

This article was downloaded by: [62.72.90.110]

On: 04 October 2013, At: 08:31

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Bolletino di zoologia

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/tizo19>

Mating and post-mating behaviour of the European amazon ant, *Polyergus rufescens* (Hymenoptera, Formicidae)

Alessandra Mori^a, Patrizia D'ettorre^a & Francesco Le Moli^a

^a Dipartimento di Biologia e Fisiologia Generali, Università degli Studi, viale delle Scienze, Parma, I-43100, Italy

Published online: 28 Jan 2009.

To cite this article: Alessandra Mori, Patrizia D'ettorre & Francesco Le Moli (1994) Mating and post-mating behaviour of the European amazon ant, *Polyergus rufescens* (Hymenoptera, Formicidae), *Bolletino di zoologia*, 61:3, 203-206, DOI: [10.1080/11250009409355886](https://doi.org/10.1080/11250009409355886)

To link to this article: <http://dx.doi.org/10.1080/11250009409355886>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>



Mating and post-mating behaviour of the European amazon ant, *Polyergus rufescens* (Hymenoptera, Formicidae)

ALESSANDRA MORI
PATRIZIA D'ETTORRE
FRANCESCO LE MOLI

Dipartimento di Biologia e Fisiologia Generali, Università degli Studi, viale delle Scienze, I-43100 Parma (Italy)

ABSTRACT

The mating and post-mating behaviour of reproductives belonging to three sympatric dulotic colonies of the obligatory slave-making ant *Polyergus rufescens* Latr. (the «Amazon») were analysed in the field near Parma (Italy) every day during the summer of 1992. Forty-two nuptial flights (of males, females, or both) were recorded, generally in sunny and hot early afternoons. Our observations show that the European amazon ant adopts a reproductive behaviour (similar to the «female calling syndrome») more diverse than that performed by the two American congeneric species. The results indicate that *P. rufescens* females (*f*) mate on the ground around their natal nest, or (*ii*) return to a dulotic colony after mating flights and wait for a raid, or (*iii*) mate directly during a raid. Because of the non-independent mode of colony foundation typical of the obligatory slave-makers, the following of a slave-raid swarm by newly inseminated young queens is considered an advantageous strategy to locate and invade host nests and to establish a new dulotic colony.

KEY WORDS: Ants - Slave-makers - *Polyergus rufescens* - Mating behaviour - Host colony location.

ACKNOWLEDGEMENTS

This research has been supported by grants from the Ministero dell'Università e della Ricerca Scientifica e Tecnologica (MURST 40% and 60% funds).

(Received 21 January 1994 - Accepted 16 March 1994)

INTRODUCTION

Although mating behaviour varies greatly among ant species, two broad classes can be recognized: the «male-aggregation syndrome» and the «female-calling syndrome» (Hölldobler & Bartz, 1985).

In the first case, males from many colonies gather at specific mating sites and produce sex-attractant pheromones simultaneously. In order to mate, females fly into the swarms, even from great distances. Multiple insemination is common in this strategy, typical of species that form large colonies and produce hundreds to thousands of reproductives every year, as in the case of *Pogonomyrmex* and *Camponotus* (Hölldobler & Bartz, 1985).

In the second kind of syndrome, females do not disperse widely, but tend to remain near their natal nest and release sex pheromones to attract the males. The colonies of female-calling species produce relatively few reproductives in a year and nuptial flights are inconspicuous and not well synchronized between the sexes (Buschinger, 1975). This strategy is typical of several phylogenetically primitive species (Hölldobler & Haskins, 1977; Haskins, 1978) and some socially parasitic and myrmecophilous myrmicine genera such as *Doronomyrmex*, *Harpagoxenus*, *Leptothorax* and *Formicoxenus* (Buschinger, 1968, 1971, 1975; Buschinger & Alloway, 1979).

More recently, the female-calling behaviour has also been described for the formicine ant *Polyergus breviceps* Emery (Topoff & Greenberg, 1988). Ants of the genus *Polyergus* (the so-called Amazon ants) are all obligatory slave-makers, which periodically organize group raids against colonies of the related genus *Formica* to sack the resident brood. A significant part of the plundered brood is reared to eclosion and is integrated into the working force of the dulotic colony (Buschinger *et al.*, 1980; Le Moli, 1980; Hölldobler & Wilson, 1990; Mori *et al.*, 1991).

Since *Polyergus* workers are specialized in raiding, they have lost the ability to perform the normal domestic tasks, and slaves are essential to maintain the colony (Sakagami & Hayashida, 1962; Mori & Le Moli, 1988). The presence of slaves is also necessary at the moment of colony founding. In fact, a *Polyergus* newly-mated female is not capable of rearing her own first brood. Therefore, before laying her eggs, she must penetrate a *Formica* colony, kill the resident queen(s), become accepted by the resident workers, which later will assist her in rearing the parasitic offspring, and appropriate the resident brood (Stitz, 1939; Topoff *et al.*, 1988; Topoff 1990a, b; Topoff & Zimmerli, 1993).

Since the first step for successful colony foundation is finding a host colony to invade, the mating and post-mating behaviour of *Polyergus* females include several adaptations for locating colonies of *Formica*. In *P. lucidus* Mayr, mating flights of both sexes occur but, after the mating, dealate females seek out a *Polyergus* colony (not

necessarily their own) in order to follow a slave-raid swarm that will lead them to a target *Formica* colony (Talbot, 1968; Marlin, 1971; Kwait & Topoff, 1984). In the other American amazon species, *P. breviceps*, most winged females do not engage in mating flights but copulate directly during a raid of their homocolonial workers. The females stop running and attract males with pheromones produced by mandibular glands. After mating, they shed their wings and continue with the swarm (Topoff & Greenberg, 1988).

At present, little is known about the reproductive biology of the European amazon ant, *Polyergus rufescens* Latr., except for some occasional observations concerning the occurrence of mating flights and the presence of females in the raiding swarms of this species (Emery, 1908, 1909, 1911; Czechowski, 1975; Mori *et al.*, 1991). In this paper, we present the results of a field study on the mating and post-mating behaviour of *P. rufescens*, paying particular attention to the behaviour and the fate of females.

FIELD CONDITIONS AND METHODS

This research was conducted during the summer of 1992. The area of study was a forage field located in the Apennines in the Province of Parma (northern Italy) at an altitude of about 700 m.

Three colonies of *P. rufescens* (named P1, P4 and P5) were monitored every day in July and August continuously from 11 a.m. to 7 p.m., but observations were also made randomly early in the morning. These colonies were populated by *F. cunicularia* Latr. workers as slaves. Colony P1 was situated at the edge of the field and was sheltered by a wooded area in its northern limit. Colony P4 was situated about 80 m from P1 with a wooded area in its western border. Colony P5 was situated in an open area approximately 75 m from P4 and 90 m from P1.

During the period of study, air (AT) and soil (ST) temperature, and relative humidity (RH) were recorded near each colony at the beginning of mating flights. In order to follow the post-mating activity of queens, a considerable number (about one hundred) of winged females from colony P1 was marked with a dot of enamel paint on the thorax, using a different colour each day.

RESULTS

In the area of study the alates were active in July and August, but the period of activity varied considerably from colony to colony. At colony P1, the activity of reproductives began on July 13 when some males shyly emerged from the nest and retracted suddenly. On three days (from July 15 to 17) only flights of males were recorded. The first females emerged from the nest on July 16 and began launching into flight on July 18. Reproductives were seen for the last time at colony P1 on July 28, but this colony was attacked by colony P4 on July 26. This intraspecific raid was characterized by fierce fights involving *Polyergus* intruders and both slave and slave-making residents. The result of the battle was the elimination of colony P1 in a few days (cf. Le Moli *et al.*, 1993). At colony P4, alate activity began on July 21 when

a few males were seen emerging from the nest and flying off. The first winged females appeared at the nest entrances on July 25, but they began to fly only on July 27. Compared to colony P1, colony P4 produced fewer males and these had disappeared after August 5, while females were active until August 8. At colony P5, mainly females were produced. The first were observed emerging from the nest on July 28, but mating flights began on July 30. Male flights occurred only on four successive days from July 31, and the number of males was very small (a total of about 20 individuals). The activity of reproductives of this colony stopped on August 28.

In the three colonies studied, a total of 42 nuptial flights were observed. Of these, 6 (14%) involved only males (3 in P1, 2 in P4, and 1 in P5); 19 (45%) involved only females (1 in P1, 3 in P4, and 15 in P5); 17 (41%) involved males and females together (7 in P1, 7 in P4, and 3 in P5). Almost all flights took place on sunny, hot and clear days (80%), but also on cloudy days (20%) mating flights occurred. The average values (with SD) of AT, ST and RH recorded at the beginning of mating flights were: $31.2^\circ \pm 1.3^\circ$ C, $32^\circ \pm 1.9^\circ$ C and $71.7 \pm 4.6\%$ for colony P1; $31.5^\circ \pm 2.8^\circ$ C, $31.8^\circ \pm 1.5^\circ$ C and $75 \pm 7.5\%$ for colony P4; $30.1^\circ \pm 2.8^\circ$ C, $28.2^\circ \pm 2.4^\circ$ C and $74 \pm 6.5\%$ for colony P5.

Typically, the activity of the winged forms began around midday when only slaves were present outside the nest. At first, the heads of some males could be seen peering from the nest entrance and gradually the males came out and began milling around the nest. Slaves often interacted with these males and tried to drag them back into the nest. In a few minutes the activity increased and the males began climbing grass blades where they tested their wings and flew off individually. Alate females appeared later than males. They came out singly, began walking around the nest area and climbing up and down grasses sometimes standing for a long time on a grass tip. Some of them launched into flight, but often the first attempt was not successful so they had to try again.

Times of starting and stopping flights varied from colony to colony. The average daylight hour (with SD in min) of initial swarming respectively for males and females was 13.12 ± 14 and 13.53 ± 22 at colony P1; 12.39 ± 21 and 12.54 ± 25 at colony P4; 13.05 ± 16 and 13.19 ± 21 at colony P5. The average daylight hour of final swarming was 14.30 ± 15 and 14.47 ± 39 at colony P1; 13.25 ± 14 and 13.42 ± 14 at colony P4; 13.35 ± 9 and 14.02 ± 30 at colony P5.

A considerable portion of alate females emerged during the period of mating flights but did not fly off. They remained in the surroundings of the dulotic nest and copulated on the ground. Probably winged females attracted males by releasing a sexual pheromone produced by the mandibular glands as in the case of *P. breviceps* (Topoff & Greenberg, 1988). In fact, we observed that after a female began opening and closing her mandibles, a male arrived making erratic movements until he succeeded in copulating. Sometimes, more than one male could ap-

proach simultaneously the same female and generally the male which copulated was the first one to arrive, though he could be disturbed by unsuccessful suitors. As a rule, multiple mating did not occur; only one female was seen copulating with eight males in rapid succession.

A total of 336 females were observed flying from the colonies, and 52 copulating on the ground near the nest. In fact, at colony P1, 94 females flew off while 38 mated on the ground; at colony P4, 127 females were seen taking part in mating flights while only three were seen copulating near the nest; finally, at colony P5, 115 females flew off and 11 mated near the dulotic nest. The average duration of copulation was 49 s (ranging from 10 to 180 s). After mating, females shed their wings in an average time of 6 min (ranging from 1 to 60 min) and then hid in the vegetation surrounding the nest. Several alate females did not come out of the nest at the time of mating flights, but emerged later, with *Polyergus* workers which were engaged in the raiding activity, and participated in the raid. In fact, a total of 156 alate females were seen during 32 slave-raids ($\bar{n} = 5$, ranging from 1 to 15). Moreover, 19 of these females copulated during a raid as recorded for *P. breviceps* (Topoff & Greenberg, 1988). Alate females would either enter the target colonies (6.4%) or return to the dulotic nest (25.6%) before the inbound column. It is worth noting that four alate females participated in the pillage of the host brood during a multiple raid, since in the inbound column they were seen carrying a *Formica* cocoon. This is the first report of brood capture during a raid by *Polyergus* alate females.

Since many females were marked before mating, it was possible to record their post-mating behaviour. After mating flights, some dealate females were observed following the route of previous raids, probably relying on the chemical trail laid down by raiders (cf. Mori *et al.*, 1991) and reaching a *Polyergus* colony, not necessarily their own, as described also for *P. lucidus* (see: Marlin, 1971; Kwait & Topoff, 1984). There they wandered around with females that copulated near the dulotic colony. Dealate females were seen approaching the nest cautiously and trying to enter it. They were always treated with hostility by all the slaves and the slave-makers they met and were driven away in a short time (see: Mori *et al.*, 1991). Probably they were waiting for a raid, since they would remain in the nest surroundings up to six days.

A total of 76 dealate females were seen participating in 28 raids ($\bar{n} = 3$, ranging from 1 to 12). Once at the target nest, 22 (29%) of these dealate females were seen penetrating the attacked colony during 10 raids, whereas another portion (35.5%) was seen returning to the surroundings of the dulotic colony with the inbound column. Therefore, it was likely that more than one dealate female could enter simultaneously the same target colony. In fact, up to six females were observed entering the same target nest but none of them was seen re-emerging from it.

DISCUSSION

An interesting feature of the reproductive biology of *P. rufescens* is the variation of relative abundance of sexual forms from colony to colony. In fact, in the area of study both colonies producing males and females (P1) and colonies producing almost exclusively females (P5) were present. These data are consistent with those on the American species *P. lucidus*, for which colonies bearing only males were also described (Marlin, 1971). The strategy of producing mostly males or females is likely to occur in some species of the genus *Formica*, whose colonies tend to have a strongly biased sex-ratio or, if a nest produces both sexes, they often emerge at different times of the season. In both cases, inbreeding is effectively prevented (cf. Pamilo *et al.*, 1978; Pamilo & Rosengren, 1983).

Our observations show that, in colonies producing both sexes, the males emerge and fly off some days before females. Moreover, when nuptial flights involving males and females occur, although the timing of the take-off overlaps between the two sexes, the males fly from the nest first. Hence, the mating flight activities are not well synchronized within the colony. It was also recorded that reproductives were active within colonies in different periods of the season, and differences in the timing of the reproductives' activity were also recorded among colonies.

On 71 occasions (52 on the ground near the nest and 19 during slave raids) it was possible to record the behaviour of females just before mating. Their mandibular movements are likely connected with the releasing of a sexual attractant pheromone, as occurs in *P. breviceps* (Topoff & Greenberg, 1988). Moreover, since multiple mating was hardly ever seen, *P. rufescens* reproductive behaviour could be considered similar to the «female calling syndrome» (Hölldobler & Bartz, 1985).

The behaviour of *P. rufescens* alate females appears to be more variable than that of the American congeneric species. In fact, *P. lucidus* females copulate mostly after mating flights (Talbot, 1968; Marlin, 1971), while *P. breviceps* females typically copulate almost always only during slave-raids (Topoff & Greenberg, 1988). By contrast, *P. rufescens* females adopt a more diverse strategy, since they copulate after mating flights, during slave raids and, in addition, on the ground close to their nest. Our observations suggest that, whatever mating strategy is adopted by *P. rufescens* females, they may take part in slave-raids. In fact, because of their parasitic mode of colony founding, *Polyergus* females must locate and invade a *Formica* nest. Following a slave-raid swarm by newly-mated young queens is an advantageous strategy to penetrate host nests and to establish a new colony. The invasion and subsequent usurpation of the host colony may be facilitated by the panic and disorganization produced by raiding swarms (Talbot, 1968; Topoff & Greenberg, 1988). Since more than one

fertilized female participates in slave-raids and penetrates simultaneously the same target colony, pleometrosis could occur. In this case, an interesting question regards how initial pleometrosis results in the monogyny typical of the slave-making ant species.

REFERENCES

- Buschinger A., 1968 - «Locksterzeln» begattungsbereiter ergatoider Weibchen von *Harpagoxenus sublaevis* Nyl. (Hymenoptera: Formicidae). *Experientia*, 24: 297.
- Buschinger A., 1971 - «Locksterzeln» und Kopula der sozialparasitischen Ameise *Leptothorax kutteri* Buschinger (Hym. Form.). *Zool. Anz.*, 186: 242-248.
- Buschinger A., 1975 - Sexual pheromones in ants. International Union for the Study of Social Insects, Symposium on Pheromones and Defensive Secretions in Social Insects. Imprimerie Univ. Dijon, pp. 225-233.
- Buschinger A., Alloway T. M., 1979 - Sexual behaviour in the slave-making ant, *Harpagoxenus canadensis* M. R. Smith, and sexual pheromone experiments with *H. canadensis*, *H. americanus* (Emery), and *H. sublaevis* (Nylander) (Hymenoptera, Formicidae). *Z. Tierpsychol.*, 49: 113-119.
- Buschinger A., Ehrhardt W., Winter U., 1980 - The organization of slave raids in dulotic ants - a comparative study (Hymenoptera; Formicidae). *Z. Tierpsychol.*, 53: 245-264.
- Czechowski W., 1975 - Mixed polycalic colony of *Formica (Serviformica) cinerea* Mayr and *Polyergus rufescens* Latr. (Hymenoptera, Formicidae). *Ann. zool.*, 33: 67-76.
- Emery C., 1908 - Osservazioni ed esperimenti sulla formica amazzone. *Rend. Sess. R. Accad. Sci. Ist. Bologna*, 12: 49-62.
- Emery C., 1909 - Nuove osservazioni ed esperimenti sulla formica amazzone. *Rend. Sess. R. Accad. Sci. Ist. Bologna*, 13: 31-36.
- Emery C., 1911 - Ulteriori osservazioni ed esperienze sulla formica amazzone. *Rend. Sess. R. Accad. Sci. Ist. Bologna*, 15: 60-75.
- Haskins C. P., 1978 - Sexual calling behavior in highly primitive ants. *Psyche*, 85: 407-415.
- Hölldobler B., Bartz S. H., 1985 - Sociobiology of reproduction in ants. In: B. Hölldobler & M. Lindauer (eds), *Experimental behavioral ecology and sociobiology*. G. Fisher Verlag, Stuttgart, New York, pp. 237-257.
- Hölldobler B., Haskins C. P., 1977 - Sexual calling in a primitive ant. *Science*, 195: 793-794.
- Hölldobler B., Wilson E. O., 1990 - *The ants*. Springer-Verlag, Berlin, Heidelberg, 732 pp.
- Kwait E. C., Topoff H., 1984 - Raid organization and behavioral development in the slave-making ant *Polyergus lucidus* Mayr. *Insectes Soc.*, 31: 361-374.
- Le Moli F., 1980 - On the origin of slaves in dulotic ant societies. *Boll. Zool.*, 47: 207-212.
- Le Moli F., Grasso D. A., D'Ettoire P., Mori A., 1993 - Intraspecific slavery in *Polyergus rufescens* Latr. (Hymenoptera, Formicidae): field and laboratory observations. *Insectes Soc.*, 40: 433-437.
- Marlin J. C., 1971 - The mating, nesting and ant enemies of *Polyergus lucidus* Mayr (Hymenoptera: Formicidae). *Am. Midl. Nat.*, 86: 181-189.
- Mori A., Grasso D. A., Le Moli F., 1991 - Eco-ethological study on raiding behaviour of the European amazon ant, *Polyergus rufescens* Latr. (Hymenoptera: Formicidae). *Ethology*, 88: 46-62.
- Mori A., Le Moli F., 1988 - Behavioural plasticity and domestic degeneration in facultative and obligatory slave-making ant species (Hymenoptera Formicidae). *Monit. zool. ital. (N. S.)*, 22: 271-285.
- Pamilo P., Rosengren R., 1983 - Sex ratio strategies in *Formica* ants. *Oikos*, 40: 24-35.
- Pamilo P., Rosengren R., Vepsäläinen K., Varvio-Aho S., Pisarski B., 1978 - Population genetics of *Formica* ants. I. Patterns of enzyme gene variation. *Hereditas*, 89: 233-248.
- Sakagami S. F., Hayashida K., 1962 - Work efficiency in heterospecific ant groups composed of hosts and their labour parasites. *Anim. Behav.*, 10: 96-104.
- Stitz H., 1939 - Ameisen oder Formicidae. In: F. Dahl (ed.), *Die Tierwelt Deutschlands*. 37. Teil. G. Fisher Verlag, Jena.
- Talbot M., 1968 - Flights of the ant *Polyergus lucidus* Mayr. *Psyche*, 75: 46-52.
- Topoff H., 1990a - Slave-making ants. *Am. Sci.*, 78: 520-528.
- Topoff H., 1990b - The evolution of slave-making behavior in the parasitic ant genus *Polyergus*. *Ethol. Ecol. Evol.*, 2: 284-287.
- Topoff H., Cover S., Greenberg L., Goodloe L., Sherman P., 1988 - Colony founding by queens of the obligatory slave-making ant, *Polyergus breviceps*: the role of the Dufour's gland. *Ethology*, 78: 209-218.
- Topoff H., Greenberg L., 1988 - Mating behavior of the socially parasitic ant, *Polyergus breviceps*: the role of the mandibular glands. *Psyche*, 95: 81-87.
- Topoff H., Zimmerli E., 1993 - Colony takeover by a socially parasitic ant, *Polyergus breviceps*: the role of chemicals obtained during host-queen killing. *Anim. Behav.*, 46: 479-486.