younger workers, which serve as social food converters by consuming prey retrieved by older nest-mates and ovipositing to feed queen and larvae. Laying trophic eggs is not exclusively restricted to callows, however. Some individuals with active ovaries are also found among the older foragers, though most have inactive ovaries and reduced fat bodies. This finding may be relevant to observations on *A. albisetosus* by McDonald and Topoff (1985) and Beshers and Traniello (1987), indicating both temporal polyethism and a remarkable degree of individual plasticity. The latter authors found that members of all but the oldest age classes perform all tasks, at least occasionally. Although we did not follow the behavioral ontogenies of *A. cockerelli* workers, the retention of active ovaries by some outside workers suggests that at least these individuals may be similarly plastic, able to switch back to queen or brood care for which trophic egg production is necessary.

Our observations of antagonistic behavior in some queenless groups suggest that competition for male production may occur. Workers may fight among themselves or, even when within-group aggression is absent, guard their eggs. Competitive behavior appears

to be correlated with worker ovarian activity. Only a few workers per colony fragment have highly active ovaries and lay most or all of the eggs; in fact, taken collectively the ovarian development of queenless workers is not consistently different from that of queenright workers laying only trophic eggs. The ovipositing individuals may attain the status of "pseudoqueens" and become subject to attack when reunited with their own queenright nestmates. While reports of aggression toward former nestmates reunited after a period of estrangement are common (Breed and Bennett 1987), the singling out of specific individual workers is unusual.

Finally, we suggest that reproduction by disinhibited queenless workers may be an important source of males in field populations, given the longevity of queenless groups, the ability of even a few survivors to rear males, and the potential for fragmentation of polydomous colonies. Strong queen control may be required to prevent worker reproduction in the colony periphery. Perhaps in large polydomous nests control is not entirely successful, and peripheral workers may contribute males to nuptial flights.

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