Anim. Behav., 1988, **36**, 159–165

Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study

LAURENT KELLER*

Museum of Zoology, Palais de Rumine, CP 448, 1000 Lausanne 17, Switzerland

and

Laboratory of Entomology, UPS, 118 rte de Narbonne, 31062 Toulouse, France

Abstract. A comparison of several physiological parameters of queens of *Iridomyrmex humilis* in experimental monogynous and polygynous colonies showed that queens in monogynous colonies became heavier, had more developed ovaries and laid about twice as many eggs. Workers in monogynous colonies were more attracted to queens, which therefore probably received more food. This may partially explain the higher weight and fecundity of queens in monogynous colonies of *Iridomyrmex humilis* and possibly other ant species. In polygynous colonies, queens differed greatly in their fecundity. These differences did not appear to be the result of a dominance hierarchy. These results are discussed from an evolutionary point of view. Two hypotheses of mutualism and colony level selection are proposed as an alternative to kin selection which is unlikely to be the exclusive selective influence in the evolution of polygyny either in *I. humilis* or in most other ant species.

Following the conventional models of evolution (Fisher 1930; Wright 1931; Haldane 1932), selection acts in favour of the genomes of individuals able to produce many surviving offspring. To increase this production, individuals compete among themselves. In social insects, cases of competition are well documented (Baroni-Urbani 1968a; Wilson 1971; Keller & Cherix 1985).

In the case of polygyny (the presence of more than one egg-laying queen in the same colony, Wilson 1974b), several authors have shown that queen fecundity is inversely proportional to their number in the colony (e.g. Michener 1964; Brian 1969; Passera 1969; Roisin & Pasteels 1985). To explain this decrease in queen fecundity, Fletcher et al. (1980) proposed two hypotheses. In *Solenopsis invicta*, the lower ratio of workers to queens found in polygynous nests compared with monogynous nests may create resource limitation for the queens, or alternatively, in nests, queens may possess a pheromonal mechanism which mutually inhibits their fecundity.

The lower fecundity of queens in polygynous colonies raises the question whether the decrease in fecundity affects all queens equally or whether it leads to the formation of a dominance hierarchy among queens. In this paper, the Argentine ant, *Iridomyrmex humilis* (Mayr), a typically polygynous species (Newell 1909; Markin 1970a), was chosen to investigate the causes of lower fecundity of queens in polygynous colonies and was used as a test of the existence of a dominance hierarchy among queens.

*Present address: Museum of Zoology, Palais de Rumine, CP 448, 1000 Lausanne 17, Switzerland.

MATERIALS AND METHODS

Seven stock colonies of *I. humilis* were collected in March 1983 in the south of France on the Mediterranean coast between Nice and St Raphael. The colonies were maintained in the laboratory in artificial nests (Passera et al., in press) at 27±2°C and at a relative humidity of 55±5%. They were fed ad libitum on a diet of meat, eggs, sugar and vitamins. Mealworms were given regularly. Each of the seven stock colonies was split into one polygynous colony, containing between five and eight queens, and a control group containing between five and eight monogynous colonies (the number of monogynous colonies in each control group was equal to the number of queens in the corresponding polygynous colony). Altogether, 42 queens were distributed in seven polygynous colonies and 42 queens in the seven control groups. Each queen was marked with Tech pen ink (Marktex) and given 0·9 cm³ of workers and brood (about 600 workers). At 10, 20, 30, 50, 80, 120 and 160 days after the beginning of the experiment, each queen was weighed and subjected to an oviposition test. In this test, each queen was isolated during 14 h in an experimental nest and the number of eggs laid during this period were counted under a dissecting microscope.

When a queen in a polygynous colony died, a queen of the corresponding group of monogynous colonies was randomly chosen and eliminated. The same procedure was used when a queen in a monogynous colony died. Consequently, the number of queens remained equal in both kinds of colonies.

On day 160, the 28 remaining queens in monogynous colonies and the 28 queens in polygynous colonies were tested for their attractiveness to workers in a manner similar to that described in Coglitore & Cammaerts (1981). Each queen was isolated in a plastic box (8·0 cm diameter) with 50 workers randomly chosen from her colony. The plastic box was closed with a lid to avoid disturbance and the inner side was coated with Fluon to prevent workers and queens from escaping. Ants were allowed 15 min to acclimatize after which time the number of workers in contact with the queens was counted once every 5 min for 1 h (12 values). The same procedure was repeated for each queen once in the morning and once in the afternoon, with different groups of workers. The attractiveness of each queen was quantified by calculating the mean of these 24 values.

Finally, each queen was dissected. Ovarian development was estimated from the number of mature oocytes (more than 0·25 mm long).

RESULTS

Queen Weight and Fecundity

Queen weight increased during the first 80 days in both monogynous and polygynous colonies (Fig. 1). But the increase in monogynous colonies was more rapid, and queens from monogynous and polygynous colonies differed significantly in weight from day 30 onwards.

Queen fecundity increased up to day 80 in both monogynous and polygynous colonies (Fig. 2). The increase in queen fecundity was again greater in monogynous colonies; the ratio of the mean rate of egg laying by queens in monogynous colonies to

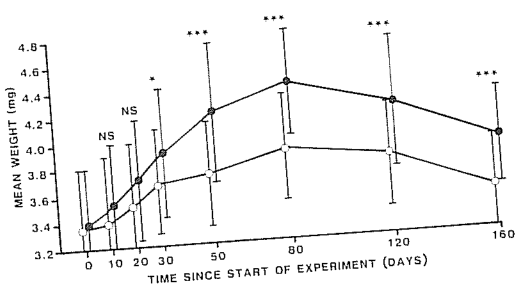

Figure 1. Mean queen weight ($\pm$SD) of queens in polygynous colonies (open circles) and monogynous colonies (closed circles). $*P<0·05$; $***P<0·001$ indicate significant differences between monogynous and polygynous colonies (t-test). The number of queens in monogynous and polygynous colonies was equal: $N=42$ at day 10, 20, 30, 50; 38 at day 80; 33 at day 120; and 28 at day 160.

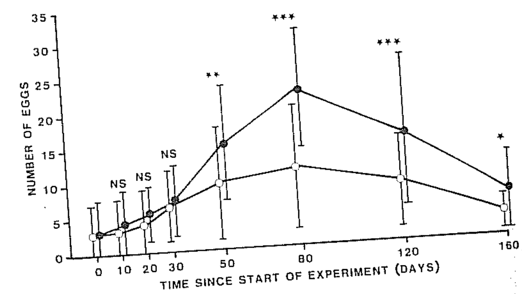

Figure 2. Mean number of eggs ($\pm$SD) laid by queens in polygynous colonies (open circles) and monogynous colonies (closed circles). The number of queens is as in Fig 1. $*P<0·05$; $**P<0·01$; $***P<0·001$.

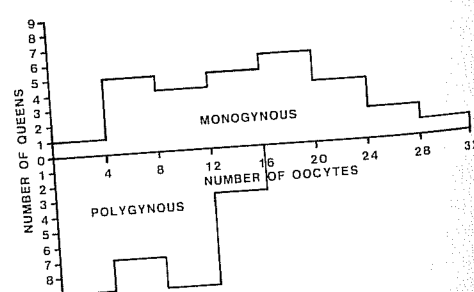

Figure 3. Distribution of number of mature oocytes per queen for 28 queens reared 160 days in polygynous colonies and 28 queens in monogynous colonies. Queens in polygynous colonies: $\bar{X}\pm SD=7·0\pm4·6$. Queens in monogynous colonies $\bar{X}\pm SD=15·2\pm7·5$. The difference between both means is significant ($t=8·85$, $df=54$, $P<0·001$).

Table 1. Volumes of workers plus brood per queen ($\bar{X} \pm$ SD) after 160 days of the experiment

Polygynous colonies			Control groups of monogynous colonies			
Colony	Number of queens	Volume of workers plus brood per queen (cm³)	Colony	Number of queens	Volume of workers plus brood per queen (cm³)	*t*-Test *P*
P_1	5	1·1	M_1	5	1·8	
P_2	5	0·9	M_2	5	1·1	
P_3	5	0·9	M_3	5	1·3	
P_4	6	1·2	M_4	6	2·0	
P_5	6	1·3	M_5	6	1·6	
P_6	7	0·7	M_6	7	1·1	
P_7	8	0·6	M_7	8	1·8	
Mean	42	$1·0 \pm 0·3$		42	$1·5 \pm 0·4$	$<0·005$

the mean rate of egg laying by queens in polygynous colonies was 160% on day 50, 190% on day 80, 190% on day 120 and 191% on day 160. A *t*-test showed a significant difference in individual queen fecundity between monogynous and polygynous colonies as early as day 50.

At the end of the experiment, the dissection of queens showed that the mean number of oocytes per queen was significantly greater in monogynous colonies than in polygynous colonies (Fig. 3). This difference in ovarian development of queens was associated with a significantly higher production of workers and brood in monogynous colonies. The volume of workers plus brood per queen increased by 11% between day 0 and day 160 in polygynous colonies, whereas this increase reached 67% in monogynous colonies (Table I).

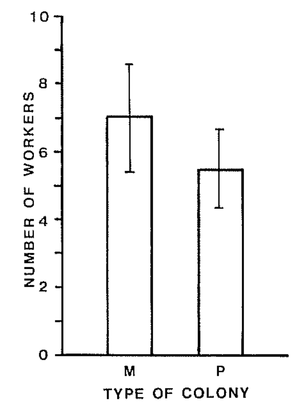

Figure 4. Mean attractiveness $\pm$ SD of queens to workers in monogynous (M) and polygynous (P) colonies. The means are significantly different ($t=3·89$, $df=54$, $P<0·001$).

Attractiveness of Queens in Monogynous and Polygynous Colonies

The tests for attractiveness performed on day 160 showed that workers were significantly more attracted to queens in monogynous colonies ($\bar{X} \pm$ SD $= 7·0 \pm 1·6$) than in polygynous colonies ($5·5 \pm 1·2$; Fig. 4).

Queen Interactions

To test the interactions among queens and to determine whether a dominance hierarchy exists, five polygynous colonies, each containing five queens on day 120, were compared with five control groups each consisting of five monogynous colonies. If there was a dominance hierarchy among queens in polygynous colonies, there should be larger differences in fecundity between queens in polygynous colonies than within the control groups in which queens were not together.

To study the differences in fecundity among queens, the five queens in each polygynous colony were ranked according to the total number of eggs laid during the six oviposition tests (see Materials and Methods; 1 = queen with the highest egg-laying rate; 5 = queen with the lowest egg-laying rate). The number of eggs was expressed in relation to this ranking system. The same procedure was applied to the five queens in each of the five control groups. Because the same data were used to generate both axes in this analysis, there was of course a negative

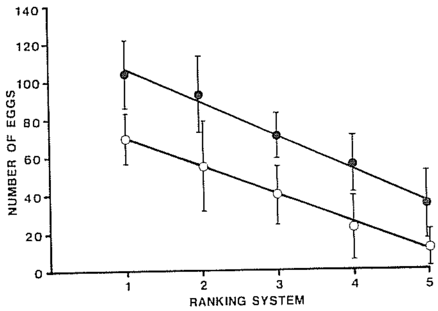

Figure 5. Mean number of eggs laid by queens as a function of the ranking system of fecundity. Open circles: queens in polygynous colonies; closed circles: queens in control groups of monogynous colonies.

correlation between ranks of queens and their egg-laying rate. Within polygynous colonies, there was a linear relationship between the ranking of queens and their egg-laying rate ($y = -15{\cdot}0x + 84{\cdot}6$; $r = 0{\cdot}81$ $P < 0{\cdot}001$; Fig. 5). In the control groups, a similar pattern with large differences in fecundity among queens was found ($y = -17{\cdot}7x + 124{\cdot}7$; $r = 0{\cdot}85$, $P < 0{\cdot}001$). The slopes of these regression lines are proportional to the differences in the egg-laying rate between queens with high and low fecundity, a steep slope indicating that there are large differences. The slopes of the two regression lines did not differ significantly ($t = 1{\cdot}96$; $df = 33$; NS) thus suggesting that there was no dominance hierarchy among queens in polygynous colonies. The differences in fecundity among queens in polygynous colonies as well as in the control groups probably resulted from intrinsic physiological differences between queens (e.g. age, genetic differences). The mean number of eggs laid during the six oviposition tests by queens was significantly higher in monogynous colonies ($\bar{X} \pm \text{SD} = 72 \pm 30$) than in polygynous colonies (40 ± 27; $t = 2{\cdot}80$; $df = 46$; $P < 0{\cdot}01$). Since the slopes of both regression lines were similar, the fecundity of all queens in polygynous colonies was reduced equally.

DISCUSSION

Queen Weight and Fecundity

Queens in monogynous colonies became heavier, had more developed ovaries and laid significantly more eggs than queens in polygynous colonies. Furthermore, brood and worker production per queen was higher in monogynous colonies.

Working on the same species, Bartels (1983) failed to show a difference in brood production between monogynous and polygynous colonies. However, a close examination of his results shows that egg production per queen in monogynous colonies was also about twice that in polygynous colonies but, due to the small sample ($N = 5$) studied, he was not able to show a significant difference.

Queen Hierarchy in Polygynous Colonies

In mature polygynous colonies, the existence of a hierarchy among queens resulting from reproductive competition can be tested by comparing their reproductive success, i.e. the number of males, queens and fertile workers they produce. In the case of *I. humilis*, I have not considered workers, because they never lay reproductive eggs (Markin 1970b; Benois 1973; Bartels 1983). In this study, the fecundity of queens was used as the criterion of their reproductive success, because, for the following reasons, the eggs laid by all queens have the same probability of developing into sexuals. First, all queens lay male-eggs in a similar ratio (Passera et al., in press; Passera & Keller, unpublished data) and second, the development of female-eggs produced by queens into queens or workers depends only on extrinsic factors such as queen inhibition and food status of the colony (Passera & Keller, unpublished data). Consequently, the female-eggs laid by each queen in a colony are equally likely to develop into new queens.

The comparison of the fecundity of queens shows that in polygynous colonies of *I. humilis*, there is no evidence of a dominance hierarchy between queens. Instead, the difference in fecundity of queens, in polygynous as well as in control groups of monogynous colonies, results from intrinsic physiological differences between the queens. This indicates that the demonstration of important physiological differences between individuals in a colony does not provide conclusive evidence of a dominance hierarchy. To demonstrate the existence of a dominance hierarchy, it is necessary to show that behavioural or physiological differences result from interactions among individuals. This can be done by showing, for example, that these differences disappear when the individuals are separated or that these differences do not exist when comparing individuals that are not interacting. In *Leptothorax curvispinosus*

(Wilson 1974a, b), queens
eat the eggs laid by other
(Evesham 1984) and in *P*
lus (Wheeler 1984) there
ences between queens. H
differences between queen
given above may possibly
differences, as in our exp
consequence of a domina
lepis pygmaea, queens rea
onies displayed no signif
fecundity (Mercier et al. 1
conclusive evidence for th
tive hierarchies resultin
between queens in mature
ants.

Queen Fecundity

In the experimental grou
to queens was the same
polygynous colonies. There
in polygynous colonies the
to queens creates a reso
queens (Fletcher et al. 19
explain the differences in q
experimental conditions.

The second hypothesis (
that queens may possess a
which inhibits egg laying
nest. In *Leptothorax gred*
Myrmecina graminicola (
Formicoxenus nitidulus (
1976), *Solenopsis invicta*
1978), *Formicoxenus hirtic*
and *Leptothorax provanch*
1980), several queens coexi
one of them inhibits the f
This functional monogyny
tive competition between q
fecundity of all queens in
reduced equally and there
archy with one or several
inhibiting the fecundity of
the lower fecundity of quee
onies seems difficult to exp
ductive competition.

The results of the test of
workers suggest a new exp
weight and fecundity of
colonies: in *I. humilis*, queens
from the workers (Markin

(Wilson 1974a, b), queens differ in their tendency to eat the eggs laid by other queens. In *Myrmica rubra* (Evesham 1984) and in *Procryptocerus scabriusculus* (Wheeler 1984) there are behavioural differences between queens. However, the behavioural differences between queens in the three examples given above may possibly be the result of individual differences, as in our experiments, rather than the consequence of a dominance hierarchy. In *Plagiolepis pygmaea*, queens reared in experimental colonies displayed no significant difference in their fecundity (Mercier et al. 1985). Hence, there is no conclusive evidence for the existence of reproductive hierarchies resulting from a dominance between queens in mature polygynous colonies of ants.

Queen Fecundity

In the experimental groups, the ratio of workers to queens was the same in monogynous and polygynous colonies. Therefore the hypothesis that in polygynous colonies the lower ratio of workers to queens creates a resource limitation for the queens (Fletcher et al. 1980), is not adequate to explain the differences in queen fecundity under my experimental conditions.

The second hypothesis (Fletcher et al. 1980) was that queens may possess a pheromonal mechanism which inhibits egg laying by other queens in the nest. In *Leptothorax gredleri* (Buschinger 1968), *Myrmecina graminicola* (Baroni-Urbani 1968b), *Formicoxenus nitidulus* (Buschinger & Winter 1976), *Solenopsis invicta* (Tschinkel & Howard 1978), *Formicoxenus hirticornis* (Buschinger 1979) and *Leptothorax provancheri* (Buschinger et al. 1980), several queens coexist in the same nest, but one of them inhibits the fecundity of the others. This functional monogyny results from reproductive competition between queens. In *I. humilis*, the fecundity of all queens in polygynous colonies is reduced equally and there is no dominance hierarchy with one or several queens preferentially inhibiting the fecundity of the others. Therefore, the lower fecundity of queens in polygynous colonies seems difficult to explain in terms of reproductive competition.

The results of the test of queen attractiveness to workers suggest a new explanation for the lower weight and fecundity of queens in polygynous colonies: in *I. humilis*, queens receive nearly all food from the workers (Markin 1970b). The data in Fig. 3 show that queens in polgynous colonies are less attractive to workers. Thus, these queens have fewer contacts with workers and consequently probably receive less food. This hypothesis, that there is a difference in the amount of food that queens receive, is supported by the fact that the increase in weight of queens was far more rapid in monogynous than in polygynous colonies (Fig. 1). Consequently, the difference in the amount of food that queens receive in monogynous and polygynous colonies may at least partially explain their difference in fecundity.

Polygyny in an Evolutionary Context

In ants monogyny is probably the primitive condition and polygyny derived (Brian 1983; Fletcher & Ross 1985). Following the theory of Hamilton (1964a), polygyny could be explained if queens are related (Hamilton 1964b; Wilson 1966, 1971; Hölldobler & Wilson 1977). In *I. humilis*, the colony structure is polydomous (i.e. the population is divided into many nests, but they are interconnected). Furthermore, nest sites often shift, split or fuse several times in the year in response to desiccation, flooding or human disturbance (Newell & Barber 1913). Queens are also very nomadic and frequently change nests (Newell & Barber 1913). Therefore, it seems unlikely that queens from the same nest are closely related. In some other ant species, there is a significant relatedness among the nestmate queens, but this relatedness is generally low (Craig & Crozier 1979; Pamilo & Varvio-Aho 1979; Pamilo 1981, 1982; Ward 1983; Crozier et al. 1984; Pamilo & Rosengren 1984), whereas in some other species, no significant relatedness can be detected in most nests (Craig & Crozier 1979; Pamilo 1981, 1982; Pearson 1982, 1983; Ross & Fletcher 1985).

Thus, in *I. humilis* and in other species where relatedness is probably low, the maintenance of polygyny seems difficult to explain exclusively in terms of kin selection. Another possibility to consider is that polygyny is not the result of altruism. In *I. humilis* as in many other polgynous species, polygyny is linked to important behavioural and ecological modifications, namely, loss of nuptial flight of the queens, mating within the nest, colony founding by budding, loss of territorial boundaries and aggression among colonies (Hölldobler & Wilson 1977). In *I. humilis*, these modifications seem very adaptive for the opportunistic nesting strategy used: frequent moving, splitting and fusion of colonies. Furthermore, in this and probably other ant species, colony founding by budding necessitates a much lower energy investment, which is adaptive in poor habitats (Keller & Passera, in press). Polygyny also seems well-suited for particular patches of habitat (Hölldobler & Wilson 1977; Pamilo & Rosengren 1984). Thus, the social organization adopted by polygynous species may present some selective advantages. This raises the question whether selection acts at the individual level (i.e. queens), or at a higher level (i.e. colony). Under selection at the individual level, the evolution and maintenance of polygyny assumes that for queens the association with other queens outweighs the costs (i.e. loss of personal fecundity). This mutualism has been invoked to explain the temporary association of queens during colony founding in social insects (e.g. Lin & Michener 1972; Bartz & Hölldobler 1982). However, in the majority of cases, either queens begin to fight when the first workers are ready to pupate or emerge, or the first workers to emerge eliminate queens until only one remains (Bartz & Hölldobler 1982). This strong aggression indicates that mutualism does not prevent reproductive competition from operating among queens during the maturation of the colony. In the case of permanent polygyny, it is still difficult to assess whether the benefits for queens of associating with other queens may outweigh the cost in loss of personal reproduction in mature colonies. The alternative explanation invokes selection at the colony level. This mode of selection has been hypothesized by Sturtevant (1938) then discussed by Lewontin (1970), Oster & Wilson (1978), Crozier (1979), Starr (1979) and West-Eberhard (1981) as a means of explaining the evolution of eusociality. Under this mode of selection there may be a selective pressure against competition among queens in polygynous colonies. Colonies in which queens compete would probably be at a disadvantage in comparison with other colonies. Although it is difficult to assess the relative importance of these alternative hypotheses, in colonies in which the degree of relatedness among queens is low, selection at the colony level is probably an important selective influence acting against competition among nestmate queens. Selection at the colony level may therefore act in concert with mutualism for the evolution of polygyny when this mode of social organization is best suited to a habitat.

ACKNOWLEDGEMENTS

I wish to thank Dr D. Cherix for his help during all the work, Drs C. Baroni-Urbani, J. J. Boomsma, J. Hausser, L. Passera, B. Pearson, Chr. Peeters, H. Richner, J. P. Suzzoni, J. F. A. Traniello, E. L. Vargo, P. Vogel and an anonymous referee for their very helpful comments, as well as Drs J. Abbey and D. Stone for improving the English. The study was supported by the Georgine Claraz Foundation, the Société Académique Vaudoise, and a grant of the University of Lausanne.

REFERENCES

Baroni-Urbani, C. 1968a. Monogyny in ant societies. *Zool. anz.*, **181**, 269–277.

Baroni-Urbani, C. 1968b. Dominance et monogynie fonctionnelle dans une société digynique de *Myrmecina graminicola* Latr. *Insectes Soc.*, **15**, 407–411.

Bartels, P. J. 1983. Polygyny and the reproductive biology of the Argentine ant. Ph.D. thesis, University of California.

Bartz, S. H. & Hölldobler, B. 1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera, Formicidae) and the evolution of foundress associations. *Behav. Ecol. Sociobiol.*, **10**, 137–147.

Benois, A. 1973. Incidences des facteurs écologiques sur le cycle annuel et l'activité saisonnière de la fourmi d'Argentine *Iridomyrmex humilis* (Mayr) (Hymenoptera, Formicidae), dans la région d'Antibes. *Insectes Soc.*, **20**, 267–296.

Brian, M. V. 1969. Male production in the ant *Myrmica rubra* L. *Insectes Soc.*, **4**, 177–190.

Brian, M. V. 1983. *Social Insects. Ecology and Behavioural Biology*. London: Chapman and Hall.

Buschinger, A. 1968. Mono- und Polygynie bei Arten der Gattung *Leptothorax* Mayr (Hymenoptera, Formicidae). *Insectes Soc.*, **15**, 217–226.

Buschinger, A. 1979. Functional monogyny in the American guest ant *Formicoxenus hirticornis* (Emery) (= *Leptothorax hirticornis*), (Hym. Form.) *Insectes Soc.*, **26**, 61–68.

Buschinger, A., Francoeur, A. & Fischer, K. 1980. Functional monogyny, sexual behavior and karyotype of the guest ant *Leptothorax provancheri* Emery. (Hym., Formicidae). *Psyche*, **87**, 1–12.

Buschinger, A. & Winter, U. 1976. Funktionnelle Monogynie bei der Gastameise *Formicoxenus nitidulus* (Nyl.) (Hym., Form.). *Insectes Soc.*, **23**, 549–558.

Coglitore, C. & Cammaerts, M.C. 1981. Etude du pouvoir agrégatif des reines de *Myrmica rubra* L. *Insectes Soc.*, **28**, 353–370.

Craig, R. & Crozier, R. H. 1979. Relatedness in the polygynous ant *Myrmecia pilosula*. *Evolution*, **33**, 335–341.

Crozier, R. H. 1979, Genetics of sociality. In: *Social Insects. Vol 1* (Ed. by H. R. Hermann), pp. 223–286. New York: Academic Press.

Crozier, R. H., P
Relatedness and
Rhytidoponera m
Behav. Ecol. Soci
Evesham, E. J. M.
and interactions
Myrmica rubra L
Fisher, R. A. 1930
Selection. Oxford
Fletcher, D. J. C., B
1980. Monogyny
sis invicta Buren.
Fletcher, D. J. C. &
reproduction in e
mol., **30**, 319–343
Haldane, J. B. S. 19
Longmans.
Hamilton, W. D. 19
behavior, I. *J. the*
Hamilton, W. D. 19
behavior, II. *J. th*
Hölldobler, B. & W
queens: an import
senschaften, **64**, 8–
Keller, L. & Cherix,
la polygynie chez
Ins. Soc., **2**, 263–2
Keller, L. & Passera
gynes of the Ar
(Mayr) in relation
ants (Hymenopter
Dev.
Lewontin, R. C. 1970
Syst., **1**, 1–18.
Lin, N. & Michener,
insects. *Q. Rev. Bi*
Markin, G. P. 1970
Argentine ant *Iri*
Formicidae), in sc
Soc. Am., **63**, 1238
Markin, G. P. 1970b
tory colonies of the
(Mayr). *Insectes S*
Mercier, B., Passera,
polygynie chez la
(Hym. Formicidae
condition expérime
349–362.
Michener, C. D. 1964
with colony size in
Soc., **11**, 317–341.
Newell, W. 1909. The
Econ. Entomol., **2**,
Newell, W. & Barbe
U.S.D.A. Bureau E
Oster, G. & Wilson,
Social Insects. Pr
University Press.
Pamilo, P. 1981. Gene
nea populations. *Be*
Pamilo, P. 1982. Gene
nous *Formica* ants.
Pamilo, P. & Rosengr

Crozier, R. H., Pamilo, P. & Crozier, V. C. 1984. Relatedness and microgeographic genetic variation in *Rhytidoponera mayri*, an Australian arid-zone ant. *Behav. Ecol. Sociobiol.*, **15**, 143–150.

Evesham, E. J. M. 1984. Queen distribution movements and interactions in a semi natural nest of the ant *Myrmica rubra* L. *Insectes Soc.*, **31**, 5–19.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

Fletcher, D. J. C., Blum, M. S., Whitt, T. V. & Tempel, N. 1980. Monogyny and polygyny in the fire ant *Solenopsis invicta* Buren. *Ann. Entomol. Soc. Am.*, **73**, 658–661.

Fletcher, D. J. C. & Ross, K. G. 1985. Regulation of reproduction in eusocial Hymenoptera. *A. Rev. Entomol.*, **30**, 319–343.

Haldane, J. B. S. 1932. *The Causes of Evolution.* London: Longmans.

Hamilton, W. D. 1964a. The genetical evolution of social behavior, I. *J. theor. Biol.*, **7**, 1–16.

Hamilton, W. D. 1964b. The genetical evolution of social behavior, II. *J. theor. Biol.*, **7**, 17–52.

Hölldobler, B. & Wilson, E. O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften*, **64**, 8–15.

Keller, L. & Cherix, D. 1985. Approche expérimentale de la polygynie chez la fourmi d'Argentine. *Actes Coll. Ins. Soc.*, **2**, 263–279.

Keller, L. & Passera, L. In press. Energy investment in gynes of the Argentine ant *Tridomyrmex humilis* (Mayr) in relation to the mode of colony founding in ants (Hymenoptera: Formicidae). *Int. J. Invert. Repr. Dev.*

Lewontin, R. C. 1970. The units of selection. *A. Rev. Ecol. Syst.*, **1**, 1–18.

Lin, N. & Michener, C. D. 1972. Evolution of sociality in insects. *Q. Rev. Biol.*, **47**, 131–159.

Markin, G. P. 1970a. The seasonal life cycle of the Argentine ant *Iridomyrmex humilis* (Hymenoptera, Formicidae), in southern California. *Ann. Entomol. Soc. Am.*, **63**, 1238–1242.

Markin, G. P. 1970b. Food distribution within laboratory colonies of the Argentine ant, *Iridomyrmex humilis* (Mayr). *Insectes Soc.*, **17**, 127–157.

Mercier, B., Passera, L. & Suzzoni, J. P. 1985. Etude de la polygynie chez la fourmi *Plagiolepis pygmaea* Latr. (Hym. Formicidae). I. La fécondité des reines en condition expérimentale polygyne. *Insectes Soc.*, **32**, 349–362.

Michener, C. D. 1964. Reproductive efficiency in relation with colony size in hymenopterous societies. *Insectes Soc.*, **11**, 317–341.

Newell, W. 1909. The life history of the Argentine ant. *J. Econ. Entomol.*, **2**, 174–192.

Newell, W. & Barber, T. C. 1913. The Argentine ant. *U.S.D.A. Bureau Entomol. Bull.*, **122**, 1–98.

Oster, G. & Wilson, E. O. 1978. *Caste Ecology in the Social Insects.* Princeton, New Jersey; Princeton University Press.

Pamilo, P. 1981. Genetic organization of *Formica sanguinea* populations. *Behav. Ecol. Sociobiol.*, **9**, 45–50.

Pamilo, P. 1982. Genetic populations structure in polygynous *Formica* ants. *Heredity*, **48**, 95–106.

Pamilo, P. & Rosengren, R. 1984. Evolution of nesting strategies of ants: genetic evidence from different population types of *Formica* ants. *Biol. J. Linn. Soc.*, **21**, 331–348.

Pamilo, P. & Varvio-Aho, S. L. 1979. Genetic structure of nests in the ant *Formica sanguinea*. *Behav. Ecol. Sociobiol.*, **6**, 91–98.

Passera, L. 1969. Interaction et fécondité des reines de *Plagiolepis pygmaea* et de ses parasites sociaux *P. grassei* et *P. xene* (Hym. Formicidae). *Insectes Soc.*, **16**, 179–194.

Passera, L., Keller, L. & Suzzoni, J. P. In press. The control of the brood male differentiation in the Argentine ant *Iridomyrmex humilis* (Mayr). *Insectes Soc.*

Pearson, B. 1982. Relatedness of normal queens (macrogynes) in nests of the polygynous ant *Myrmica rubra* L. *Evolution*, **36**, 107–112.

Pearson, B. 1983. Intra-colonial relatedness amongst workers in a population of nests of the polygynous ant, *Myrmica rubra* Latr. *Behav. Ecol. Sociobiol.*, **12**, 1–4.

Roisin, Y. & Pasteels, J. M. 1985. Polymorphism and polygyny in the Neo-Guinean termite *Nasutitermes princeps* Desneux. Insectes Soc., **32**, 142–157.

Ross, K. G. & Fletcher, D. J. C. 1985. Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, **117**, 349–356.

Starr, C. K. 1979. Origin and evolution of insect sociality: a review of modern theory. In: *Social Insects. Vol. 1* (Ed. by H. R. Hermann), pp. 35–80. New York: Academic Press.

Sturtevant, A. H. 1938. Essays on evolution. II. On the effects of selection on social insects. *Q. Rev. Biol.*, **13**, 74–76.

Tschinkel, W. R. & Howard, D. F. 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.*, **3**, 297–310.

Ward, P. S. 1983. Genetic relatedness and colony organization in a species complex of Ponerine ants. II. Patterns of sex ratio investment. *Behav. Ecol. Sociobiol.*, **12**, 301–307.

West-Eberhard, M. J. 1981. Intragroup selection and the evolution of insect societies. In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 3–17. New York: Chiron Press.

Wheeler, D. E. 1984. Behavior of the ant, *Procryptocerus scabriusculus* (Hymenoptera: Formicidae) with comparison to other Cephalotines. *Psyche*, **91**, 171–192.

Wilson, E. O. 1966. Behaviour of social insects. *Symp. Roy. Entomol. Soc., Lond.*, **3**, 81–96.

Wilson, E. O. 1971. *The Insect Societies.* Cambridge, Massachusetts: Harvard University Press.

Wilson, E. O. 1974a Aversive behavior and competition with colonies of the ant *Leptothorax curvispinosus*. *Ann. Entomol. Soc. Am.*, **67**, 777–780.

Wilson, E. O. 1974b. The population consequences of polygyny in the ant *Leptothorax curvispinosus*. *Ann. Entomol. Soc. Am.*, **67**, 781–786.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics*, **16**, 77–158.

(Received 5 December 1986; revised 18 February 1987; MS. number: 2941)