

Short communication

**Nuptial flights and calling behaviour in the ant
Leptothorax acervorum (Fabr.)**

N. R. Franks^{*1}, A. B. Sendova-Franks¹, M. Sendova-Vassileva² and L. Vassilev²

¹ *School of Biological Sciences, University of Bath, Bath BA27AY, England*

² *Faculty of Physics, University of Sofia, "Anton Ivanov" No. 5, 1126 Sofia, Bulgaria*

Key words: Nuptial flights, sexual behaviour, polygyny, Leptothoracini.

Summary

We describe in detail a very large nuptial flight of the ant *Leptothorax acervorum* at an open hilltop site in Britain. The mating behaviour of these ants involved not only a large mating swarm but also sexual/calling behaviour by the females. The females left the flight to land on vertical objects, where they took up a characteristic calling posture, in which females of closely related species are known to release pheromones that are sexually attractive to males. That *Leptothorax acervorum* has a complex mating behaviour involving both large nuptial flights and sexual calling has important consequences for the interpretation of the evolution of polygyny in this species and social parasitism in its close relatives.

Introduction

The mating systems and social systems of ants, bees and wasps are often intimately related. In ants, for example, colonies can be headed by a single queen (monogyny) or multiple queens (polygyny), and in both cases each queen may be singly or multiply mated. Both the mating systems and the number of queens affect patterns of relatedness and the strength of kin selection acting upon the various members of the society (Hölldobler and Wilson, 1990). Both, therefore, have profound consequences for social evolution among insects. For example, if ant queens mate away from their maternal nest, it seems unlikely that assemblages of queens within a single colony can be closely related, simply because they are unlikely to be able to find their way back to their own relatively small maternal nest. Unfortunately, however, of the vast majority of ant species, there are relatively few observations of the mating behavior (Hölldobler and Wilson, 1990).

* For reprint requests.

Here, we present detailed observations of a large mating swarm of *Leptothorax acervorum*. These observations are important for several reasons. First, they are the first from the United Kingdom, even though this is one of the most widely distributed of British ants (Baroni Urbani and Collingwood, 1976). Second, *L. acervorum* has colonies that can be extremely polygynous (Buschinger, 1974), and in Sweden such cohabiting queens are quite closely related to one another (Stille et al., 1990).

Observations

The nuptial flight was encountered on July 17th, 1990, at 9.30 GMT at the summit of Holyhead Mountain (Holy Island, Anglesey, North Wales) and had a duration of at least one and a half hours. In a small area, within a radius of less than 15 m of the very summit of the mountain, enormous numbers of *L. acervorum* virgin queens and males were undertaking a nuptial flight. The climatic conditions included a cloudless blue sky, an extremely light breeze and an air temperature of about 20 to 22 °C.

The flight consisted of a definite aggregation of very large numbers of sexuals. Many of the females quickly landed at the top of any vertically prominent objects, including ourselves and stems of the short vegetation. Some of the females showed aggression towards one another, so that on relatively flat objects, such as the backs of our shirts, they came to be rather beautifully overdispersed. However, elsewhere, for example on grass stems or our hair, the females remained in small but tight clusters. After they had remained still for a few seconds, each female took up a calling posture, characteristic of many leptothoracine females, with the body straight but angled, so that the head was pointing obliquely downwards and the gaster upwards, with the sting protruding and extended. In such a calling posture, females in closely related species release pheromones that attract the males (Buschinger, 1975). Soon, some of the calling females were attended by males, which throughout the period of observations remained in the minority by at least 1 to 10. Mating occurred quickly at the site at which the female had called a male, and each pair remained *in copula* for approximately 1 minute.

Discussion

The only other published observations of a nuptial flight of *Leptothorax acervorum* are those of Buschinger (1971). On September 9th, 1969, at the summit of the Grosser Ossi (1293 m) in the Bavarian Forest, he observed several dozen sexuals of *L. acervorum* among a swarm of a *Myrmica* species. The mating behaviour he observed was very similar to that we recorded on Holyhead mountain, with females landing and exhibiting sexual calling behaviour. There were three major differences in his observations. First, the Bavarian nuptial flight occurred much later in the year, possibly because of the greater altitude and the later maturation of the ant sexuals. Second, the venue in Germany was surrounded by more or less dense forest, possibly providing many good nest sites for this species. Third, even though the habitat was potentially much richer for these ants, there were far fewer sexuals involved in the Bavarian nuptial flight.

The nuptial flight described in this paper is noteworthy because Holyhead Mountain is rather different from typical habitats for *L. acervorum*. It is treeless within an area of at least 1.5 km in radius in any direction from the summit, and the geology and flora of Holyhead Mountain consists of rather hard quartzites and a short heath of closely browsed gorse and heather. This is unlikely to be an ideal habitat for large numbers of colonies of this species. For this reason, the numbers of sexuals involved in the flight suggests strongly that they must have gathered from a considerable distance.

It is highly unlikely that newly inseminated queens that participate in such a large nuptial flight can find their way back to their own parental colony. Hence, at sites such as that at Holyhead Mountain, a straightforward explanation of polygyny in *L. acervorum* colonies involving the re-adoption of closely related queens is unlikely to be sufficient, unless small numbers of queens do not participate in the flight, but mate in the vicinity of their parental nests. Such mixed mating strategies may be of tremendous importance in the evolution of ant social parasites (Bourke and Franks, 1991; Franks and Bourke, 1990; Buschinger, 1990) of which *L. acervorum* is both a host and a close relative to an unusually large number.

Our confirmation of Buschinger's (1971) observations that *L. acervorum* females have both a nuptial flight and calling behaviour is important, because these two mating systems are often considered to be mutually exclusive (Hölldobler and Bartz, 1985). For example, the social parasites of *L. acervorum*, the workerless inquiline *Doronomyrmex kutteri*, *Doronomyrmex goesswaldi* and *Doronomyrmex pacis* and the slave-maker *Harpagoxenus sublaevis*, all of which occur in continental Europe, but not in the British Isles, use calling behaviour in the immediate vicinity of the parasitized nests from which they first emerge (Buschinger, 1975). Indeed, almost all *H. sublaevis* females are wingless, and can therefore only move relatively short distances. In such relatively rare parasites, calling behaviour may serve to attract males from other parasitized colonies in the immediate neighbourhood, and enable the parasitic female to mate without leaving a local high-density patch of suitable host colonies. However, the free living *L. muscorum* and *L. gredleri* also have calling behaviour (Buschinger and Alloway, 1979).

Since *Leptothorax acervorum* has sexual calling, and may be close in its general behaviour to the ancestral species that gave rise to its parasites, sexual calling may be a primitive trait in this whole clade of ants (Buschinger, 1971; Buschinger and Alloway, 1979; Buschinger, personal communication). This in turn is important, because, as Bourke and Franks (1991) have suggested, mixed strategies of mating in ants may have a central role in the evolution of social parasites, especially workerless inquilines. If, for example, small females mate near to their maternal nest, while larger ones mate at greater distances, and there is facultative polygyny in established colonies, small females may effectively become intraspecific parasites, always relying on the larger queens to found colonies that they then infiltrate. Later, such small queens, specializing in polygyny, may become reproductively isolated. At this stage, such small queens will form part of a separate obligately parasitic species (Bourke and Franks, 1991). Buschinger (1990) has also recently reviewed the possible evolutionary importance of polygyny as a key trait in the ancestors and hosts of the social parasites in the leptothoracines, and the possibility of sympatric speciation that

this trait might facilitate. The complex mating strategy that we have observed in *L. acervorum* including a nuptial flight and calling behaviour is exactly the type of sexual behaviour that West Eberhard (1986) has suggested as being important in speciation events involving alternative adaptations.

Acknowledgements

We wish to thank Alfred Buschinger and Andrew Bourke for their very helpful comments and many suggested improvements to an earlier draft of this manuscript.

References

- Baroni Urbani, C. and C. A. Collingwood, 1976. A Numerical analysis of the distribution of British Formicidae (Hymenoptera, Aculeata). *Verhandl. Naturf. Ges. Basel* 85:51–91.
- Bourke, A. F. G. and N. R. Franks, 1991. Alternative adaptations, sympatric speciation, and the evolution of parasitic, inquiline ants. *Biological Journal of the Linnean Society*. 43:157–178.
- Buschinger, A., 1971. "Locksterzeln" und Kopula der sozialparasitischen Ameise *Leptothorax kutteri* Buschinger (Hym., Form.). *Zool. Anz. Leipzig* 186:242–248.
- Buschinger, A., 1974. Monogynie and Polygynie in Insektensozietäten. In: *Sozialpolymorphismus bei Insekten* (G. H. Schmidt, Ed.), Wissenschaftliche Verlagsgesellschaft m.b.H., Stuttgart 974 p.
- Buschinger, A., 1975. Sexual pheromones in ants. In: *Pheromone and defensive secretions in social insects*. Proc. Symp. IUSSI, Dijon, pp. 225–233.
- Buschinger, A., 1990. Sympatric speciation and radiative evolution of socially parasitic ants – Heretic hypotheses and their factual background. *Z. zool. Syst., Evolut.-forsch.* 28:241–260.
- Buschinger, A. and T. M. Alloway, 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.
- Franks, N. R. and A. F. G. Bourke, 1990. The evolution of inquiline ant parasites: the interspecific versus the intraspecific hypothesis. In: *Social Insects and the Environment*. (G. K. Veeresh, B. Mallik and C. A. Viraktamath, Eds.), Oxford & IBH Publishing Co., New Dehli, pp. 149–150.
- Hölldobler, B. and S. Bartz, 1985. Sociobiology of Reproduction in Ants. Karl v. Frisch Symposium. (M. Lindauer and B. Hölldobler, Eds.), *Fortschritte der Zoologie*. 31:91–107. Fischer Verlag, Stuttgart, New York, pp. 237–258.
- Hölldobler, B. and E. O. Wilson, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts. 732 pp.
- Stille, M., B. Stille and P. Douwes, 1990. Polygyny, relatedness and nest founding in the polygynous myrmicine ant *Leptothorax acervorum* (Hymenoptera: Formicidae) *Behavioral Ecology and Sociobiology* 28:91–96.
- West Eberhard, M. J., 1986. Alternative adaptations, speciation, and phylogeny (A Review). *Proceedings of the National Academy of Sciences, U.S.A.* 83:1388–1392.

Received 7 November 1990;

Revised 25 March 1991;

Accepted 6 April 1991.