Insectes Sociaux, Paris
1986, Volume 36, n° 2, pp. 106-115

SOCIAL ORGANIZATION AND REPRODUCTION IN *OCYMYRMEX FORELI* (FORMICIDAE : MYRMICINAE)

J.C. FORDER and A.C. MARSH (*)

Department of Zoology, University of the Witwatersrand, P.O. Wits 2050, Johannesburg, South Africa

Reçu le 29 juin 1987 Accepté le 20 juin 1988

SUMMARY

Colonies of *Ocymyrmex foreli* contained 16-1586 adults of which 4-20 % were ergatoid queens the remainder being sterile workers. Each colony contained one inseminated ergatoid queen only and colonies were monogynous. Workers and virgin queens were similar in size and appearance but had distinctive ovaries; queens had significantly more ovarioles than workers, with mated queens having more ovarioles than virgins.

Virgin queens and workers had similar behavioural repertoires, differing only with respect to the frequencies with which the various behaviours were performed. In terms of allogrooming and trophallactic exchanges, mated queens received the most and gave the least, workers gave the most and received the least and virgin queens were intermediate in their receiving: giving ratios.

Colony production was positively correlated with mean monthly rainfall and hence primary and secondary productivity. The continuous production of queens throughout they ear and the ability of unmated queens to adopt worker-like roles are considered to be adaptations that ensure colony reproduction and foundation in unpredictable, energy-poor arid environments.

ZUSAMMENFASSUNG

Soziale Organisation und Fortflanzung bei Ocymyrmex foreli **Formicidae-Myrmicinae)**

Kolonien von *Ocymyrmex foreli* bestehen aus 160-1586 adulten Ameisen, von denen 4-20 % ergatoide Königinnen sind. In jeder Kolonie existiert nur eine begattete Königin, die Kolonien sind monogyn. Arbeiter und unbegattete Weibchen sind von gleicher Größe und Gestalt, haben aber unterschiedlich ausgeprägte Ovarien; die Königinnen haben bedeutend mehr Ovariolen als die Arbeiter, während die begattete Königin wiederum mehr Ovariolen besitzt als die unbegatteten Weibchen.

* Present address and address for correspondence: Department of Zoology, University of Namibia, Private Bag 13301, Windhoek 9000, Namibia.

Unbegattete Weibchen und Arbeiter haben ähnliche Verhaltensweisen, sie unterscheiden sich nur in der Häufigkeit, mit der die verschiedenen Verhaltensweisen in Erscheinung treten. Im Hinblick auf gegenseitige Pflege und Futteraustausch erhalten die begatteten Königinnen am meisten und geben am weingsten ab, Arbeiter geben am meisten ab und erhalten am wenigsten, und das Verhältnis Abgabe/Aufnahme bei unbegatteten Weibchen liegt dazwischen.

Die Produktion der Kolonien konnte mit dem durchschnittlichen monatlichen Niederschlag und damit der primären und sekundären Produktion positiv in Übereinstimmung gebracht werden. Ergatoide Königinnen wurden während desganzen Jahres erzeugt. Diese fortlaufende Poduktion von Königinnen und dazu die Fähigkeit der unbegatteten Weibchen, Arbeiter-Rollen zu übernehmen, werden als Anpassung betrachtet, die die Vermehrung und Erhaltung der Kolonien in unvorhersehbaren Umständen und in energiearmen, ariden Umebungen wie dem Habitat der meisten Angehörigen des Genus *Ocymyrmex* sichert.

INTRODUCTION

Most members of the myrmicine ant genus *Ocymyrmex* inhabit hot, arid localities of the Ethiopian zoogeographical region in southern and eastern Africa (BOLTON, 1981). Relatively little is known about their general biology (see MARSU, 1985a; 1985b; 198 for aspects of the ecology, behaviour and physiology of *O. barbiger* = *robustior*) and their reproductive biology is enigmatic. Males are winged and common at night throughout most of the year (ARNOLD, 1916) but neither ARNOLD (1916) nor EMERY (1922) were able to distinguish a distinct reproductive caste amongst females *. They did, however, notice wingless "variant" females and proposed that these might be ergatoid queens. Subsequently, BOLTON (1981) declared that the "variants" were the ergatoid females but his conclusion was not based on an examination of ovarian structure, the critical evidence needed to distinguish the reproductive caste from the sterile worker caste. "Variants" differed from "normal" females with regard to head sculpture pattern, size and shape of scape and shape of frontal lobes.

Here we examine the reproductive biology of *O. foreli*, a species which occurs in relatively high altitude grasslands in southern Africa. Our major objectives were to determine (1) whether or not "variants" belonged to a distinct ergatoid queen caste, (2) whether colonies were polygynous or monogynous, (3) whether there were any behavioural differences between classes

* Currently, there is a controversy over whether ant castes should be defined according to role (BUSCHINGER, 1987) or morphology (PEETERS, 1987). To prevent confusion and misunderstanding, BUSCHINGER and CROZIER (1987) have suggested that scientists, studying caste problems, should clearly outline their position with regard to the controversy. Here, we have opted for a morphological definition of caste. Irrespective of external morphology, a queen is an individual that has a distinctive ovarian structure relative to a worker and possesses a spermatheca. Virgin queens are uninseminated and mated queens inseminated individuals.

of female and (4) to monitor the annual cycle in reproductive activity and social structure.

MATERIALS AND METHODS

A colony of *O. foreli* was excavated each month from February 1986 to January 1987 inclusive at a site near Johannesburg (26 00'S; 28 03' E) with a long term rainfall mean of 634 mm pa. The total number of adults and the proportion that were males, callows, "normal" and "variant" females were determined. The gasters of about six recently killed females from both classes were measured and dissected each month, with the exception of February 1986. Measurements taken were the length and maximum width from which gaster volume was calculated assuming an ellipsoid shape. Data on gaster volume were analysed using Student's t-test. The number of ovarioles and length of any mature eggs was recorded. In an attempt to locate their spermathecae, 160 "normal" and 221 " variant" females were dissected from the colony excavated in February. Data on ovariole number and eggs size were analyzed using Wilcoxon 2-sample tests. If evident, spermathecae were removed, squashed on a glass slide and viewed under a phase contrast microscope for sperm. Similar data were collected from three other *Ocymyrmex* species at Tosca in the northern Cape (25 54'S; 23 57'E) which receives approximately 400 mm of rain pa. Nests were excavated at Tosca in April and December 1986.

Temporal trends in the social structure of *O. foreli* in relation to long-term (18 years) mean monthly rainfall and monthly rainfall data for the study period, were analyzed using Sperman's rank correlation. Rainfall data for the principal study site was obtained from the Weather Bureau, Pretoria.

To determine whether there were any behavioural differences between "normal" and "variant " females, on *O. foreli* colony comprising 234 adults, and all the brood found in the excavated nest, was established in an observation nest situated within a wooden foraging arena (1.2 × 1.2 m) in a laboratory. The nest was maintained at 28° C and 70 % RH and one end of the arena was maintained at 36-40° C during the day to stimulate foraging activity. The ants were offered a diet of water, sugar-water, cockroaches, termites and meal worms. Females were marked with enamel paint so that "variants" could be distinguished from "normal" females and foragers from non-foragers. Data were collected by scanning all colony members at five minute intervals and noting what each ant was doing. Observations were made at random throughout the day over a period of five days until a total of 180 scans was obtained. For behaviours carried out by solitary individuals, the mean number of behavioural events per ant in each class was calculated and expressed as a relative frequency to facilitate interclass comparisons. The number of interactions between individuals (allogrooming and trophallaxis) were scored and the beneficiary noted. To determine whether there were any interclass differences, the data were analysed using Wilcoxon 2-sample tests.

RESULTS

"Normal" females, i.e., individuals with vertical head sculpturing, had one ovariole per ovary and these were generally undeveloped, although the ovaries of 12 of the 272 individuals examined contained 1-5 developing and/or mature oocytes (*table I*). All of the "normal" females appeared to be uninseminated since ther spermathecae could not be found and were either

Table I. — Numbers of ovarioles per ovary in various classes of female *Ocymyrmex* species [X ± SD (N)].

Tabelle I. — Die Anzahl der Ovariolen pro Ovar in den verschiedenen Klassen von weiblichen *Ocymyrmex* [X ± SD (N)].

	Foreli	*Picardi*	*Flaviventris*	*Sphinx*
Mated queen	17.09 + 1.53 (12)	18.00 + — (1)	8.00 + — (1)	18.00 + — (1)
Virgin queen	14.88 + 2.18 (55)	15.06 + 4.88 (6)	7.37 + 3.00 (10)	14.79 + 3.12 (29)
Worker	1.00 + 0.00 (12)	1.00 + 0.00 (5)	1.00 + 0.00 (10)	1.00 + 0.00 (29)

absent or very reduced. In contrast, "variant" females, i.e., individuals with horizontal head sculpturing, had a large number of ovarioles (*table I*). The majority of the 259 "variants" dissected had no eggs in their ovaries and were not inseminated. However, each colony contained one "variant" that had more ovarioles than the other variants (*table I*; $p < 0.002$) and these were packed with eggs at all developmental stages, including many fully developped eggs. In all cases, the spermathecae of these individuals were engorged with sperm. Thus, it is apparent that "variants" represent ergatoid queens, "normal" females are sterile workers and colonies are monogynous. Mature eggs of mated queens were no different in size to worker eggs (*table II;* $p > 0.05$) however, worker eggs tended to be transparent relative to the opaque queen eggs. It remains unknown whether worker eggs are trophic eggs, male eggs or both. Except for head sculpture patterns, all females looked similar. Mated queens were readily distinguished by their physogastric condition, their gasters being on average 2.7 times larger than those of virgin queens or workers (*table II*; $p < 0.001$). The gaster volumes of virgin queens and workers were indistinguishable ($p > 0.10$). In mated queens the gastral tergites and sternites were separated by an opaque-white intersegmental region. The white coloration was due to the large egg mass being visible through the transparent intersegmental membranes. Virgin queens and workers occasionally had swollen gasters due to the retention of fluid in the gut, but their intersegmental regions were translucent.

Table II. — Gaster volume and mature egg length in various classes of female *O. foreli* [X ± SD (N)].

Tabelle II. — Gastervolumen und Länge reifer Eier bei den verschiedenen Klassen von weiblichen *O. foreli* [X ± SD (N)].

	Gaster volume (mm^3)	Egg length (mm)
Mated queen	3.83 + 0.98 (8)	0.85 + 0.31 (20)
Virgin queen	1.42 + 0.43 (36)	— — —
Worker	1.42 + 0.48 (37)	0.82 + 0.23 (20)

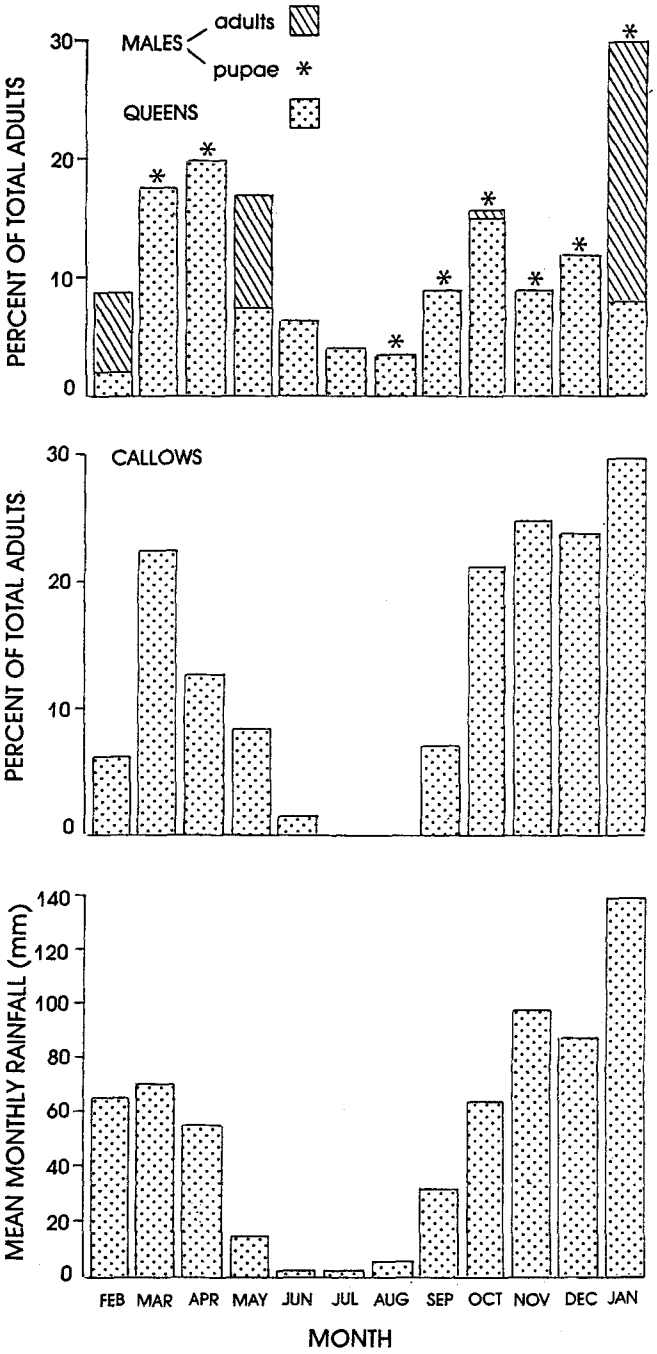

Fig. 1. — Monthly variation in rainfall and the abundance of males, queens and callows in *O. foreli*. * = male brood present.

Abb. 1. — Schwankungen der mittleren monatlichen Regenmenge im Laufe des Jahres und die Häufigheit von Männchen, Königinnen und Jungtieren bei *O. foreli*.

Similar results were obtained for the other *Ocymyrmex* species examined, *picardi, sphinx* and *flaviventris*. Workers were uninseminated, had one ovariole per ovary and two *O. picardi* workers had eggs (*table I*). Ergatoid queens had large numbers of ovarioles; virgin having undeveloped ovaries and mated queens having fully developed ovaries and engorged spermathacae. Mated queens hard very distended gasters and distinctive opaque-white intersegmental regions.

The colony size of *O. foreli* varied from 160-1586 adults with the majority of individuals being sterile workers. Males were found in all months excepting the mid-winter months of June and July (*fig. 1*). Males were exceptionally abundant in January 1987, comprising 22 % of all adults in the colony excavated. Virgin ergatoid queens were present throughout the year but their abundance was considerably reduced in winter, May to August and in February 1986 (*fig. 1*). Ergatoid queens constitued 4-20 % of the total colony membership during the study period. There was no correlation between the production of sexuals and rainfall ($p > 0.05$), but distinct trends were apparent with regard to queen production (*fig. 1*). Callow production, a measure of reproductive activity, was however positively correlated with long-term mean monthly rainfall ($p < 0.001$) and with monthly rainfall during the study period ($p < 0.01$).

Six categories of behaviour were sufficiently common to enable statistical comparisons between virgin ergatoid queens and workers ; foraging, guarding,

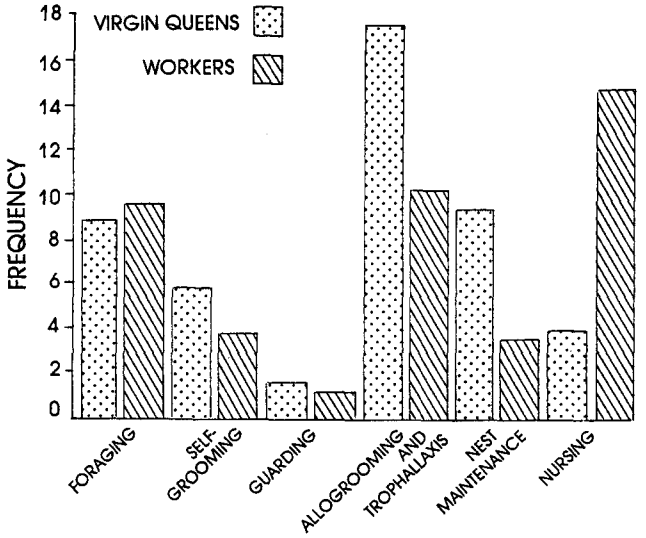

Fig. 2. — Frequency with which *O. foreli* virgin queens and workers performed various behaviours.

Abb. 2. — Haüfigkeit, mit der unbegattete ergatoide Weibchen und Arbeiter von *O. foreli* verschiedene Verhaltensweisen ausführen.

i.e., ants remaining stationary at or near the nest entrance, nest maintenance, brood care, selfgrooming, and interactions between individuals, i.e., allogrooming and trophallaxis. Behavioural repertoires were the same in workers and virgin queens but the frequencies with which the two castes of females performed the behaviours was different (*fig. 2*, $p < 0.01$). Workers foraged and nursed brood more than virgin queens, whereas virgin queens selfgroomed, guarded, maintained the nest and interacted more than workers. 660 trophallactic interactions and 1466 instances of allogrooming were observed during the study. Recipients during trophallactic exchanges were recognized by their soliciting behaviour whereby they opened their mandibles and antenated the donor rapidly and respectively. The mated queen benefitted most from trophallactic and allogrooming exchanges, followed by the virgin queens (*table III*). Workers received the least and gave the most. In both exchanges, virgin queens gave more to other virgin queens than to workers and workers gave more to virgin queens than to other workers. Interactions between the mated queen and virgin queens were relatively infrequent.

Three other behaviours were noted but occurred too rarely to permit intercaste comparisons. Egg laying by the mated queen was observed three times and oophagy by the mated queen was seen once. Aggression between workers, when one individual rushed at another causing the other to retreat, was seen on four occasions.

Table III. — Trophallactic and grooming benefit per individual, for the mated queen, virgin queens and workers in an *O. foreli* colony. The data are derived from 660 trophallactic exchanges and 1466 grooming interactions.

Tabelle III. — Der individuelle Gewinn bei Fütterung und Pflege für die begattete Königin, die unbegatteten ergatoiden Weibchen und die Arbeiter in einer *O. foreli*-Kolonie. Die Daten wurden aus 600 Fällen von Futteraustausch und 1466 Fällen der gegenseitigen Pflege gewonnen.

Trophallaxis		Donating			
		Mated queen	Virgin queen	Worker Total	Total
Receiving	Mated queen	—	0.0	19.0	19.0
	Virgin queen	0.0	0.8	3.5	4.3
	Worker	0.0	0.5	2.4	2.9
Allogrooming		Grooming			
Groomed	Mated queen	—	2.0	31.0	33.0
	Virgin queen	0.0	1.5	9.0	10.5
	Worker	0.0	1.0	5.4	6.4

DISCUSSION

Although ergatoid queens are extremely worker-like in appearence, they are clearly distinct in terms of ovarian structure. Correlated with this ovarian distinction is a clearcut reproductive division of labour, with the mated queen acting as the primary reproductive and only a possibility that workers produce male eggs. Insemination appears to be necessary for reproduction to occur in *Ocymyrmex* species; of the large numbers of queens examined, only inseminated individuals exhibited ovariole hypertrophy and produced large numbers of eggs. The existence of more ovarioles in mated queens than virgin queens is enigmatic. Insemination may trigger increased ovarian development, implying that queens have equal chances of becoming inseminated and of thus becoming the primary reproductive. Alternatively, certain queens may have more developed ovaries prior to insemination and may for an unknown reason be more attractive to males thereby enhancing their chances of becoming the primary reproductive.

Virgin queens behaved in a worker-like manner and formed a significant component of the forager force. The presence of working, but potentially reproductive, females has previously been recorded in several ant genera, *Myrmica, Leptothorax, Formicoxenus, Harpagoxenus* (BUSCHINGER, 1987) and *Camponotus* (B.A. CURTIS, pers comm). *Ocymyrmex* appears to be unique in terms of the high proportion of queens relative to workers. Although there were intercaste differences in the frequencies with which various behaviours were performed in *O. foreli*, these may be artefacts of age polyesthism and not an intrinsic intercaste difference. In terms of trophallactic interactions and allogrooming, queens received preferential treatment over workers. The mated queen benefitted most from these interactions and did not perform "work" like the other virgin queens.

Colony production in *O. foreli* is associated with the wetter, warmer months when primary production is high. That colony production followed long-term mean monthly rainfall more closely than rainfall during the study period, suggests that colony production is inherently seasonal. It would be of interest to know whether such patterns occur in *Ocymyrmex* species that live in highly unpredictable desert environments.

The presence of apterous ergatoid queens is well known amongst certain arid-adapted, and other, ant species (BOLTON, 1986). An intriguing aspect of the social organization of *Ocymyrmex* species concerns the adaptive value of year-round production of ergatoid queens in numbers which exceed reproductive needs. Most *Ocymyrmex* species occupy arid or semi-arid habitats (BOLTON, 1981) and we believe that the adaptive value of year round production of queens is related to the unpredictable nature of year round arid environments. In such environments mating and colony founding conditions occur unpredictably because of their association with rainfall (HÖLLDOBLER et

BARTZ, 1985). Furthermore, arid environments are characterized by low productivity. To ensure reproductive success, sexuals need to be produced continuously even though the majority do not realize their reproductive potential.

Role flexibility in *Ocymyrmex* queens may have evolved to minimize the otherwise vast drain of resources that producing large numbers of sexuals would represent to a small colony. Thus if a queen remains a virgin beyond some as yet undetermined critical age she switches roles and begins to behave as a worker thereby contributing positively to the colonies ergonomic efficiency. The almost identical morphology of *Ocymyrmex* queens and workers (BOLTON, 1981) probably ensures that they can perform the same tasks with the same efficiency. Similar selective pressures may be operative in ponerine species that lack a queen caste; inseminated workers (gamergates) adopting the roles of reproductives and uninseminated individuals acting as workers (PEETERS et CREWE, 1984; 1985).

The above scenario could apply to most members of the genus which occur in unpredictable environments. The environment of *O. foreli* is, however, relatively predictable and despite this predictability, ergatoid queens were produced throughout the year. Possibly the production of sexuals in *O. foreli* reflects its generic origins in unpredictable environments and may be a neutral characteristic in its present environment.

ACKNOWLEDGEMENTS. — The study was supported by grants from the C.S.I.R. and Senate Research Committee of Witwatersrand University (A.C.M.) and a Senior BURSARY, Witwatersrand University (J.C.F). We thank M. KEEPING for assistance with statistical analyses, Barry BOLTON for identifying the ants and H. ROBERTSON and an anonymous reviewer for valuable comments on the manuscript.

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