Ethology Ecology & Evolution 6: 507-517, 1994

Reproduction and division of labour in *Leptogenys schwabi* Forel (Hymenoptera Formicidae), a polygynous, queenless ponerine ant

S.J. Davies [1], M.H. Villet [1,3], T.M. Blomefield [2,4] and R.M. Crewe [1]

[1] *Department of Zoology, University of the Witwatersrand, P.O. Wits, 2050 South Africa*
[2] *Department of Zoology, University of Natal, Pietermaritzburg, 3200 South Africa*

Received 24 November 1993, accepted 30 September 1994

The combination of polygyny and natural queenlessness is uncommon in ants. The ponerine ant *Leptogenys schwabi* Forel 1913 has no morphologically or anatomically distinct reproductive castes and several mated workers in each colony, providing a model for the study of the effect(s) of polygyny on the social organization of a naturally queenless species of ponerine ant. *L. schwabi* also presents a case of queenlessness that is useful in comparative evolutionary studies of natural queenlessness because it is phylogenetically independent of previously-studied examples.

Virgin laying workers were few unless mated workers were experimentally removed from the colony, indicating that their reproductive physiology is regulated by the mated workers. No physical interactions or oophagy were seen, implicating a pheromonal mechanism of regulation. The combination of queenlessness and polygyny did not affect the general pattern of division of labour. This may be attributed to the inhibitory influence exerted by mated workers over virgin workers that forestalls the disruptive effects of reproductive competition among virgin workers.

KEY WORDS: Ponerinae, reproduction, polygyny, queenlessness, polyethism.

[3] Current address: Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 South Africa.
[4] Current address: Infruitec, Private Bag X5013, Stellenbosch, 7599 South Africa.

INTRODUCTION

Queen ants generally inhibit reproduction by their workers, and the experimental removal of queen(s) from a colony permits reproductive competition between workers that can affect division of labour (COLE 1981, OLIVEIRA & HÖLLDOBLER 1990). Many ant species of the subfamily Ponerinae are naturally, obligately queenless, and in a number of these cases the inhibitory role of the queen is filled by a single mated worker in each colony (Table 1); the remaining workers show undisrupted division of labour (VILLET 1990a, 1991a, 1991b, 1992a). Other naturally queenless ponerine species have several-to-many mated workers in each colony (Table 1), which has been suggested to reflect a modified form of reproductive organization that does not include active regulation of reproductive activity by mated colony members (PEETERS & CREWE 1985a). Although there is evidence to the contrary in *Ophthalmopone berthoudi* Forel 1890 (VILLET 1992b), this has not been generally tested. Furthermore, the effect of this form of sociality on division of labour in naturally queenless ponerines has not been quantified.

There is evidence that colonies of the African ponerine ant *Leptogenys schwabi* Forel 1913 are naturally, obligately queenless (BLOMEFIELD 1979, ZINI 1985) and contain several reproductively-active mated workers (ZINI 1985). The species thus offers a chance to examine division of labour and regulation of reproduction in a species with several mated workers in each colony. The occurrence of natural queenlessness in *L. schwabi* is also useful to an understanding of the evolutionary loss of the queen caste (VILLET 1992a, 1992c) for the following reason. One of the main drawbacks of the comparative method in evolutionary biology is that each case under comparison should have a phylogenetically independent origin (GITTLEMAN 1989). The phylogenetic position of *L. schwabi* within the African species of *Leptogenys* Roger 1861 (BOLTON 1975) indicates that queenlessness is a derived trait in this genus, since at least 10 African congeners (and indeed all species once placed in the subgenus *Lobopelta* Mayr 1862 for which these data are known) have a morphologically distinct, ergatoid queen caste (WHEELER 1933; BOLTON 1975; PEETERS 1991, 1993; VILLET et al. 1991). *L. schwabi* therefore provides a case of natural queenlessness that is phylogenetically independent of cases in other genera (Table 1).

MATERIALS AND METHODS

Fifteen natural colonies of *L. schwabi* were collected between August 1975 and March 1976 from World's View (29°31'S 30°31'E), Msunduze (29°33'S 30°25'E), and Wartburg (29°27'S 30°33'E). These sites are in the mist belt of Natal; their mean annual rainfalls are all over 800 mm. These colonies were used to examine the general demography of the species, and no dissections of workers were done.

Two colonies were collected in 1991 from Mkuzi Game Reserve, Natal, South Africa (27°40'S 32°15'E). These colonies (colony 1 and colony 2) were kept in the laboratory for behavioural studies. The larger colony was split randomly into two (colonies 1A and 1B) immediately after collection. They were all housed in modified, four-chambered Lubbock nests partially filled with soil and placed in large foraging arenas. Each nest was covered with a sheet of red perspex and kept at about 27 °C and about 60% humidity. The ants were fed harvester termites daily.

Each ant was examined for qualitative morphological indications of its caste, such as the presence of ocelli, a distinctive thoracic or petiolar profile, or an enlarged gaster (WHEEL-

Table 1.

Species of ponerine ants with queenless colonies.

Species	Gyny	Habitat preference	Reference
Ectatommini			
*Rhytidoponera**			
numerous species[1]	P or ?(P)	arid shurbland to rain forest	WARD (1981, 1983, 1984), PAMILO et al. (1985)
Platythyreini			
*Platythyrea**			
P. arnoldi[2]	P	seasonal savanna	VILLET (1993)
P. schultzei	M	seasonal savanna	VILLET (1991a)
P. cribrinodis	M	seasonal savanna	VILLET (1992c)
P. brevidentata	M	seasonal savanna	VILLET (1991b)
P. lamellosa	M	seasonal savanna	VILLET et al. (1990)
Ponerini			
Dinoponera			
D. gigantea	M	forest	HASKINS & ZAHL (1971)
D. australis	M	forest	FOWLER (1985)
D. quadriceps	(P)	evergreen forest	DANTAS DE ARAUJO et al. (1988, 1990)
Streblognathus			
S. aethiopicus	M	seasonal grassland	WARE et al. (1990)
Diacamma			
D. rugosum	M	seasonal forest	FUKUMOTO et al. 1989
D. nr. *rugosum*	M	?	MOFFETT (1986)
D. australe	M	dry woodland	PEETERS & HIGASHI (1989)
D. sp.	M	woodland	PEETERS & TSUJI (1993)
Hagensia			
H. havilandi	M	evergreen forest	VILLET (1992a)
H. peringueyi	M	montane scrub	VILLET (unpublished)
*Pachycondyla**			
P. tridentata[2]	P	?	SOMMER & HÖLLDOBLER (1992)
P. laevissima	M	coastal fynbos	ROBERTSON & VILLET (unpublished)
P. granosa	M	montane scrub	VILLET (unpublished)
P. pumicosa	M	montane scrub	VILLET (unpublished)
P. soror	?	seasonal savanna	LONGHURST (1977), VILLET (unpublished)
P. krugeri	M	seasonal savanna	WILDMAN & CREWE (1988), VILLET & WILDMAN (1991)
P. sublaevis	M	dry woodland	ITÔ & HIGASHI (1991)
P. porcata	M	rain forest	WARD (1983), pers. comm.
Ophthalmopone			
O. berthoudi	P	seasonal savanna	PEETERS & CREWE (1985a)
O. hottentota	P	arid shurbland	PEETERS & CREWE (1985b)
*Leptogenys**			
L. schwabi	P	evergreen forest	ZINI (1985)

* = genus with queenright species too; M = one mated worker/colony; P = many mated workers/colony; (P) = secondary mated workers join founding mated worker; [1] some species, e.g. *R. confusa* and *R. chalybaea*, have queens, but not in the same nests as mated workers; [2] these species have alate queens that share their nests with mated workers.

ER 1933, BOLTON 1975, PEETERS 1991, VILLET et al. 1991). To seek quantitative indications of castes, the length of the antennal scape and the minimum width between the eyes of every ant in two colonies were measured with an Olympus OSM optical micrometer and a Wild M3 stereomicroscope.

A catalogue of mutually exclusive behaviours was compiled from observations of colonies 1A, 1B, 2 and an experimental colony (colony 3) described below. To quantify the pattern of labour, each of the 78 surviving ants in colony 2 was marked with a binary code using enamel model paint so that each individual was distinct, and 50 scan samples of the activities of each ant were made over 3 days, beginning 8 days after the colony was collected.

The reproductive system of every ant in colonies 1A, 1B and 2 was dissected immediately following the completion of scan sampling of colony 2. Ants that died before this were frozen and dissected later with the rest. Ovariole length and the length of the largest oocyte (if any) in each ovary were measured, and the condition of the ovaries and the presence of *corpora lutea* were noted. The spermathecae were crushed between a microscope slide and coverslip and examined under a Leitz Labrolux 11 phase-contrast microscope for sperm. The lengths and widths of a sample of laid eggs were also measured.

An experimental colony (colony 3) composed only of virgin ants was made up from 37 ants which eclosed in the laboratory colonies. The virgins could be easily identified because they were unmarked, while the original workers had been marked. The experimental colony was fed to excess on termites, and 4 weeks later the reproductive systems of every ant in the colony were dissected.

All of the eggs were removed from colonies 1A and 1B, and the number of eggs laid 11 days in each nest was counted. Using the number of virgin and mated reproductives in each colony, as determined from the dissection data, the average daily laying rate per reproductive was calculated. The same datum for colony 3 was calculated 21 days after the colony was created.

RESULTS

Field observations

Colonies of *L. schwabi* were found in mixed mistbelt bush, mixed closed riverine bush, and fig forest composed chiefly of *Acacia xanthophloea* Bentham and *Ficus sycomorus* Linnaeus. They were located on or near the ground, in soft, alluvial soils, in shallow, rocky, dry soils, or in rotting wood. The nests in alluvial soil were less than 30 cm deep, with no obvious passages or chambers, while those in dry, rocky soils included chambers beneath stones, connected by obvious passages, and galleries extending to a depth of 45 cm. Colony size ranged from 32 to 338 individuals (Table 2). The production of male pupae began in late September (Table 2), and adult males eclosed in captive colonies in early October.

Several parties of 4-6 workers each were found and followed back to their nests. The ants followed one another in loose formation with frequent leader-changes. Individuals often wandered as much as a meter from the group, so that the formation broke down, usually without encountering prey. This behaviour was never seen in captivity, and ants also foraged alone in the field.

Foragers preyed largely on isopods (*Philoscia* sp.) and termites (*Odontotermes latericius* Haviland), but also collected unidentified amphipods. Termites predominated during September and October, when the first rains fell and the foraging activity of termites increased. On only one occasion in 200 hr of observation was another taxon brought to the nest: a spider which was later discarded. The entrances of natural nests were surrounded by the skeletons of amphipods and isopods. The ants were fed successfully on both isopods and termites in the laboratory.

Table 2.
Composition of natural colonies of *L. schwabi* at different times of year.

Date	Eggs	Larvae	Cocoons				Workers	Males
			Pre-pupae	Workers	Males	Total		
28 Aug 1975	*	0	0	0	0	0	144	0
28 Aug 1975	*	0	0	0	0	0	160	0
8 Sep 1975	*	0	0	0	0	0	181	0
24 Sep 1975	*	69	0	2	11	13	183	0
24 Sep 1975	*	43	0	0	9	9	165	0
7 Oct 1975	*	100	12	42	72	126	338	0
12 Oct 1975	*	128	12	12	110	134	185	0
5 Jan 1976	*	*	16	24	4	44	105	2
5 Jan 1976	*	*	0	32	1	33	32	0
5 Jan 1976	*	*	6	69	0	75	123	0
12 Mar 1976	0	0	0	148	0	148	201	0
15 Mar 1976	0	0	0	103	0	103	192	0
20 Mar 1976	0	0	0	105	0	105	250	0
26 Mar 1976	0	0	0	124	0	124	165	0
27 Mar 1976	*	*	0	66	0	66	320	0
Mar 1991	0	13	?	?	?	31	124	0
Mar 1991	63	23	?	?	?	146	260	0

* = too numerous to count; ? = not counted.

Reproduction

Seven ants out of 260 from colony 1 (1A + 1B) and six out of 146 from colony 2 were mated, and all of these had active ovaries containing oocytes and *corpora lutea*. One mated worker in colony 1 and five in colony 2 had red fluid in their poison sacs, as distinct from colourless fluid in the sacs of all of the other ants. However, mated ants did not differ from virgins in either scape length (t-test, unequal variances; t = 0.0271; P = 0.7870) or interocular width (t = 0.0608; P = 0.9517). All ants had three ovarioles per ovary and morphology characteristic of the worker caste of *Leptogenys*; no quantitative or qualitative evidence of a morphologically or anatomically distinct queen caste could be found.

Three virgin ants in colony 1A and four in colony 1B had developed ovaries and developing oocytes. No males were produced in either subcolony, implying that the virgins did not lay eggs, but this is not certain. No virgin ants in colony 2 had even developing ovarioles or oocytes.

In colony 3, all of the 37 newly-eclosed ants were virgins. Six of these (16.2%) had developed ovaries; two had both oocytes and *corpora lutea* in their ovaries; two had developing oocytes but no *corpora lutea*; and two more had ovaries with *corpora lutea* but no oocytes. Eggs appeared in this colony at least 12 days after it was constructed.

Laid eggs measured 1.15 mm (SD = 0.05; n = 75). The size of eggs did not differ significantly between virgin reproductives from colony 3 and mated reproductives in the field-caught colonies (n = 75 and 40, respectively; t = 0.1895; P = 0.8500). The mean rate of egg laying in colonies 1A and 1B was 31/11/7 = 0.4 and 116/11/7 = 1.5

eggs/day/reproductive ant, respectively. Colony 2 was not sampled because it was being used for behavioural observations. The oviposition rate of the virgin workers in colony 3 was 77/21/6 = 0.6 eggs/day/reproductive. Oophagy was absent.

Division of labour

During more than 30 observer-hours of observations, 25 distinct behaviours were recorded (Table 3), none of which were unusual. The ethograms of mated and virgin workers differed (Table 3). No cases of oophagy, trophallaxis or behavioural dominance were seen.

The pattern of division of labour was quantified from the scan samples (lasting 24 observer-hours) using a centroid-linkage hierarchical cluster analysis (SARLE 1985). Four methods were used to identify the number of clusters which would represent the most information. According to the cubic clustering criterion (SARLE

Table 3.

Catalogue of behaviours and ethogram modified to show frequencies of act and task performance in *L. schwabi* mated and virgin ants in a natural colony of 78 ants (figures indicate the relative occurrence of each act or task for each group of individuals; the total number of acts recorded was 3889).

Behaviour		Ethogram	
Code	Description	Virgin	Mated
BA	be antennated	0.0056	0.0029
BG	be groomed	0.0243	0.0460
CA	antennate cocoon(s)	0.0184	0.0029
CC	carry cocoon	0.0068	—
CG	groom cocoon(s)	0.0257	—
CR	rest with cocoon(s)	0.0229	0.3477
EA	antennate ball of eggs and larvae	0.0023	—
EC	carry ball of eggs and larvae	0.0155	0.0086
EG	groom ball of eggs and larvae	0.0023	—
EL	lay egg	—	*
FA	antennate prey	0.0054	—
FC	carry prey	0.0243	0.0029
FF	feed	0.1070	0.0316
NC	carry soil	0.0251	—
NE	dig	0.0079	—
NG	guard nest entrance	0.0367	—
NI	inspect nest	0.0082	0.0029
RA	rest alert	0.2166	0.0460
RI	rest inside nest	0.1649	0.2443
RO	rest outside nest	0.0045	—
SG	groom self	0.0554	0.0718
WA	antennate worker	0.0178	0.0374
WC	carry worker	0.0017	—
WG	groom worker	0.0291	0.0489
WI	walk inside nest	0.1063	0.1063
WO	walk outside nest	0.0198	—

* = observed, but not during quantification of ethogram.

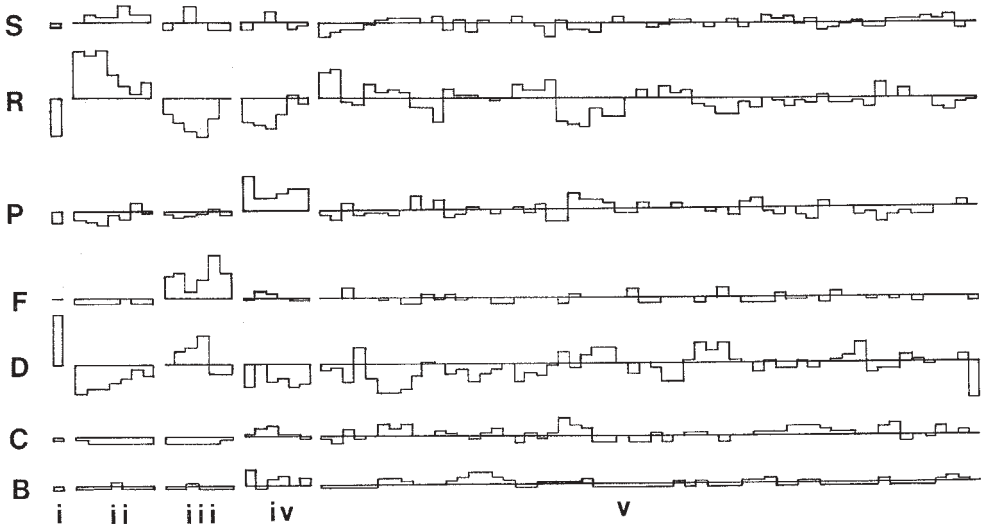

Fig. 1. — Histograms showing individual task performance frequencies of all 78 workers in colony 2 relative to the colony average. The individuals are ordered according to their position in the cluster analysis; groups *i-v* correspond to the roles discussd in the text. B, egg and larval care (EC, EG, EA); C, care of cocoons (CC, CG, CA); D, nest-related behaviour (NC, NE, NG, NI, WC, WI); F, foraging (FC, WO); P, personal behaviours (FF, FI, SG); R, resting behaviours (CR, RA, RI, RO); S, social interactions (BA, BG, WA, WG).

1985), the most information was contained in six clusters, with an additional local peak at one cluster; the PSF and PST2 methods (SARLE 1985) identify the most information in 2 and 4 or 5 clusters respectively; the 0.7 level of dissimilarity used by VILLET (1990a, 1991b, 1992a) and VILLET & WILDMAN (1991) also identified five clusters. Five clusters was taken as the best description of the data: four groups of ants and one worker whose behaviour was unique in the colony.

The behavioural roles associated with each cluster were characterized by comparing the individual ethograms of the workers in each cluster to the mean ethogram of the whole colony (Fig. 1). The behaviourally unique individual group (i) engaged in a high frequency of guarding behaviour; group (ii) contained ants that were usually seen resting, and that were identified by dissection as mated workers; workers in group (iii) performed the most foraging and nest maintenance; ants of group (iv) specialized in brood care; and group (v) contained behaviourally unspecialized virgin ants.

DISCUSSION

The term *polygyny* is a homonym that generally denotes male promiscuity, but in relation to insect sociobiology, denotes the presence of several mothers together in a colony. This homonymy is unfortunate because it has probably contributed to the neglect of studies of the incidence and effects of male promiscuity in the social

insects. However, in the sense that it denotes the presence of more than one mother in a colony, colonies of *L. schwabi* are polygynous (Zini 1985). This study confirms this, and provides evidence that reproduction by virgin workers is regulated by mated workers in this species, and that polygyny does not appear to have affected the general pattern of division of labour.

Queens of *L. langii* Wheeler 1923 have wings (Wheeler 1923), and represent the ancestral condition in the genus. The central African *L. ergatogyna* Wheeler 1922 has queens that lack wings, but have a thoracic morphology associated with flight (Wheeler et al. 1922). All other known *Leptogenys* queens have reduced, wingless, worker-like thoraxes. However, even when the queen caste of a species of *Leptogenys* is wingless and worker-like, it retains a suite of morphological traits that distinguish it from the worker caste. These include the presence of ocelli or at least traces of them, a convex (rather than flat) profile to the meso- and metanota, shorter petioles that incline forward, and more voluminous gasters (Wheeler 1933, Bolton 1975, Peeters 1991, Villet et al. 1991). None of these traits were found in mated specimens of *L. schwabi*, and colonies were composed entirely of workers.

It is not known how prevalent queenlessness is within the genus. Wheeler (1933) could not find queens in Australian colonies of *L. clarki* Wheeler 1933, and further reported, "nor has it been possible to detect a differentiated female or queen in any of the described species of Leptogenys *sens. str.* We may therefore conclude that such a form does not exist. The same is true for the species assigned to the subgenera Machærogenys and Odontopelta" (Wheeler 1933: 85). He cited *L.* (= *Odontopelta*) *turneri* Forel 1900 in support of his claim. Although the subgeneric divisions are no longer recognized (Bolton 1975), Wheeler's generalization remains unchallenged, and obligate queenlessness may therefore be the norm in several other species of *Leptogenys*.

The queenright species of *Leptogenys* appear to be all monogynous (Villet et al. 1991, Peeters 1993). The loss of the queen caste in *L. schwabi* is therefore associated with a difference in the mechanisms regulating the numbers of reproductive ants in each colony: there was more than one mated worker per colony, and virgin laying workers were found in natural colonies.

However, there is evidence that mated workers of *L. schwabi* have an inhibitory influence on reproduction by conspecific virgin workers: a much larger proportion (16.2%) of virgin ants with active ovarioles was found in the experimental colony lacking mated workers than in the natural colonies (2.7% in colony 1 and 0.0% in colony 2), which included mated workers. Similarly, the presence of mated workers of the polygynous, obligately queenless ponerine *Ophthalmopone berthoudi* inhibits laying by virgin workers (Villet 1992b), so that virgin reproductives are very scarce or absent in natural colonies (Peeters & Crewe 1985a: 31). The 12-day period before eggs appeared in the experimental nest can be interpreted as a period during which the ovaries and oocytes of virgins developed after being inhibited by mated workers in the natal colony. Furthermore, there is an inverse relation between the percentage of mated workers (2.7%, 4.1% and 0.0% respectively) and the percentage of reproductively active virgins (2.7%, 0.0% and 16.2% respectively) in the three laboratory colonies. Since the laboratory nests were of similar volumes, the effect could be due to the ratio of mated ants to virgins, or to a "pheromonal titre" effect caused by nest volume (Villet 1992b).

No aggressive behaviours were seen, and reproductives did not engage in more physical interactions than did non-reproductive workers, ruling out physical

contests such as has been reported in some other ponerines (PEETERS & HIGASHI 1989, OLIVEIRA & HÖLLDOBLER 1990, ITÔ & HIGASHI 1991, MEDEIROS et al. 1992, SOMMER & HÖLLDOBLER 1992, VILLET 1992a, PEETERS & TSUJI 1993). Oophagy, which has been found in some ponerines (e.g. OLIVEIRA & HÖLLDOBLER 1990), and trophallaxis were not seen. If regulation does occur, a volatile pheromone is the most likely mechanism, and levels of polygyny may be regulated by the ambient titres of the pheromone in the nest (VILLET 1992b).

As in queenless, monogynous ponerines (VILLET 1990a, 1991a, 1991b, 1992a; VILLET & WILDMAN 1991), although mated workers of *L. schwabi* are behaviourally distinct from virgin workers, the general pattern of division of labour is unremarkable: workers of each species are organized into several roles relating to brood, nest maintenance and foraging, with an inactive "reserve" (cf. FRESNEAU 1984); and mated workers contributed little or nothing to colony maintenance. Polygyny has had no qualitative effect on division of labour.

Although *L. schwabi* provides an example of a queenless species that is phylogenetically independent of those previously studied, until we know more about the biology of its close relatives, the significance of the ecology of *L. schwabi* for our understanding of the evolutionary origins of queenless societies of ponerine ants must remain unclear (VILLET 1992a, 1992c). In particular, it is not clear whether *L. schwabi* evolved directly from an ancestor that had winged queens or ergatoid queens, or was already obligately queenless. Ergatoid queens have not been reported in some genera containing mated workers, so that it is likely that the transition was from There is great diversity in the habitats (Table 1) and biologies of the species already studied and it may be found that, as with the evolution of ergatoid queens in the ponerines (VILLET 1991c), there is more than one evolutionary pathway to the queenless condition.

ACKNOWLEDGEMENTS

We would like to thank J. Descroizilles, F. Duncan, D. Fletcher, T. van der Leij, R. Lincoln, A. Nelson, A. Turner and A. Wackernagel for their help with various parts of this work, Y. Itô, C. Peeters and an anonymous referee for their comments, and the Natal Parks Board for permission to collect ants in Mkuzi Game Reserve. The project was funded by the Foundation for Research Development, Pretoria, and the Communication Biology Research Group, University of the Witwatersrand, Johannesburg.

REFERENCES

BLOMEFIELD T.M. 1979. A test of the competitive exclusion principle. *Unpublished M.Sc. Dissertation, University of Natal, Pietermaritzburg, South Africa*.

BOLTON B. 1975. A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian region, with a review of the Malagasy species. *Bulletin of the British Musuem (Natural History)* 31: 237-305.

COLE B. 1981. Dominance hierarchies in *Leptothorax allardycei* ants. *Science* 212: 83-84.

DANTAS DE ARAUJO C., FRESNEAU D. & LACHAUD J. 1988. Premiers résultats sur l'éthologie d'une fourmi sans reine: *Dinoponera quadriceps*. *Actes Colloques des Insectes Sociaux* 4: 149-155.

Dantas de Araujo C., Fresneau D. & Lachaud J. 1990. Données biologiques sur la fondation des colonies de *Dinoponera quadriceps* (Hymenoptera: Formicidae). *Actes Colloques des Insectes Sociaux* 6: 281-286.

Fowler H. 1985. Populations, foraging and territoriality in *Dinoponera australis* (Hymenoptera, Formicidae). *Review of Brasilian Entomology* 29: 443-447.

Fresneau D. 1984. Developpement ovarien et statut social chez une fourmi primitive *Neoponera obscuricornis* Emery (Hym.-Form., Ponerinae). *Insectes Sociaux* 31: 387-402.

Fukumoto Y., Abe T. & Taki A. 1989. A novel form of colony organisation in the 'queenless' ant *Diacamma rugosum*. *Physiological Ecology, Japan* 26: 55-61.

Gittleman, J. 1989. The compartive approach in ethology: aims and limitations, pp. 55-83. In: Bateson P. & Klopfer P., Edits. Perspectives in ethology. Vol. 8. *New York: Plenum.*

Haskins C. & Zahl P. 1971. The reproductive pattern of *Dinoponera grandis* Roger (Hymenoptera: Ponerinae) with notes on the ethology of the species. *Psyche* 78: 1-11.

Itô F. & Higashi S. 1991. A linear dominance hierarchy regulating reproduction and polyethism of the queenless ant *Pachycondyla sublaevis*. *Naturwissenschaften* 78: 80-82.

Longhurst C. 1977. Behavioural, chemical and ecological interactions between West African ants and termites. *Ph.D. Thesis, Southampton University, England.*

Medeiros F.N.S., Lopes L.E., Moutinho P.R.S., Oliveira P.S. & Hölldobler B. 1992. Functional polygyny, agonistic interactions and reproductive dominance in the neotropical ant *Odontomachus chelifer* (Hymenoptera, Formicidae, Ponerinae). *Ethology* 91: 134-146.

Moffett M. 1986. Evidence of workers serving as queens in the genus *Diacamma* (Hymenoptera: Formicidae). *Psyche* 93: 151-152.

Oliveira P. & Hölldobler B. 1990. Dominance orders in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae). *Behavioral Ecology and Sociobiology* 27: 385-393.

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

Peeters C.P. 1991. Ergatoid queens and intercastes in ants: two distinct adult forms which look morphologically intermediate between workers and winged queens. *Insectes Sociaux* 38: 1-15.

Peeters C.P. 1993. Monogyny and polygyny in ponerine ants with or without queens, pp. 234-261. In: Keller L., Edit. Queen number and sociality in social insects. *Oxford: Oxford University Press.*

Peeters C.P. & Crewe R.M. 1985a. Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial organisation. *Behavioral Ecology and Sociobiology* 18: 29-37.

Peeters C.P. & Crewe R.M. 1985b. Queenlessness and reproductive differentiation in *Ophthalmopone hottentota*. *South African Journal of Zoology* 20: 268.

Peeters C. & Higashi S. 1989. Reproductive dominance controlled by mutilation in the queenless ant *Diacamma australe*. *Naturwissenschaften* 76: 177-180.

Peeters C.P. & Tsuji K. 1993. Reproductive conflict among ant workers in *Diacamma* sp. from Japan: dominance and oviposition in the absence of the gamergate. *Insectes Sociaux* 40: 119-136.

Sarle W.S. 1985. The cluster procedure, pp. 255-315. In: Joyner S., Edit. SAS Users' Guide: Statistics. *Cary, North Carolina: SAS Institute Incorporated.*

Sommer K. & Hölldobler B. 1992. Coexistence and dominance among queens and mated workers in the ant *Pachycondyla tridentata*. *Naturwisseschaften* 79: 470-472.

Villet M.H. 1990a. Social organization of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): II. Division of labour. *South African Journal of Zoology* 25: 254-259.

Villet M.H. 1990b. Qualitative relations of egg size, egg production and colony size in some ponerine ants. *Journal of Natural History* 24: 1321-1331.

Villet M.H. 1991a. Social differentiation and division of labour in the queenless ant *Platythyrea schultzei* Forel 1910 (Hymenoptera Formicidae). *Tropical Zoology* 4: 13-29.

Villet M.H. 1991b. Reproduction and division of labour in *Platythyrea* cf. *cribrinodis* (Gerstaecker 1858) (Hymenoptera Formicidae): comparisons of individuals, colonies and species. *Tropical Zoology* 4: 209-231.

VILLET M.H. 1991c. Colony foundation in *Plectroctena mandibularis* F. Smith, and the evolution of ergatoid queens in *Plectroctena* (Hymenoptera: Formicidae). *Journal of Natural History* 25: 979-983.

VILLET M.H. 1992a. The social biology of *Hagensia havilandi* (Forel 1901) (Hymenoptera Formicidae), and the origin of queenlessness in ponerine ants. *Tropical Zoology* 5: 195-206.

VILLET M.H. 1992b. Does mating trigger egg laying in the ant *Ophthalmopone berthoudi* Forel (Hymenoptera Formicidae)? *Ethology Ecology & Evolution* 4: 389-394.

VILLET M.H. 1992c. Exploring the biology of obligate queenlessness: social organization in platythyreine ants, pp. 291-294. In: Billen J., Edit. Biology and evolution of social insects. *Leuven: Leuven University Press*.

VILLET M.H. 1993. Co-occurence of mated workers and a mated queen in a colony of *Platythyrea arnoldi* (Hymenoptera: Formicidae). *South African Journal of Zoology* 28: 56-57.

VILLET M.H., CREWE R.M. & DUNCAN F.D. 1991. Evolutionary trends in the reproductive biology of ponerine ants (Hymenoptera: Formicidae). *Journal of Natural History* 25: 1603-1610.

VILLET M.H., HART A. & CREWE R.M. 1990. Social organisation of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): I. Reproduction. *South African Journal of Zoology* 25: 250-253.

VILLET M.H. & WILDMAN M.H. 1991. Division of labour in the obligately queenless ant *Pachycondyla* (= *Bothroponera*) *krugeri* Forel 1910 (Hymenoptera Formicidae). *Tropical Zoology* 4: 233-250.

WARD P.S. 1981. Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae). II. Colony origin, seasonal cycles and reproduction. *Psyche* 88: 109-126.

WARD P.S. 1983. Genetic relatedness and colony organisation in a species complex of ponerine ants I. Phenotypic and genotypic composition of colonies. *Behavioral Ecology and Sociobiology* 12: 285-299.

WARD P.S. 1984. A revision of the ant genus *Rhytidoponera* in New Caledonia. *Australian Journal of Zoology* 32: 131-175.

WARE A.B., COMPTON S.G. & ROBERTSON H.G. 1990. Gamergate reproduction in the ant *Streblognathus aethiopicus* Smith (Hymenoptera: Formicidae: Ponerinae). *Insectes Sociaux* 37: 189-199.

WHEELER W.M. 1923. The occurence of winged females in the ant genus *Leptogenys*, with descriptions of new species. *American Museum Novitates* 90: 1-16.

WHEELER W.M. 1933. Colony-founding among ants, with an account of some primitive Australian species. *Cambridge, Massachusetts: Harvard University Press.*

WHEELER W.M., BEQUART J., BAILEY I., SANTSCHI F. & MANN W. 1922. Ants of the American Museum Congo expedition: a contribution to the myrmecology of Africa. *Bulletin of the American Museum of Natural History* 45: 1-1055.

WILDMAN M. & CREWE R. 1988. Gamergate number and control over reproduction in *Pachycondyla krugeri* (Hymenoptera: Formicidae). *Insectes Sociaux* 35: 217-225.

ZINI M.A. 1985. The role of worker reproduction in two species of ponerine ants (*Leptogenys* Roger) (Formicidae: Hymenoptera). *Proceedings of the Congress of the Entomological Society of Southern Africa* 5: 47-48.