PSYCHE

Vol. 93 1986 Nos. 1-2

FUNCTIONAL QUEENS IN THE AUSTRALIAN GREENHEAD ANT, *RHYTIDOPONERA METALLICA* (HYMENOPTERA: FORMICIDAE)*

BY PHILIP S. WARD

Department of Entomology,
University of California,
Davis, CA 95616, U.S.A.

INTRODUCTION

In most species of the Indo-Australian ant genus, *Rhytidoponera,* deciduously winged queens are rare or absent, their place being taken by reproductively functional workers (Whelden, 1957, 1960; Haskins & Welden, 1965; Ward, 1981, 1984; Pamilo *et al.,* 1985). A polygynous colony structure, with several mated workers in lieu of a queen, is the normal mode of colony organization in the common Australian greenhead ant, *Rhytidoponera metallica* F. Smith (Whelden, 1960; Haskins & Whelden, 1965; Haskins & Haskins, 1983), and queenright colonies of this species have not been reported. A few alate or dealate females are known in collections, and Haskins & Whelden (1965) noted the sporadic production of alate queens in laboratory colonies of *R. metallica.* However behavioral observations by these authors suggested that the queens had lost the ability to found colonies. In this paper I document the occurrence of functional queens in *R. metallica,* describe colony foundation and growth under laboratory conditions, and discuss the significance of occasional queen production in this species.

**Manuscript received by the editor February 26, 1986.*

METHODS

Field observations were made at several Queensland localities in August–September, 1983, of which the following sites are discussed below: (1) 10 km SE Kenilworth (26°40′S, 152°47′E), 340 m, dense *Eucalyptus* forest; (2) Mt. Coot-tha, near Brisbane (27°29′S, 152°58′E), 160 m, mixed wet sclerophyll forest; and (3) St. Lucia, Brisbane (27°30′S, 153°01′E), 15 m, urban parkland on the University of Queensland campus. Voucher specimens of *Rhytidoponera metallica* from these localities have been deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra and the Museum of Comparative Zoology (MCZ), Harvard University. Evidence suggests that *R. "metallica"* is composed of a complex of sibling species (Crozier, 1981; cf. Brown, 1958), and the southeastern Queensland populations may not be conspecific with *R. metallica* sens. str. (type locality: Adelaide, South Australia).

Field-collected queens of *Rhytidoponera* from St. Lucia were maintained in the laboratory in moist plaster-of-Paris nests. Each nest consisted of a glass-covered chamber with the dimensions 40 × 25 × 5 mm, in a block of plaster measuring 85 × 55 × 10 mm. A single exit, 4 mm wide, led to a foraging arena 85 × 110 mm in area. After a colony size of approximately 50 workers was attained, colonies were provided with larger nests. Colonies were fed small arthropods (mostly *Drosophila*) on a daily basis and droplets of honey about once a week. A small quantity of clean sand was provided to allow construction of a cocoon-spinning matrix for the first larvae. Censuses of brood and adults were taken every 3 weeks for the first 9 weeks of colony development, and at weekly intervals thereafter for the first year of growth.

RESULTS

Field observations

While conducting field work in eastern Queensland in August–September, 1983 I frequently encountered foraging workers of *Rhytidoponera metallica* (s.l.), and I dissected several typical, worker-reproductive colonies, i.e. colonies with workers and (sometimes) males, but no queens. At three locations in southeastern Queensland I unexpectedly encounted alate queens of *R. metallica*:

(1) While collecting for a period of one hour in *Eucalyptus* forest 10 km SE Kenilworth (25 August, 1983), I located a single *Rhyti-*

doponera metallica colony under a rotten log; a partial excavation (about two-thirds of the colony) yielded 157 workers, 17 alate queens, and numerous larvae. No males or dealate females were seen.

(2) During several hours of field work in wet sclerophyll forest on Mt. Coot-tha (1 September, 1983), devoted primarily to the task of locating colonies of the very timid species, *R. anceps* Emery, I noted more than a dozen, scattered, individual alates of *R. metallica* resting on low vegetation (leaves, grass stalks, tree roots, etc.), apparently in the aftermath of one or more mating flights. About half of these alates were females (five queens were collected and preserved).

(3) On the University of Queensland campus, St. Lucia, between 28–31 August, 1983, there was considerable flight activity of *R. metallica* alates. Most of these alates were males: they were observed in moderate numbers (30–40 males at any given time) around *R. metallica* nest entrances on a campus lawn at mid-day. Most individuals were dispersing skyward, but a few males were observed approaching nests in a low, cruising flight, 20–50 cm above the ground. Four alate females of *R. metallica* were also noted: three of these were running on campus sidewalks, the fourth was resting on a grass stalk. The alate queens were observed between noon and 3:00 p.m., and none was associated with a specific nest. Three of the *R. metallica* queens were collected; one died within 5 days, and subsequent dissection showed that she was uninseminated. The two remaining queens (acc. nos. 6280 and 6281) were kept in vials with a small quantity of earth and leaf litter. They shed their wings, excavated crude cells, and began laying fertile eggs. On September 17, 1983 the queens were relocated in plaster-of-Paris nest chambers. I also collected a single dealate queen of *R. chalybaea* Emery on 1 September, 1983 in a University of Queensland lecture hall (acc. no. 6297). This queen was treated in the same manner as the *R. metallica* queens, and provided a convenient standard for colony growth and development, since colony-founding queens are a normal occurrence in this species (Ward, 1983).

Development of queenright colonies: incipient stages

The preceding observations established that the early stages of colony-founding behavior have been retained in *R. metallica* queens, i.e. they can mate, disperse, undergo dealation, and exca-

vate nests. Laboratory observations demonstrated that this can be followed by normal haplometrotic colony development.

Both the *R. metallica* and *R. chalybaea* queens readily accepted the plaster-of-Paris nests, and began raising worker brood. The queens of both species foraged in their arenas for food, and accepted both honey and fresh arthropods. Struggling *Drosophila* adults (held in the foraging arena with a pair of fine forceps) were approached with outstretched mandibles, captured, stung, and returned to the nest.

The *R. metallica* queens appeared to be no less dexterous than the *R. chalybaea* queen in capturing and handling prey, or in caring for larval brood. As the larvae matured, queens of both species used sand grains to construct cocoon-spinning matrices for the larvae. Initially the development of brood proceeded at a similar rate in all three colonies, with eggs, larvae, and cocoons present by the tenth week (late November, 1983; Table 1).

Some behavioral differences were noted between the two species: the *R. metallica* queens were observed foraging more frequently during daytime hours than the *R. chalybaea* queen; the *R. metallica* queens established their middens in the nest entrance, thus partially closing it, whereas the *R. chalybaea* queen scattered most of her refuse just outside the nest entrance; and the *R. metallica* queens defecated widely (frequently in the foraging arena) whereas the *R. chalybaea* queen concentrated her fecal deposits at one location (c. 25 mm^2) inside the nest chamber. These minor (and perhaps idiosyncratic) differences hardly diminish the overriding similarity between the two species in early colony development.

After about twelve weeks, and just prior to the eclosion of workers, colonies of the two species of *Rhytidoponera* began to diverge in their patterns of development. The first *R. metallica* workers appeared to have difficulty eclosing from their cocoons—possibly because of inept assistance on the part of the queens—and there was appreciable early worker mortality both as pharate adults in cocoons and as eclosed adults. No such difficulties were evident in the *R. chalybaea* colony, whose worker population increased at considerably faster rate than that of the two *R. metallica* colonies (Table 1). Moreover the *R. chalybaea* colony displayed regular (although increasingly dampened) cycles of brood development, with bouts of egg-laying followed by pulses of larval growth, cocoon formation, and adult eclosion, whereas such cycles appeared to be

Table 1. Development of incipient queenright colonies of *Rhytidoponera* under laboratory conditions. Under columns E, L, C, and W are given the numbers of eggs (approximate), larvae, worker cocoons, and adult workers observed, respectively, at each census period.

	chalybaea 6297				*metallica* 6280				*metallica* 6281			
Date	E	L	C	W	E	L	C	W	E	L	C	W
12.x.83	18	—	—	—	20	1	—	—	20	1	—	—
2.xi.83	5	11	2	—	20	12	—	—	8	20	—	—
22.xi.83	3	10	8	—	5	17	6	—	0	10	6	—
29.xi.83	3	7	9	—	5	21	7	—	5	14	8	—
6.xii.83	7	6	11	—	5	18	8	—	8	14	8	—
13.xii.83	18	4	13	—	0	18	10	—	7	14	8	—
20.xii.83	25	4	13	1	1	15	11	—	9	12	9	—
27.xii.83	29	3	12	4	3	14	13	—	8	10	10	—
3.i.84	25	6	12	5	0	13	12	—	5	6	12	—
10.i.84	25	8	8	7	0	15	13	—	5	9	9	1
17.i.84	25	10	6	9	4	10	14	—	5	9	10	1
24.i.84	23	17	5	9	10	8	10	—	10	8	9	1
31.i.84	20	26	3	13	11	5	10	—	14	7	8	—
7.ii.84	10	27	5	13	12	4	8	—	14	5	11	—
14.ii.84	10	22	11	13	18	3	8	1	17	4	9	2
21.ii.84	15	24	17	13	20	5	8	—	15	4	7	3
28.ii.84	20	15	24	14	22	7	8	—	18	6	7	3
6.iii.84	27	15	32	15	12	9	7	1	20	12	6	4
13.iii.84	32	15	34	18	10	16	6	4	17	14	5	5
20.iii.84	40	17	33	22	4	26	5	5	18	14	6	7

disrupted in the *R. metallica* colonies (compare respective columns of Table 1).

Because of the delay in successful emergence of workers, the *R. metallica* queens continued to forage for about two months after the *R. chalybaea* queen ceased such activity. In both species the foraging activity of the queen declined gradually, over a period of several weeks after the first successful eclosion of workers. For three weeks after her first daughter appeared the *R. chalybaea* queen continued (with decreasing frequency) to capture and sting prey (*Drosophila* adults) held at, or near, the nest entrance. During the equivalent transition period, the *R. metallica* queens continued to make forays into the foraging arena and to capture prey. The sequence of events in colony #6280 is summarized in Table 2; similar observations were made on colony #6281.

Table 2. Observations on foraging activity of the queen and first eclosing workers in *R. metallica* colony #6280. Day #1 (3.iii.1984) is the day of first successful eclosion of a worker.

Day #	No. of adult workers in colony	Foraging activity of queen and workers
1-2	1 (callow)	Queen foraging. Worker confined to nest.
7	2 (1 callow)	Queen foraging. Workers confined to nest.
10	4	Queen took prey (*Drosophila*) at nest entrance.
11-12	4	Queen foraging. Workers confined to nest.
13	4	Worker foraging in arena (first time), captured a subdued *Drosophila* adult; queen removed prey from worker at nest entrance, then proceeded to forage in arena herself.
14-17	4-5	Queen and one worker in foraging arena.
22-27	6-8	Queen and several workers foraging and taking prey, the workers more active than the queen.
28	8	Last observation of queen in foraging arena (thereafter queen confined to nest, and all foraging conducted by workers).

Subsequent growth and development of queenright colonies

The growth rates of the *R. metallica* colonies were rather slow and uneven, relative to that of *R. chalybaea* (Figure 1). One year after colony initiation, the two *R. metallica* colonies had worker populations of 41 and 27 individuals, respectively, while the *R. chalybaea* colony had a worker population exceeding 200. Since the colonies were fed *ad libitum,* food availability is not likely to have been a limiting factor in the slower growth of the *R. metallica* colonies. In fact, all three colonies grew at a rate faster than that inferred for incipient queenright colonies of *R. chalybaea* (and a related species, *R. confusa* Ward) in the field (Ward, 1981).

The *R. metallica* colonies appeared to function similarly during the first year of development. Then a marked divergence took place, apparently due to queen infertility in colony #6280. In mid-October, 1984 (week 56) this colony stopped producing eggs, and the amount of brood began declining. By mid-January, 1985 (week 66), with a population of 50 workers (and one male of unknown parentage), this colony contained no eggs or larvae, and only one cocoon (worker). On January 22, the queen was observed in a sexual calling posture (gaster raised, head and mesosoma lowered) inside the nest;

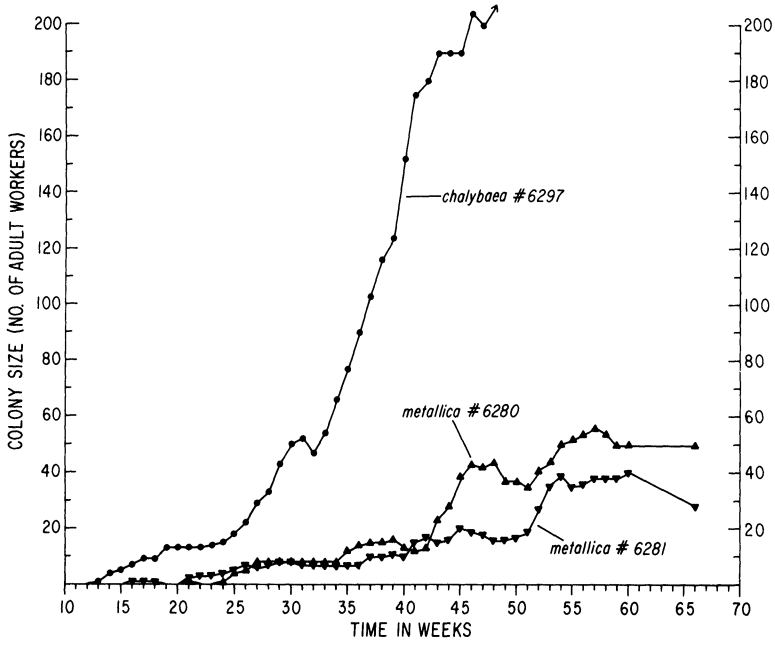

Figure 1. Colony size (number of adult workers) of developing, queenright colonies of *R. metallica* and *R. chalybaea,* as a function of time in weeks since colony initiation.

at the same time she was being spread-eagled by two workers who were tugging on opposite legs. Ten minutes later the queen was dragged and bitten on the tip of her gaster by a worker. The following day the queen was still being molested by workers, who bit her on the legs and gaster. On January 24, the queen was found dead inside the nest. A few days later her disarticulated body had been dumped in a midden pile in one corner of the foraging arena. In the meantime there began a spate of intersibling rivalry among a group of 15–20 workers inside the nest who repeatedly "boxed" one another with their antennae. These rapid antennation movements were very similar to those which occur among mated workers in polygynous, worker-reproductive colonies of the *R. impressa* group (Ward, 1983, p. 293).

One week after the death of the queen in colony #6280, workers began "calling" for males in the characteristic sex pheromone-

releasing posture (Hölldobler & Haskins, 1977). As many as six workers were observed calling simultaneously, both inside and outside the nest. Workers calling inside the nest were subject to repeated rapid antennation of the gaster, sides of body, and head, by other workers. When antennated in front, the calling worker would reciprocate the gesture, while maintaining the calling posture. Workers calling in the foraging arena outside the nest were not the object of rapid antennation by other workers.

The sexual calling behavior of workers continued, with increasing intermittency, for the next six months. During this time, two additional adult males were produced, but no workers. There was no indication that sib mating occurred—males showed no apparent interest in their calling nestmates. The colony continued to decline in size, no additional workers were produced, and, at time of writing (January, 1986), it consisted of 35 workers, 1 male, 2 larvae and several eggs.

By contrast, colony #6281 remained a viable queenright colony. The queen continued to produce fertile eggs, and was not molested by her daughters. There was no obvious conflict among workers (i.e. no spate of antennal boxing or other forms of aggression), and workers did not exhibit sexual calling behavior. At time of writing, the colony was continuing to grow and comprised the queen, about 120 workers, and abundant brood.

Discussion

These findings demonstrate that the deciduously winged females of *Rhytidoponera metallica* have not lost the potential to function as queens, despite their sporadic occurrence in nature. Under laboratory conditions the two *R. metallica* colonies remained queenright for at least a year, and the queens and workers adopted conventional roles of egg-layer and forager, respectively. On the other hand the *R. metallica* colonies grew more slowly than the incipient queenright colony of *R. chalybaea,* and the colony-founding foraging phase of the queens was correspondingly extended. Hence there remains some uncertainty about the efficacy of colony foundation by *R. metallica* queens in nature.

One of the *R. metallica* colonies experienced death of the queen, apparently a case of matricide triggered by queen infertility. Since the workers began calling for males soon after the queen's death,

and continued to do so for six months, it seems likely that, under natural conditions, replacement of the queen by mated workers would be readily accomplished. Ward (1983) alluded to the possibility that some worker-reproductive (Type B) colonies in the *Rhytidoponera impressa* group are derived from orphaned queenright (Type A) colonies, and the present observations provide direct evidence that such a transition can occur in *R. metallica.* Moreover they suggest that reproductive activity on the part of the queen, rather than her mere presence, is necessary for the suppression of hostile takeover attempts by her daughters.

The reverse process, production of colony-founding queens by worker-reproductive colonies, seems certain to have occurred. No mated dealate queen was found in the queen-producing colony from 10 km SE of Kenilworth, and indeed no functional queenright colonies of *R. metallica* have been reported in the field, even though this species is one of the commonest Australian ants.[1] Haskins & Whelden (1965) reported the occasional production of female alates in worker-reproductive colonies of *R. metallica* which had been maintained in the laboratory for several years. These females failed to function as queens but this could have been due to the absence of favorable conditions for mating and dispersal.

Queen production might be viewed as an infrequent, alternate dispersal strategy employed by worker-reproductive *R. metallica* colonies in response to environmental conditions which favor long-range dispersal over short-range movement (colony fission). The unusually large production of queens in Queensland in August–September, 1983 occurred after a period of drought associated with the 1982–83 El Niño. Alate queens appeared in one of Haskins' laboratory colonies after a shift in diet (C. P. Haskins, pers. comm.). The

[1]Among the limited number of *R. metallica* queens in collections, the majority of specimens are alates; the dealate specimens which I have examined contain no information about their reproductive status. During a five year period of collecting ants in eastern Australia (1974–78; 1980) I encountered (and subsequently dissected) *R. metallica* queens only twice. One of these was a mated dealate female wandering on the ground by herself (colony-founding?) in open *Eucalyptus* woodland, 14 km E Grenfell, New South Wales (29. X. 1975, P. S. Ward #1406); the other was a single uninseminated (spermatheca empty, ovaries poorly developed) dealate female in a colony with 173 workers and brood, under a stone in dry sclerophyll forest, at Bathurst, N.S.W. (18. X. 1975, P. S. Ward #1374).

extreme rarity of mature queenright colonies in nature could be attributed to a frequent transition to the worker-reproductive (Type B) colony structure, coupled with the sporadic production of queens in the first place. That *R. metallica* queens still function as dispersal units is suggested by the widespread retention of queen production. Among material in the ANIC and MCZ, there are alate or dealate females of *R. metallica* (s.l.) from Western Australia, South Australia, New South Wales, and Queensland, i.e. throughout the range of this species (or species complex). Queens have also been collected throughout most of the geographical distribution of *R. victoriae* André, another species whose mature colonies are predominantly or entirely worker-reproductive.

It is worth reiterating that queens are entirely unknown in the majority of *Rhytidoponera* species (including the large, robust-bodied forms found primarily in xeric habitats), and in such species aerial dispersal of females is impossible. If queens *are* effective aerial dispersers in *R. metallica* and other occasional queen-producers (including *R. clarki* Donisthorpe, *R. inornata* Crawley, *R. tasmaniensis* Emery, and *R. victoriae*), then this should result in differential patterns of habitat island and offshore island occupancy by the two groups of *Rhytidoponera.* There are not sufficient data available to test this prediction—and the test would be complicated by differing habitat preferences of members of the two groups—but records in the ANIC do show that *R. metallica* and related species are found on a variety of small islands off the coasts of Western Australia, New South Wales and Queensland.

Summary

In colonies of the Australian greenhead ant, *Rhytidoponera metallica* (s.l.), female reproductive activities are almost invariably assumed by workers. Queens (deciduously winged females) are rarely produced, and were heretofore considered non-functional. Field observations in southeastern Queensland in August and September, 1983 revealed an unusually high frequency of alate queens in several localities. Two of three alate queens, collected while dispersing in the vicinity of male mating flights, proved to be inseminated. In the laboratory these mated queens both established functional queenright colonies under non-claustral, haplometrotic conditions. The *R. metallica* colonies grew more slowly than an

incipient, queenright colony of *R. chalybaea* (a species in which functional queens are common), but a clear division of labor developed between the egg-laying queen and foraging workers.

One *R. metallica* colony suffered death of the queen in its second year of development. This was followed by a spate of intersibling rivalry and frequent sexual calling behavior on the part of the workers. The other colony continued to function as a viable queenright colony, and showed no signs of intracolony strife or reproductive attempts by workers.

These observations show that *R. metallica* queens have retained their colony-founding and reproductive potential, despite their sporadic occurrence in nature. This suggests that long-range dispersal via winged queens remains an occasional viable option for worker-reproductive colonies of *R. metallica.*

Acknowledgements

The University of California provided financial support for this work. I thank Ross Crozier, Caryl Haskins and Christian Peeters for comments on the manuscript.

References

Brown, W. L. 1958. Contributions toward a reclassification of the Formicidae II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. Harvard, **118**: 175–362.

Crozier, R. H. 1981. Genetic aspects of ant evolution. *In* Atchley, W. R. and D. Woodruff (Eds.). Evolution and speciation. Essays in honor of M. J. D. White. Cambridge: Cambridge Univ. Press, pp. 356–370.

Haskins, C. P. and W. M. Whelden. 1965. "Queenlessness", worker sibship, and colony versus population structure in the formicid genus *Rhytidoponera.* Psyche, **72**: 87–112.

Haskins, C. P. and E. F. Haskins. 1983. Situation and location-specific factors in the compatibility response in *Rhytidoponera metallica.* Psyche, **90**: 163–174.

Hölldobler, B. and C. P. Haskins. 1977. Sexual calling behavior in primitive ants. Science, **195**: 793–794.

Pamilo, P., R. H. Crozier, and J. Fraser. 1985. Inter-nest interactions, nest autonomy, and reproductive specialization in an Australian arid-zone ant, *Rhytidoponera* sp. 12. Psyche, **92**: 217–236.

Ward, P. S. 1981. Ecology and life history of the *Rhytidoponera impressa* group II. Colony origin, seasonal cycles, and reproduction. Psyche, **88**: 109–126.

Ward, P. S. 1983. Genetic relatedness and colony organization in a species complex of ponerine ants. I. Phenotypic and genotypic composition of colonies. Behav. Ecol. Sociobiol., **12**: 285–299.

WARD, P. S. 1984. A revision of the ant genus *Rhytidoponera* in New Caledonia. Aust. J. Zool., **32**: 131–175.

WHELDEN, R. M. 1957. Anatomy of *Rhytidoponera convexa*. Ann. Ent. Soc. Amer., **50**: 271–282.

WHELDEN, R. M. 1960. Anatomy of *Rhytidoponera metallica*. Ann. Ent. Soc. Amer., **53**: 793–808.