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Michał Woyciechowski

Nuptial flights in several ant species and their aerial aggregations *(Hymenoptera, Formicidae)* *

[With 4 text-figs]

Loty godowe kilku gatunków mrówek i ich powietrzne zgrupowania *(Hymenoptera, Formicidae)*

Abstract. Winged ants of the genus *Myrmica*, *Leptothorax* and *Formica*, were observed and caught as they gathered to swarm on the Wysoka summit (1052 m a.s.l.) in the Polish Carpathians, during the six years' study. Variation in the male biased sex ratios of different species has been ascribed to multiple copulation by males, which remain in the swarming sites much longer than the females. The number of individuals caught and the swarming period changed from year to year, while the composition and participation of species differed in the particular stated capture sites remaining unchanged in the following years.

INTRODUCTION

Vital activities, such as reproduction, usually involve patterns of behaviour that are precise and constant for a given species. This does not mean that only one strategy can be evolutionary stable. In some species of ants two mating behavioural strategies can occur within one population (Marikovsky 1961) or even in the same nest (Kinomura & Yamauchi 1987, Fortelius et al. 1987). However, a characteristic form of sexual behaviour is usually practiced by most individuals of a particular species.

Certain species of ant mate within the nest (Kannowski 1959); this is the typical situation for those parasitic species. Winged sexuals of many other species leave the nest and copulate nearby (Kannowski 1959, 1963; Talbot 1971, Breen 1979). Both strategies suggest that ants experience local mate competition — LMC (Hamilton 1964, Alexander & Sherman 1977).

Another type of behaviour is known as „male patrolling behaviour". This occurs when males seek females by waiting for them outside the nest (Kannowski 1959, 1963, Kannowski & Johnson 1969). In yet other species, winged castes congregate on common swarming sites some distance from the nest

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(CHAPMAN 1954, KANNOWSKI 1963, MARIKOVSKY 1961, HUBBARD & NAGEL 1976). This method has evolved despite the greater risk of mortality, since it offers individuals a wide choice of partners, while avoiding kin mating and LMC (WOYCIECHOWSKI 1987). The results of a six-years' study of species use this last strategy are described in this paper.

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II. RESEARCH AREA AND METHOD

Observations were made each year, from 1982 to 1987, in southern Poland in the Małe (Lesser) Pieniny range on the Wysoka summit (1053 m a.s.l.). The area and the method used have already been described (WOYCIECHOWSKI 1987). In this study, winged castes were caught in four traps situated about three metres above the surface of the summit. This small rocky peak, about 50 m² in area, dominates the surrounding compact forest covering the mountain from 900 m a.s.l. upwards. In 1982, captures were only made in two traps; trap I was placed above rocks and trap II was situated on the edge of bushes covering part of the summit. The two remaining traps were placed above those bushes: trap III on the top of a small spruce, trap IV above the crown of a small maple. The distances between consecutive traps are respectively 2.4 m, 1.3 m, 2.6 m, and 5.8 m between extreme traps. The traps consisted of glass bottles of 3.5 cm diameter, partly filled with alcohol. They were usually emptied twice, in the middle and at the end of each month, or occasionally just at the end of a month. The period of occurrence and the maximum activity of sexual castes was therefore estimated for half-month time intervals.

The species composition of ants caught in the traps and the clouds of many thousands of winged individuals seen on the Wysoka summit suggest that most of them flew to the swarming site not from surrounding forest but from far-away sheep pastures. This would involve flying at a height of more than 150 m above a several hundred meters' stretch of forest (WOYCIECHOWSKI 1985, 1987).

For the comparison of sexes of different species, the chi-square test was used giving the value of its statistics (χ^2) and the probability of zero hypothesis assumption (P). YATES'S correction was applied where necessary. Resemblance matrices were calculated using JACCARD'S formula, and the relationship between object were summarized in the form of a dendrogram derived from the uniweighted-pair-group method using arithmetic averages — WPGMA (SNEATH & SOKAL 1973 pp. 230—234).

III. RESULTS

The six years' captures on the Wysoka summit yielded more than 15 ant species belonging to three genera. These consisted of 10 species of *Myrmica*, three species of *Formica*, and at least two species of *Leptothorax*, of which only

Table I

Period of nuptial flights (dots) and of their maximum intensity (line) on the Wysoka summit in 1982—1987. (N — the number of alates of both sexes caught)

Species	May	June	July	Aug.	Sep.	Oct.	N
Myrmica rubra LINNAUES, 1758			···———	———	———	···	5214
M. ruginodis NYLANDER, 1846			···———	———	———	···	73
M. scabrinodis NYLANRER, 1846			···———	———	———	···	1338
M. sabuleti, 1860			···———	———	———	···	1755
M. schencki EMERY, 1895			···———	———	———		115
M. lobicornis NYLANDER, 1864			·····	·····			9
M. specioides BONDROIT, 1918				···			1
M. sulcinodis NYLANDER, 1846				·····			4
M. rugulosa NYLANDER, 1846				·····	·····		2
M. sp.					···		2
Leptothorax acervorum FABRICIUS, 1793		———	———	———	·····		1657
L. s. str. sp.			·····	·····	·····		52
Formica rufa LINNAEUS, 1761	·····	———	———	···			34
F. exsecta NYLANDER, 1846			·····	·····			12
F. sanguinea LATREILLE, 1798			···———	···			69

one species, *L. (Mychothorax) acervorum*, could be distinguished with certainly. Other species of *Leptothorax* s. str. were combined as a single group because there were difficulties to identify males and because of their small numbers. This last group was dominated by *L. nigriceps*. The number of species caught and the time of their appearance and greatest activity are presented in Table I.

The time of appearance varied in different years, in some species by as much as three months. The length of the swarming period, though usually shorter, sometimes lasted for 2.5 months. The peak of a particular species also differed between years by as much as 1.5. month (Tab. I). The fact that less numerous species were usually seen over much shorter periods than abundant ones was probably due to the low probability of catching them outside their periods of maximum activity, rather than from a particular synchronization of their nuptial flights in the entire local population.

In order to find out which species carried out their nuptial flights in phenologically-similar time periods, the percentage of individuals trapped in consecutive captures was calculated for each species in particular years. The results obtained for the nine most numerous species are presented as a dendrogram (Fig. 1). They form two discrete groups of species that swarm in spring/summer or summer/autumn. The former includes all species of *Formica* and *L. acervorum*; the latter group consists of all species of *Myrmica* (Fig. 1). Species of the subgenus *Leptothorax* s. str. were caught during both periods (Tab. I). It should be noted, that during the 5 years of studies more than 10 thousand alates fell into the total traps area, less than 40 cm^2. This gives some insight into the great number of alates on the sworming site each year.

It is well-known that ant swarms contain many more males than females.

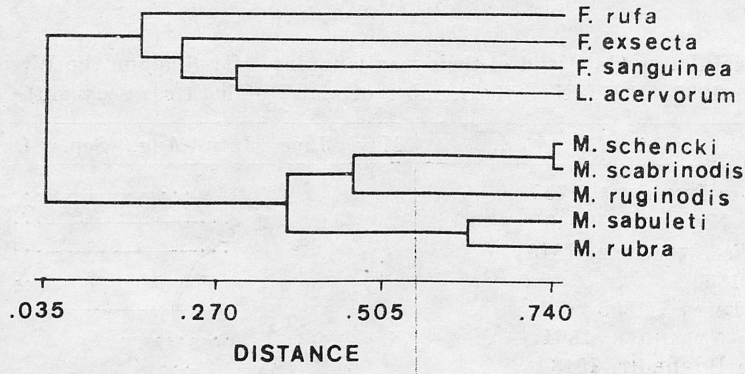

Fig. 1. Dendrogram comparing the flight activity of sexuals castes. Distances beteeen nine most frequently caught species based on the time of their appearance in 1982—1987

Table II

Number of individuals (N) of both sexes and differences in sex ratios (χ^2) in the four most frequently caught species in 1982—1987 (* — $P<0.05$, ** — $0.01<P<0.001$, *** — $P>0.001$, at df = 1)

Species	N	χ^2
♂	5204	
Myrmica rubra		
♀	10	106.363***
♂	1299	
M. scabrinodis		6.885**
♀	39	
♂	1744	24.990***
M. sabuleti		3.038*
♀	11	
♂	1649	0.112*
L. acervorum		28.345*
♀	8	

Comparisons of the sex ratio were carried out using the four most numerous species. The greatest imbalance was observed in *M. rubra*, where the ratio was 520 males per one female. In other species, one female corresponded to 33 males in *M. scabrinodis*, 159 in *M. sabuleti*, and 206 in *L. acervorum*. Differences in the sex ratio of various species are significant (Tab. II).

Swarming ants were observed above the whole mountain summit from early morning onwards on warm summer days. Different species occupied specific sites and also appeared at different time of day. Most swarms were concentrated above small treetops, but *M. ruginodis*, which appeared at noon, sought their partners on rocks. In order to check which species form such concentra-

tion of individuals during swarming, a dendrogram was plotted on the basis of the contribution of each of the species in different traps in consecutive years (Fig. 2). The compared results formed two groups, which suggests that the number and the composition of species is very different above rock (trap I) and above trees (traps III and IV). Trap II represents the border between these two areas.

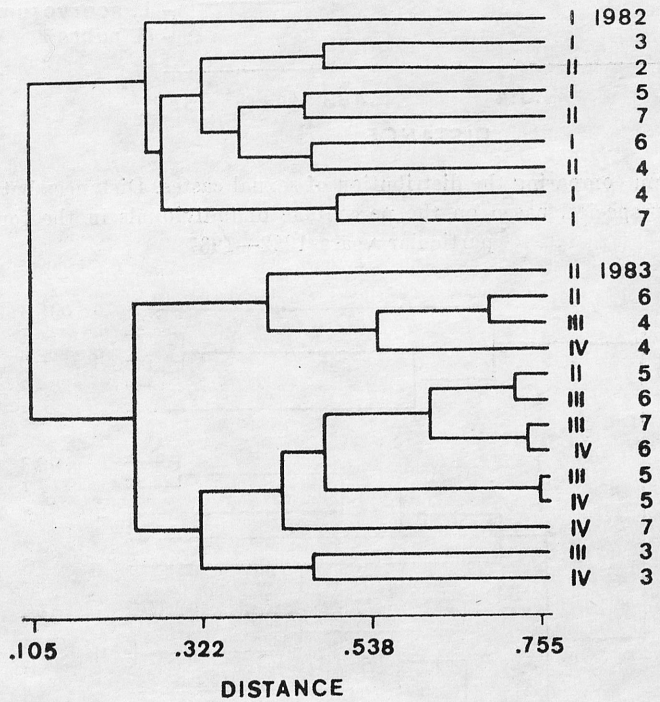

Fig. 2. Dendrogram comparing the content of traps. Distances between four traps in 1982—1987, based on the number of alates of all species caught

The nine most numerous species were also checked for similarities in spatial distribution, by calculating the percentage of individuals of each species caught in each of the four traps in the consecutive years. The results were then compared by plotting a dendrogram (Fig. 3). The species could be divided into two basic groups, of which one included two species. *M. ruginodis* and *M. schencki*, that mainly swarmed above rocks (trap I), and the other consisted of species that were more often caught above bushes. Within this group, *F. exsecta* and *F. sanguinea* were most frequently caught above the spruce (trap III), while *F. rufa*, *M. sabuleti*, *M. scabrinodis*, *M. rubra* and *L. acervorum* formed the majority of ants caught in trap IV, in the crown of the maple.

Another dendrogram was made to check whether the relative numbers remained constant between species from one year to another. This incorpo-

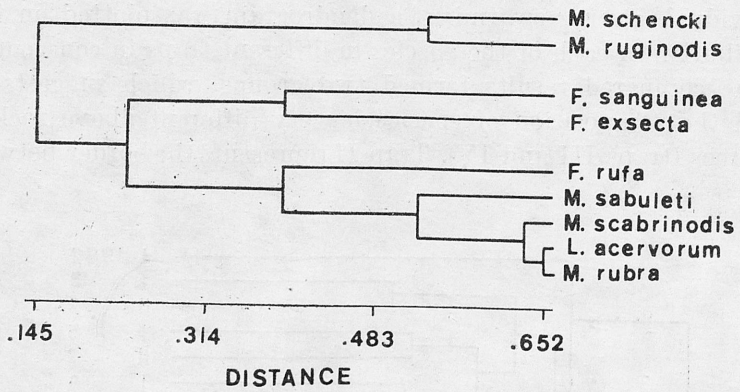

Fig. 3. Dendrogram comparing the distribution of sexual castes. Distances between nine most frequently caught species, based on the percentage of individuals in the four traps, in the particular years 1982—1987

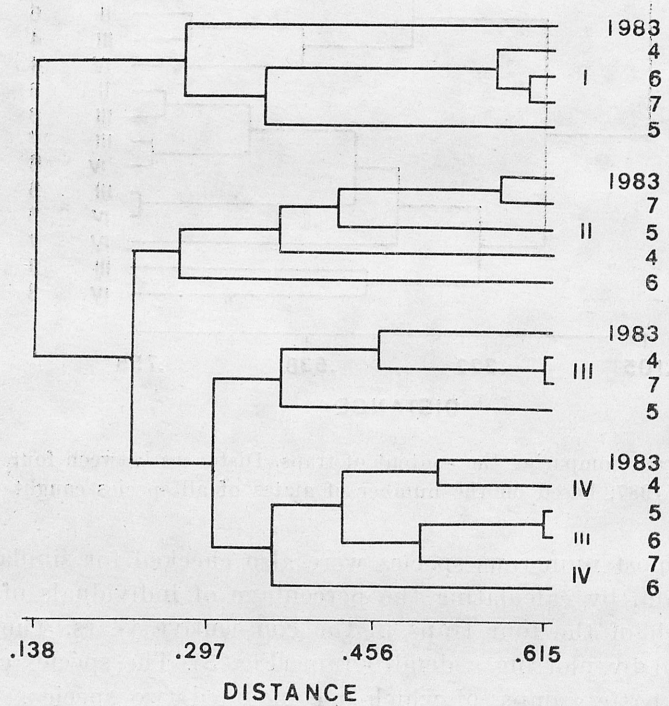

Fig. 4. Dendrogram comparing the distribution stability of sexual castes. Distances between traps in the following years 1983—1987, based on the percentage of each species caught in the four traps

rated all the species caught during the five concesutive years when four traps were used (Fig. 4). Four groups have been distinguished in the dendrogram, each of them representing a different trap during these years, with the exception of trap III, were the results from 1986 are closer to those in traps IV.

Thus the percentage of individuals of a given species in a particular trap is more stable than their actual numbers (Fig. 2). This dendrogram (Fig 4) also supports the earlier conclusions that above trees (traps III and IV) the species composition differs from that above rocks (trap I). There also exists a distinct borderline which separates the two swarms each year (trap II).

IV. DISCUSSION

The results of this study suggest that all the *Myrmica*, as well as many other species of ants, have a strategy for mating that results in a low probability of kin encounters, for many individuals are drawn together from a large number of different nests. Indeed, so concentrated are the swarms, that three new species of *Myrmica* to the Małe Pieniny mountain range were discovered among the winged sexuals, in addition to the seven species that had previously been found when traditional methods of locating ants, such as searching for nests and workers, were employed (Pętal 1974, Woyciechowski 1985).

The method used is therefore valuable in the evaluation of the diversity of *Myrmica* species. However, care should be taken if the results are to be used quantitatively. This is because in some species, such as *M. schencki*, all the sexuals from a very large area appear to assemble at a single site, whereas in other species, such as *M. ruginodis* and *M. rugulosa*, the swarms are more local in character. This conclusion is based on the discovery that *M. schencki* was caught in a much larger proportion to other species on the Wysoka summit than could be expected from the number of its nests in the neighbourhood (Woyciechowski 1985). On the other hand, *M. rugulosa* and *M. ruginodis* swarm in many other places, including small peaks, rocks, or even separate stones (Woyciechowski, unpubl.). It might be surmised, then, that the more numerous species form more local swarming sites than do those species that are encountered occasionally. Such behaviour would confirm the tendency of many ants to avoid their kin when mating.

The high proportion of male *Myrmica* that were found in the swarms (Tab. II) is greater than the true ratio of sexuals that emerge from nests (Elmes 1982). This imbalance probably results from the fact that individual males have the potential to mate many more times than the females (Kannowski 1963, Woyciechowski 1990), and so remain within the swarming cluster longer than females.

The southfacing slopes around Wysoka are interspersed with northfacing hillsides that have a distinctly colder microclimate. This results in a mosaic of habitats (Grodzińska 1970), and might be the reason why the time of appearance of sexual castes in a given species not only varies annually (Tab. I), but may also extend over 2.5 months in the same year this does not negate the distinct influence of favourable weather conditions on flight activity, as established by (Boomsma & Leusink 1981). Visible differences in appearance

times would rather be observed within whole groups of species (Fig. 1). The phenological sequences of sexual castes in particular species often vary from year to year. It can only be concluded, therefore, that both *Formica* and *Myrmica* species tend to have nuptial flights at the same time (Tab. I) as has already been noted by KANNOWSKI (1963).

This study shows that particular place, as well as the time of season, are important for the sexuals of different species. As has already been mentioned, *M. ruginodis* sexuals seek their partners by running on rock or plant surfaces, while other species usually pair in flight. Among the latter, certain species have particular swarming sites which might be shared by more than one species (Fig. 3). The area of concentration of a particular species does not change from year to year (Fig. 2) and is determined by the structure of the vegetation or the terrain. Irrespective of fluctuations in the number of sexual castes produced each year, the area occupied by a particular species remains more or less unchanged, and only the density of individuals varies (Fig. 4).

Institute of Systematics and Evolution of Animals
Polish Academy of Sciences
Sławkowska 17, 31-016 Kraków, Poland

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STRESZCZENIE

W latach 1982—1987 na szczycie Wysokiej (1052 m n.p.m.) w Małych Pieninach dokonano odłowów i obserwacji kast seksualnych mrówek w czasie rójki. Uskrzydlone osobniki chwytano do 4 pułapek umieszczonych około 3 m nad powierzchnią gruntu.

W czasie sześciu lat prowadzenia odłowów schwytano 10 gatunków z rodzaju *Myrmica*, 3 gatunki z rodzaju *Formica*, z licznych gatunków należących do rodzaju *Leptothorax* wyróżniono zaś tylko *L. acervorum* (tab. I). Regułą jest zdecydowana dominacja samców wśród rojących się osobników (tab. II), co uznano za efekt wielokrotnej kopulacji samców, przebywających w związku z tym w miejscu rójki znacznie dłużej niż to robią samice.

Okres lotów godowych dla gatunków z rodzaju *Formica* i *Leptothorax acervorum* jest zbliżony i przypada na koniec wiosny i początek lata, podczas gdy gatunki z rodzaju *Myrmica* odbywają swą rójkę w drugiej połowie lata i na początku jesieni (tab. I, ryc. 1). Skład i liczba odłowionych gatunków różni się zdecydowanie w zależności od miejsca odłowu (ryc. 2). *M. schencki, M.*

ruginodis odbywają swą rójkę nad odkrytymi skałami, gdy *M. rubra, M. scabrinodis, M. sabuleti, L. acervorum, F. sanguinea, F. exsecta* i *F. rufa* gromadzą się głównie nad krzakami porastającymi część wierzchołka góry (ryc. 3). Miejsce rójki poszczególnych gatunków jest nie tylko wyraźnie określone, ale też stałe z roku na rok (ryc. 4). Roczne wahania liczebności kast seksualnych wpływają raczej na zagęszczenie rojących się owadów, nie zaś na przestrzeń, w której odbywają swą rójkę.

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