

## Attraction of the sexes in *Formica lugubris* Zett (Hymenoptera: Formicidae)

D. Cherix<sup>1</sup>, D. J. C. Fletcher<sup>2</sup>, D. Chautems<sup>1</sup>, W. Fortelius<sup>3</sup>, G. Gris<sup>1</sup>, L. Keller<sup>1,4</sup>,  
R. Rosengren<sup>3</sup>, E. L. Vargo<sup>5</sup> and F. Walter<sup>6</sup>

<sup>1</sup> Museum of Zoology, Palais de Rumine, P.O. Box 448, 1000 Lausanne 17, Switzerland

<sup>2</sup> Department of Biology, Bucknell University, Lewisburg, Pennsylvania, USA

<sup>3</sup> Institute of Zoology, University of Helsinki, Helsinki, Finland

<sup>4</sup> Museum of Comparative Zoology, Harvard, Massachusetts, USA

<sup>5</sup> Department of Zoology, University of Texas, Austin, USA

<sup>6</sup> Institute of Organic Chemistry, University of Hamburg, Hamburg, Germany

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### Summary

Sexuals of *Formica lugubris* fly to mating places, where females attract males by using a sex pheromone. Females collected on the nest surface before departing on a mating flight are much less attractive than those collected on the mating place after the mating flight, suggesting that the mating flight triggers the release of the sex pheromone. Olfactory cues are essential for males to locate females while they patrol. Males probably use visual cues to locate females once they have alighted nearby them. Males are also attracted by aggregations of other males on the ground, probably because one or several females are likely to be close to male aggregations.

### Introduction

Mating flight plays a major role in reproduction and dispersal of most social insect species. Mating flights (or nuptial flights) have been described for many species of eusocial Hymenoptera. In honey bees (*Apis mellifera* L.) virgin queens fly to places where males congregate in order to mate (Ruttner, 1962), and they mate with a number of males in succession. In contrast males of stingless bees (Meliponini) swarm around the entrance of a nest containing a virgin queen before she departs on the mating flight, and she mates with only one male. In both cases mating occurs on the wing. In bumblebees on the other hand, the mating flight is curtailed; queens mate on the ground close to the nest in which they were reared (Michener, 1974).

Among ants, mating swarms, in which numerous males and females participate simultaneously, have been described for various species, for example, *Formica rufa* (Marikovski, 1961), *Leptothorax longispinosus* and a *Myrmica* species (Leprince and

Francoeur, 1986), as well as several species in the genera *Myrmica*, *Leptothorax* and *Formica* (Woyciechowski, 1990). However, not all ant species mate in large swarms. In his classic paper, Kannovski (1963) described the flight activities of Formicine ants. He divided the typical sequence of activities relating to flight in this subfamily into 13 different phases ranging from preparation of the nest for the emergence of sexuals, through pairing to egg laying by the newly mated queen and, based on this sequence, he discerned a number of different kinds of mating flights.

During our long-term study of the reproductive strategies of red wood ants (see Cherix et al., 1991) we have demonstrated that males and females of *Formica lugubris* meet at mating places, where males patrol on the wing apparently searching for newly arrived females. At these mating places, females attract males by releasing a sex pheromone, the components of which (undecane, tridecane, and Z-4-tridecene) have recently been identified (Walter et al., 1993). In order to gain a better understanding of the attractiveness of females, we have investigated the possibility that cues other than a sex pheromone may be involved.

## Material and methods

We placed 20 sexuals (males or females) in plastic cages ( $10 \times 10 \times 6.5$  cm deep) having a wire mesh screen on two sides and on top. In some experiments, these screens were covered with a second screen that eliminated all visual cues but still permitted the passage of olfactory cues. To measure the attractiveness of sexuals held in these cages (20 per cage in each case), we counted the number of individuals landing in an area ( $50 \times 50$  cm) demarcated by plastic-coated wire with a cage at the center. Pairwise comparisons were made with controls consisting of an empty cage in a separate square. For each comparison, counts were terminated as soon as 10 individuals had landed in one of the squares and the time that had elapsed was recorded. Each type of comparison was repeated 10 times and t-tests were employed to test whether there was a statistically significant difference in the mean numbers of males that had landed per unit time. The comparisons were made at two mating places within a supercolony of *F. lugubris* in the Swiss Jura mountains during the mating flights of June, 1989 and 1990.

## Results

### 1. Attractiveness of males to other males

Two types of comparisons were made: (1) boxes with males versus empty boxes (control); (2) boxes with males versus boxes with females collected on the surfaces of nests during pre-flight activity.

Males are significantly attracted by other males at mating places, but males are not as attractive as females which, under the conditions of our experiment, attracted more than twice as many males per unit time (Tab. 1).

**Table 1.** Attractiveness of caged males versus controls (empty boxes) and of caged males versus caged females. See text for details of methods

	No. of landings	Time (min)	t	df	p
Males	8.5 ± 2.3	9.4 ± 5.7	6.63	18	<0.001
Controls	2.8 ± 1.6				
Males	4.5 ± 3.1	5.2 ± 3.7	5.48	18	<0.001
Females	9.9 ± 0.3				

**Table 2.** Attractiveness of caged females from different sources versus controls (empty boxes) and versus each other. See text for details of methods

Source of females	No. of landings	Time (min)	t	df	p
Nest surface	9.1 ± 1.9	4.5 ± 3.7	4.03	18	<0.001
Controls	3.6 ± 4.1				
Mating place	10.0 ± 0.0	2.9 ± 2.0	25.3	18	<0.001
Controls	1.4 ± 1.1				
Mating place	10.0 ± 0.0	3.0 ± 2.3	15.2	18	<0.001
Nest surface	2.2 ± 1.6				

## 2. Attractiveness of females to females

Here, three types of comparisons were made: (1) cages with females collected from a nest surface during pre-flight activity versus empty boxes (controls); (2) cages with females collected at the mating place versus empty boxes (controls); (3) boxes with females collected from a nest during pre-flight activity versus boxes with females collected at the mating place. Both females collected from the nest surface and those that had flown to a mating place were attractive to males. However, females collected on the mating place were much more attractive than those that had not yet flown (Tab. 2).

## 3. Olfactory and visual cues

As described previously (Cherix et al., 1991), males display a patrolling behavior (see also Kannonvski and Johnson, 1969). When they detect a female, they do not fly directly to her, but alight nearby and walk to her. This lead us to suppose that visual cues may be of minor importance, at least at a distance. To test this hypothesis, we used small airtight transparent plastic boxes. When a female was surrounded by males, we captured her with as little disturbance as possible to the males and placed her in the plastic box next to the males. Under these circumstances all the males flew off in from 30 to 60 seconds even though they could presumably still see the queen. This experiment was repeated 5 times with similar results.

As an additional experiment, males and females were caged in boxes with a double layers of wire mesh (i.e., it is impossible to see through, but it permits the

**Table 3.** Attractiveness of caged males and females from the mating place to flying males in the absence of visual cues. See text for details of methods

	No. of landings	Time (min)	t	df	p
Males	8.6±3.1	8.0±1.9	1.95	8	NS
Controls	4.4±3.2				
Females	10.0±0.0	1.6±0.8	00	18	< 0.001
Controls	0.0±0.0				

passage of olfactory cues). Cages with males were not significantly more attractive than control cages, whereas cages with females were significantly more attractive than control cages (Tab. 3).

## Discussion

The results are in general agreement with the hypothesis that after arriving at a mating place females attract males via an olfactory cue, with visual cues being of minor, or no, importance, at least up to the time males alight close to a female.

Another important point is that females collected on the nest surface before they had flown were much less attractive to males at the mating places than were females that had already flown to the mating places. A similar phenomenon was reported by Kannovski and Johnson (1963) for *F. ulkei*. This suggests that flight triggers the production of the sex pheromone of *F. lugubris* and possibly *F. ulkei*. In all probability, this mechanism, in the case of *F. lugubris* at least, is the simple, but controlled, release of undecane and other components of the sex pheromone from the Dufour's gland of the female.

When visual cues were eliminated in experiment 3, there was no statistically significant difference in the attractiveness of caged males and the controls as there had been in experiment 1, in which visual cues were present. This suggests that some kind of visual cue may be involved in the aggregation of males at a mating place, as has been demonstrated, for example, in the formation of drone congregation areas in honey bees, *Apis mellifera* (Zmarlicki and Morse, 1963; Ruttner, 1966). Males possibly use high density of males on the ground as a sign that a female might be close or in the middle of the male aggregation.

Finally, Hölldobler and Bartz (1985) described two broad classes, or syndromes, of mating flights among ants: (i) the female-calling syndrome, characteristic of phylogenetically primitive species, in which females remain fairly close to the nest and release pheromones that attract males to them; and (ii) the male-aggregation syndrome, in which males from many colonies gather at specific mating sites. Females then visit these sites and mating occurs. Since these are broad categories, there are many variations on the two themes. One variation of the male-aggregation syndrome is cited by Hölldobler and Wilson (1990) and concerns the mating flights of *Formica obscuripes*. Talbot (1972) observed that males and females fly to "swarming

grounds". There the males fly back and forth in search of females, which alight on low vegetation and signal their presence to the males by means of pheromones.

The behavior of *F. lugubris* resembles this variation, but differs from it in the following respects: 1) The aggregations of males are loose in that they are often well spread out and they persist for many days, or even for two to three weeks, if weather conditions are favorable. 2) Males patrol close to the ground, usually not more than 30 cm above it and often less. 3) Females mate on the ground, and whereas some fly off after mating, others shed their wings and walk away from the mating place (D. Cherix, D. Chautems and L. Keller unpublished).

Although *F. lugubris* is by no means a phylogenetically primitive ant, with regard to the pheromonal attraction of males by females at mating sites not very far from their nests, the mating behavior of this species could be classified under the female-calling syndrome of Hölldobler and Bartz (loc. cit.), but with respect to the loose congregation of males at specific mating sites it could equally well be classified under the male-aggregation syndrome. Thus, the intermediate behavior of the species suggests that the two mating syndromes may represent the extremes of a behavioral spectrum rather than two discrete kinds of behavior.

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