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Alternative reproductive strategies
in *Formica lugubris* Zett. (Hymenoptera Formicidae) *

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A long term study on the reproductive strategies of *Formica lugubris* (*Formica rufa* group) has revealed many new important facts. Within a supercolony the sex-ratio is strongly female biased. Some of the sexuals mate on the nest surface, whereas others fly from the nest. Those sexuals participating in flights aggregate in particular meadow sites (mating places). On these places females attract males by releasing a sex pheromone.

KEY WORDS: reproductive strategy, *Formica lugubris*, ants, sex-ratio, sex pheromone, polygyny.

Colony reproduction in most ant species takes place through a mating and dispersal flight followed by initiation of a new colony by a mated female foundress. Polygynous species like *Formica lugubris* have the alternative option of founding new daughter nests by budding or splitting of the mother colony. The latter strategy may be linked to limited dispersal of sexuals and leads to the formation of a polydomous or super-colony consisting of a number of interconnected nests. Adoption of the budding strategy need not mean however, that the species abandons mating flights or dispersal, since a single species may exhibit one or more alternative mating strategies (Thornhill & Alcock 1983).
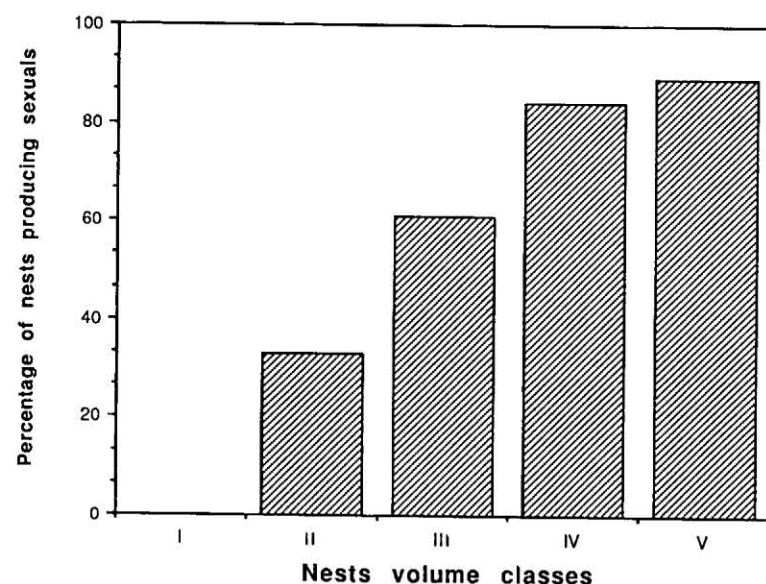
Fig. 1. — Proportion of nests of different size classes (modified from TOROSSIAN 1979) producing sexuals in 1988.

Our study addresses the relationship between different modes of colony founding and alternative mating and dispersal strategies among individual sexuals of *F. lugubris*. We have also investigated the genetic subdivision to behavioural parameters such as brood recognition, aggression between workers, acceptance and killing of young queens and cooperation between neighbour nests of a super-colony.

Most of our investigations were counducted in the Swiss Jura Mountains where *Formica lugubris* is abundant (CHERIX & BURGAT 1979). Above an altitude of 1200 m it forms polygynous and polydomous colonies (GRIS & CHERIX 1977). Our studies have mainly concerned one super-colony consisting of about 1200 interconnected nests occupying an area of 70 ha. This super-colony is located on the north-western slope of the Jura at an elevation of 1400 m (see CHERIX 1980). Due to the hard climatic conditions of this area (yearly mean temperature about 4 °C) the activity of ants outside their nest is restricted to 150 days a year.

Production of sexuals and sex-ratio. The sunbath period normally begins at the end of April for the most exposed nests, but may last for most of the month of May. The first sexual pupae appear at the middle of May and the first alates at the beginning of June. Alate males are generally present in the nest before alate females, but both sexes can be found up to the end of June. Over a 2-year period we sampled about 180 nests of the super-colony to get an idea of the proportion of nests producing sexuals in relation to their size and highest internal temperature. There is a strong tendency for bigger nests to have higher temperatures than smaller ones but this correlation was not significant. We observed that the proportion of nests producing sexuals is partly related to their size (Fig. 1). Moreover this proportion.was high, ranging from 33 to 89% depending on the sampled area.
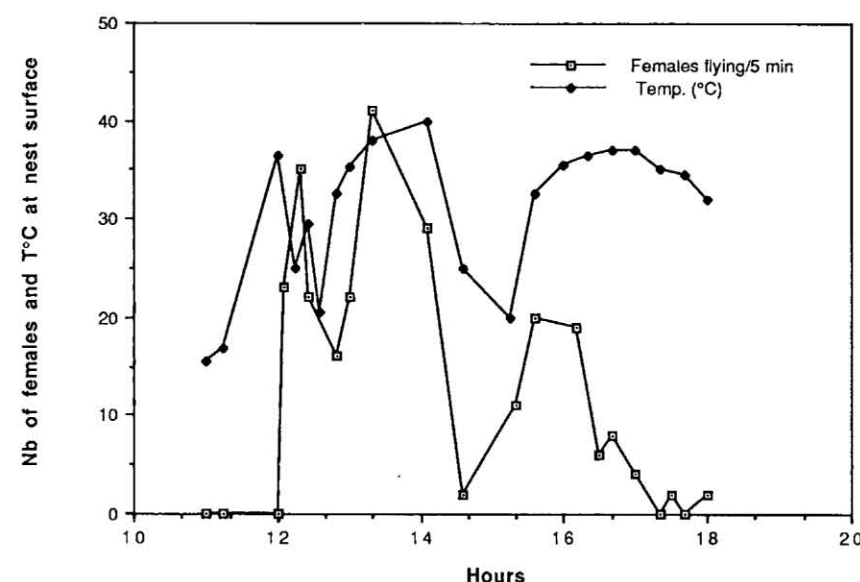
Fig. 2. — Number of females flying from the nest for 5 min periods in relation to temperature at nest surface and time of day (25 June 1987).

The sex-ratio was also sampled in order to study firstly how the sex allocation of individual nests is related to proximate factors like nest temperature and nest size, and, secondly, to address the ultimate questions of how the sex-ratio relates to the reproductive strategies. Most nests are «specialized» so that the nest either produces a strongly male-biased or a strongly female-biased brood. Males tend to appear before females in nests producing both sexes, which necessitated sampling to be restricted to the pupal period before the emergence of adult sexuals. We found that the population sex-ratio, calculated as an average for all samples nests, was female-biased, as there were fewer male-biased nests. Our data indicate furthermore that most female-biased nests produce a few males.

The presence of sexuals on the nest surface as well as their flight are temperature dependent (CHERIX et al. 1989). At 11 °C both males and females begin to appear on the nest surface. The temperature must reach 18 °C before males and females fly. Flight.may occur at any time of the day (from 9 a.m.-6 p.m.) (Fig. 2) depending also on the temperature at the nest surface and other conditions. One of these conditions is related to glycogen content. Glycogen is the major source of energy used by *F. lugubris* sexuals for flying (PASSERA et al. 1990). Males and females contain about the same level of glycogen, suggesting that they may fly similar distances.

Mating sites. After flying from the nest, sexuals clearly do not land at random locations, but they concentrate on certain sites where copulation takes place (mating places) (Fig. 3). These mating places are short-grass meadows where sexuals arrive from shortly after 9 a.m. on sunny days. Males search for females by patrolling at about 50 cm above the ground. Once females reach the mating place, they land and

are soon surrounded by several males and then mate with one or more of them. However it is not yet known if sperm transfer occurs in all matings. While patrolling, males locate females by means of a sex pheromone released by females (Fig. 4). Major constituents of this pheromone were shown to attract males which quickly land in the vicinity of the emitting source. After mating, some queens dealate and disperse on foot, whereas others fly away. These females have only small fat reserves (KELLER & PASSERA 1989) and are therefore not capable of founding colonies independently. They have two alternatives, either to try to enter a nest of the same species (see below) or parasitize a nest of *Serviformica* spp. (KUTTER 1977).

The flight activity of sexuals drastically decreases after 2 p.m. on sunny days and even before if clouds appear. Whereas most queens seem to leave mating places before nightfall, some males stay overnight and may be observed the following morning feeding on pollen and/or nectar of *Alchemilla* sp. plants which are very common on the mating places.

Intranidal mating and killing of young foreign queens. One cause of polygyny is probably intranidal mating, i.e., mating either inside the nest or on its surface. In the relatively few nests which produce large numbers of both sexes, females can often be seen to mate with nestmate males on the mound surface. These females then re-enter the nest suggesting that they then dealate and become functional egg-layers in their parental nest. This is supported by the fact that during the mating flight period, many newly-mated dealate queens are found in the upper portions of these nests away from the older queens which remain deep inside. Such newly-mated queens are also found in nests producing exclusively females, through to a much lesser extent, probably reflecting the relative scarcity of males in these nests.

In addition to mating on the mound surface, experiments in which males and females were placed in cages and then inserted into the mound demonstrated that mating can occur within the dark confines of the interior well below the nest surface.

While some females fly to mating stations, a possible alternative option is to seek out and be adopted into foreign nests either before or after mating. To determine whether such an hypothesis might be viable, young winged females were introduced into foreign nests. Virgin females, which do not appear to foreign nests, were accepted, provided that female sexuals were already present in the host nest. However, young mated females were generally killed. It thus seems unlikely that young queens are successfully adopted into foreign nests.

Intraspecific mating barriers. A total of 93 nests within the area were analyzed electrophoretically with respect to polymorphic enzymes of workers (in collaboration with Dr Pekka Pamilo). The results showed unexpectedly the occurence of two genetically distinct types. Interconnected nests forming a polycalic system seem to belong to one or the other of those types but our maps of nest distribution show that different types sometimes occur rather close to each other. Behavioural tests (see ROSENGREN & CHERIX 1981), based on workers carrying pupae of sexuals to an artificial nest, showed that workers accept pupae from alien nests only if they belong to the same genetical type. Our data indicate restrictions of gene flow between ants of those two types, although the mechanism and its relation to the mating behaviour remain to be studied.

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Fig. 3 — One of the mating places of the super-colony of *F. lugubris.*

Fig. 4. — Attractiveness of female alates in a box with excited males running on the top.

Concluding remarks. While most ant species exhibit only a single mating strategy, *F. lugubris* has several different strategies. Some sexuals take part in mating and dispersal flights, whereas others mate intranidally, either on the mound surface or in the interior of the nest. The relative costs and benefits associated with each of these different strategies is currently under investigation.

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Ultrastructural organization of the exocrine glands in ants *

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Ants, and social insects in general, are characterized by their very well developed exocrine system. According to their cellular arrangement, the numerous glands either belong to the epithelial type, or are composed of bicellular units, each comprising a secretory cell and a duct cell. The ultrastructural organization with regard to the uptake, biosynthesis and discharge of the secretory products is very similar in both types, and generally involves surface increasing foldings of the plasmalemma. The cuticle, that forms part of each glandular cell, is mostly provided with pore canals. Pheromone producing glands are characterized by numerous mitochondria, a well developed Golgi apparatus and an extensive smooth endoplasmic reticulum in their secretory cells. The often abundant multilamellar inclusions may correspond with secretory material. Glands producing venomous substances or performing digestive functions, on the other hand, are characterized by their well developed granular endoplasmic reticulum.

KEY WORDS: morphology, ultrastructure, exocrine glands, ants, Formicidae.

Communication between individuals forms a universal and indispensable condition of animal life. Its importance becomes especially evident in animal societies, where social life relies on precise interactions between its individual members. Social insects have developed one of the most sophisticated communication systems, in which information is conveyed by chemical substances or pheromones, which originate from exocrine glands. The number and diversity of these glands in social insects in general, and ants in particular, are impressive, with glands occurring in all parts of the body. Worker ants can easily contain 20 or more major glands in their small bodies, and hence can be considered as walking glandular batteries.

In spite of their obvious diversity, however, all glands can be classified in two distinct morphological types, according to their ultrastructural organization (Fig. 1). Most simple are the epithelial glands, in which the secretory cells are arranged in a