| EKOLOGIA POLSKA <br> (EKOI. pol.) | 24 | 4 | $577-592$ | 1976 |
| :---: | :---: | :---: | :---: | :---: |

Michal WOY CIECHOWSKI and Alicja MISZTA<br>Department of Nature Protection, Polish Academy of Sciences, Cracow Institute of Botany, University of Silesia, Katowice

## SPATIAL AND SEASONAL STRUCTURE OF ANT COMMUNITIES IN A MOUNTAIN MEADOW


#### Abstract

Three species predominated in ant communities inhabiting a mountain pasture: Myrmica scabrinodis Nyl., M. lobicornis Nyl. and Lasius flavus Fabr. The numbers of their foragers reached a maximum in June and July. The activity of M. scabrinodis increased with temperature. Generally, the foragers had clumped distribution. In M. scabrinodis it was related to their numbers and to the species diversity of all foraging ants. The carrying capacity of the habitat, degree of its utilization, threat from the outside and food specialization are considered the main factors responsible for a stable nest location and the size of nests.


## Contents

1. Introduction
2. Study area and methods
3. Results
3.1. Numbers and activity of ants
3.2. Species diversity of foragers
3.3. Joint occurrence of different species of foraging ants in a sample
3.4. Distribution of foragers
4. Discussion
5. Summary
6. Polish summary (Streszczenie)
7. References

## 1. INTRODUCTION

In grassland ecosystems ants represent an exceptionally abundant group of animals both by the number of species and by their density. This is probably a reason why these ecosystems have frequently been investigated by students of ants.

Literature data on the biology of ants are very rich already. The effect of ants on soil conditions and floral composition is known (Gaspar 1972, Jakubczyk, Czer-
wiński and $\mathrm{Pe}_{\varepsilon} \mathrm{tal}$ 1972). The contribution of ants as predators to reduction of small invertebrate animals is considerable ( Kajak et al. 1972). The effect of ant predation is intensified due to the fact that their consumption rate is correlated with the available food supply in the habitat ( P eq tal 1968 ).

Numerous myrmecological studies were generally conducted in large areas including different ecosystems. They provide useful information on the fauna of ants, their species diversity or their communities. The conclusions of these studies generally confirm in a way the assumptions, as the differences observed reflect directly differences among habitats. Information on the ecology of ant populations is not so rich. It is usually obtained by direct observations of nests, generally under laboratory conditions, or the distribution and numbers of nests are recorded. To analyse population processes, it seems useful to observe individual ants searching the area. In most ant species they provide food for the whole nest, therefore, their role is of basic importance. Foraging ants are the first individuals subjected to continuous variations of habitat conditions, and they must immediately respond to these changes. In addition, they must transmit much of information from the habitat to individuals inside the nest (Dobrzańska 1958).

In the temperate zone, seasonal changes occurring in climax communities or in the communities during slow succession are considerably more pronounced than those occurring from year to year. Therefore, observations of the behaviour of animals and their responses throughout the growing season seem to be of basic importance in the population studies of insects. Because the response of small animals to subtle, generally imperceptible environmental factors is little known, possibly large amounts of data should be collected in similar habitats.

To compare the present results with literature data, the materials were collected by a stañdard method used in many studies on epigeic invertebrate fauna ( Peq tal and Pisarski 1966). Primarily foraging individuals were observed, with special emphasis on factors which could be related to the size of ant populations. The study was carried out in the plots located in similar and homogeneous habitats, throughout the growing season.

## 2. STUDY AREA AND METHODS

The study was carried out in the Jaskowa meadow located on the southern slope of the Skrzyczne mountain ( $1,257 \mathrm{~m}$ above sea-level) belonging to the Silesian Beskid range of the Western Beskids. The 60 -ha meadow was cleared within the lower mountain zone before 17 th century (C eller 1972). It is a mat-grass, Hieracio-Nardetum meadow, characteristic of poor, sour soils.

This meadow is grazed by sheep from May to September each year. At night the sheep are penned up in sheep-folds moved every 3-4 days. The meadow is mown from time to time. Its southeastern edge has been afforested in recent years.

Six similar, $100-\mathrm{m}^{2}$ plots were selected in the central part of the meadow to exclude the effect of the ecotone. The distances between the plots exceeded 40 m . They were situated about 900 m above sea-level on the southern slope, the inclination of which varied from 5 to $15^{\circ}$ (Fig. 1).

Plant communities in five of the plots were represented by the Hieracio-Nardetum association, only plot 2 being covered with a degraded fresh mountain meadow Gladiolo-Agrostietum.

Insects were caught by the Barber traps, i.e., plastic cups 7 cm in diameter and 0.351 in volume. There were 100 numbered traps in each plot. They were uniformly distributed


Fig. 1. The map of the Jaskowa meadow with the study plots
$A$ - study plots, $B$ - tourist routes, $C$ - meadows, $D$ - spruce forests, $E$ - beech forests
throughout the plots at a distance of 1 m from one another, but the nests of ants were omitted. About 40 ml of $4 \%$ formalin were put inside the traps to kill and preserve animals. The insects were moved from each trap to a separate test-tube with $75 \%$ alcohol.

A total of 11 catches were done from 1st May to 11 th October, 1973, i.e., one catch every fortnight, on the average. The dates of catches and mean air temperatures on the days of sampling are shown in Table I.

Table I. Timing of catches and daily mean temperatures during the catches

| No. <br> of catch | Date of catch (1973) | Daily mean temperature <br> $\left({ }^{\circ} \mathrm{C}\right)$ |
| :---: | :---: | :---: |
| 1 | 1 May-4 May | 12.3 |
| 2 | 23 May-25 May | 7.0 |
| 3 | 9 June-11 June | 8.6 |
| 4 | 25 June-27 June | 13.5 |
| 5 | 7 July-9 July | 12.4 |
| 6 | 26 July-28 July | 8.0 |
| 7 | 9 Aug.-11 Aug. | 12.0 |
| 8 | 21 Aug.-23 Aug. | 10.1 |
| 9 | 9 Sept.-11 Sept. | 9.4 |
| 10 | 26 Sept.-28 Sept. | 3.7 |
| 11 | 11 Oct.-13 Oct. | lack of data |

The temperatures were taken from the meteorological station located on the Skrzyczne mountain at a distance of about two kilometers from the plots. The catches lasted two days, except for the first one which lasted three days. After these two (or three) days insects were removed almost simultaneously from all the plots, so that the duration of a single catch was the same.

In addition, in May and June all the plots were searched to locate ant nests. For this purpose belts 1 m in breadth were established in each of the plots, and each portion of the soil was thoroughly examined. It is probable, however, that not all nests were found.

The data for the whole season presented in Tables and Figures are based on the distribution of foraging ants in four plots. To characterize particular ant species, additional materials were used from the first two catches in plots 5 and 6 .

In plot 2 there is no catch 9 because sheep were penned up in it at that time. The results obtained in this plot during the next catches were different than in the other plots and not comparable to them.

In plots 3 and 5 nearly 80 kg of industrial dust from an ironwork were distributed. The percentage of components that could be harmful was: $5.40 \% \mathrm{Al}_{2} \mathrm{O}_{3}, 0.20 \% \mathrm{MgO}, 0.60 \% \mathrm{~S}$, $0.38 \% \mathrm{Mn}$ and $0.26 \% \mathrm{Zn}$. Because the amount of dust was small, and frequent rainfall could wash off a substantial part of it, we assumed that the dust had no effect on the numbers and distribution of foraging ants. Thus, these plots were considered as being equal to the others.

Generally, the relationships analysed in this paper are not rectilinear, therefore, they are tested by the Spearman rank correlation coefficient. To analyse the joint occurrence of foragers of different species, the Pearson coefficient $r$ was used. When describing these two correlation coefficients $\rho$ and $r$, number of samples $N$ and probability of the null hypothesis $P$, which characterizes the significance of the correlation, are given.

## 3. RESULTS

3.1. Numbersandactivity of ants

A total of 2,905 specimens belonging to 11 ant species were caught in the plots. In addition, 381 ant nests of six species were located (Table II).

Both the foragers caught in the traps and the nests were predominated by three species: Myrmica scabrinodis, M. lobicornis and Lasius flavus.

Seasonal changes in the numbers of captured ants were similar in all the plots. The highest activity of the dominant M. scabrinodis was observed in the second half of June, M. lobicornis was most frequently caught in June and July, the foragers of L. flavus in June and in the first half of July (Fig. 2). The numbers of M. lobicornis (Fig. 2) are presented together with those of other species occurring in most of the plots at very low densities, so that they cannot change the shape of the curve for M. lobicornis. The numbers of nests and foragers caught at the same time are compared for the three dominant species (Fig. 3). Because the number of the plots was not sufficient, it was not possible to find a significant correlation between these variables, and the results are presented only in the form of a graph in which the points for the six plots are presented for each species. The number of foragers caught per nest of the genus Myrmica is many times higher than in L. flavus.

Relationship between the number of ants caught and the mean daily air temperature on the day of the catch was showed for the dominant species (Table III). Significant positive correlation was found for M. scabrinodis in plots 3 and 4 . In plot 1 , where the number of catches was the lowest, and in plot 2 , where the number of ants caught was the lowest, the correlation was not significant. For the remaining species the correlation between the temperature and the number of individuals caught was not significant.

Table II. Numbers of foragers caught $(n)$ and density of colonies $(N)$ per $100 \mathrm{~m}^{2}$

|  |  |  |  |  |  |  |  |  | Tot |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 1 | 2 | 3 | 4 | 5* | 6* | $n$ | $N$ |
| 1 | Manica rubida Latr. | $n$ | 1 |  | 1 |  |  |  | 2 |  |
| 2 |  | $n$ | 341 | 55 | 809 | 348 | 63 | 64 | 1,680 |  |
| 2 | Myrmica scabrinodis Nyl. | $N$ | 17 | 12 | 36 | 18 | 14 | 35 |  | 113 |
| 3 | M. lobicornis Nyl. | $n$ | 75 | 23 | 130 | 103 | 21 | 47 | 399 |  |
|  | M. lobicornis Nyl. | $N$ | 1 | 3 | 3 | 5 | 2 | 7 |  | 21 |
| 4 | M. laevinodis Nyl . | $n$ |  | 57 | 1 |  | 8 |  | 66 |  |
| 5 | Te | $n$ |  |  | 7 |  |  |  | 7 |  |
|  | Teiramoriam caespiam | $N$ |  |  |  |  |  |  |  |  |
| 6 | Formica lemani Bondr. | $n$ | 8 |  |  |  |  |  | 8 |  |
| 7 | F. polyctena Foerster | $n$ | 4 |  |  |  |  |  | 4 |  |
| 8 | $F$, sanguinea Latr. | $n$ |  |  |  | 5 |  |  | 5 |  |
| 9 | Camponotus herculeanus L | $n$ |  | 2 | 1 | 1 |  |  | 4 |  |
| 10 |  | $n$ | 154 | 47 | 124 | 335 | 38 | 26 | 724 |  |
| 10 | Lasius flavus Fabr. | $N$ | 40 | 5 | 18 | 49 | 55 | 52 |  | 219 |
| 11 | L. niger L. | $\stackrel{n}{n}$ | 1 | 2 | 2 |  |  | 1 | 6 | 1 |
| Total |  |  |  |  |  |  |  |  | 2,305 | 381 |

*Numbers of individuals caught at the first two catches.



Fig. 2. Numbers of foragers caught $n$ at successive catches $t$ in the plots (numbers of the plots are circled) 1-Myrnica scabrinodis, 2 -Lasius flavus, 3-other species


Fig. 3. Numbers of the nests $N$ and ants caught at the first two catches $n$ of Myrmica scabrinodis (1), Myrmica lobicornis (2) and Lasius flavus (3) in six plots

Table III. Relationship between the air temperature and the number of ants caught, expressed by the Spearman rank correlation coefficient $\rho$ Significance of the coefficient is indicated by asterisk - ${ }^{*} 0.01<P<0.05$

| Species | Plots |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 |
| Myrmica scabrinodis | 0.3667 | 0.4909 | $0.6485^{*}$ | $0.6061^{*}$ |
| M. lobicornis | 0.5917 | 0.4182 | 0.4990 | 0.3636 |
| Lasius flavus | 0.5708 | 0.5545 | 0.3212 | 0.5030 |

### 3.2. Species diversity of foragers

Assuming that the species diversity is a function of the number of species and their domination structure, it can be described by the formula:

$$
H^{\prime}=-\sum_{i=1}^{n} p_{i} \ln p_{i}
$$

where: $p_{i}$ is the proportion of individuals of species $i$ and $n$ denotes number of species. It is so called Shannon's index modified by Lloyd, Zar and Karr (1968) and based on information theory (Witkowski 1970). This index of diversity contains information on the number of species and their proportion to the total number of individuals caught. Figure 4 shows seasonal changes in the species diversity of foraging ants. Although the number of


Fig. 4. Species diversity of foraging ants $H$ 'at successive catches $t$ in plots $1-4$

Table IV. Species diversity of foraging ants, expressed by the Shannon index $\boldsymbol{H}^{\prime}$, in particular plots for the whole season

| Plots |  |  |  |
| :---: | :---: | :---: | :---: |
| 1 | 2 | 3 | 4 |
| 1.5061 | 2.0615 | 1.0973 | 1.4874 |

samples in each plot was large, the diversity index, calculated on the basis of two-day observations, varied considerably. To obtain a reliable characteristics and to compare the plots, the diversity index was calculated for all the catches together. The species diversity calculated in this way is a result of the changes occurring throughout the season (Table IV). The lowest diversity was found in plot 3 , where the predominating M. scabrinodis accounted for $74.8 \%$ of the total number of ants caught. In plot 2, where the proportions of among the four predominating species were similar, the diversity index was the highest.

### 3.3. Joint occurrenceofdifferentspecies of foraging antsin asample

Joint occurrence of different species may be a result of similar habitat requirements or interspecific interactions. The Pearson correlation coefficient $r$ may be used to describe this relationship. Because the distribution of the coefficient $r$ deviates from the normal distribution, for graphic representation the Fisher's $z$ transformation for correlation coefficients was used, which is normally distributed (Guilford 1964). The coefficient $z$ is calculated from the formula:

$$
z=\frac{1}{2}[\ln (1+r)-\ln (1-r)]
$$

Table V. Correlation between the occurrence of Myrmica scabrinodis and Lasius flavus in the same samples, expressed by the Pearson coefficient $r$
Significance of the coefficient is indicated by the asterisks $-{ }^{*} 0.01<P<0.05,{ }^{*}{ }^{*} P<0.01$

| Plots |  |  |  |
| :---: | :---: | :---: | :---: |
| 1 | 2 | 3 | 4 |
| $0.2713^{*} *$ | -0.1566 | 0.1763 | $0.1961^{*}$ |



Fig. 5. Correlation between the occurrence of Myrmica scabrinodis and Lasius flavus in the same samples, expressed by the Fisher coefficient $\dot{z}$ at successive catches $t$ in plots $1-4$ $P$ - limit within which correlation coefficients are not significantly different than zero (null hypothesis, $P<0.05$ )

Correlation of the joint occurrence was analysed for all the species caught. The correlation between the occurrence of the two dominant species M. scabrinodis and L. flavus should be noted (Table V, Fig. 5). Fisher's transformation varies from catch to catch, and it indicates for a positive significant relationship only in four cases. It can be readily found, however, that in three plots out of four, the foragers of M. scabrinodis and L. flavus can meet each other more frequently than it could be expected from the random distribution. Only in plot 2 , where the density of these species was the lowest, the coefficient $z$ has negative values for most catches, but it is statistically insignificant. The results based on two-day catches are confirmed by the results calculated for the whole season (Table V). Correlation between the occurrence of M. scabrinodis and L. flavus is positive and in two plots significant. The correlation coefficient $r$ in plot 2 suggests that, unlike in the other plots, these two species exclude themselves in the same samples.

### 3.4. Distribution of foragers

The distribution of foragers in particular samples was calculated to find in which way the area under study was searched by foraging ants. Because the species caught were represented by different numbers of individuals, according to the time and site of sampling, the Morisita index $I$ was used to analyse their distribution. According to Southwood (1966) this index does not depend on the size of samples, though if the number of zero samples is high (small density) it does not provide reliable estimates. The value of the index $I$ was calculated from the formula

$$
I=N \frac{\sum_{i=1}^{N} n_{i}\left(n_{i}-1\right)}{\Sigma x(\Sigma-1)}
$$

where: $N$ is the number of samples, $n_{i}$ is the number of individuals in sample $i$, and $\Sigma x$ is the sum of individuals caught in all samples. The values of $I$ higher than one indicate for a clumped distribution, equal to one show random distribution, and lower than one are for uniform distribution. The dispersion of $I$ is the highest when the numbers of individuals caught are small. For this reason only the results for the most abundant species such as M. scabrinodis and L.flavus are presented here. The distribution of foragers of the two species in the traps is presented for the plots with the highest densities, i.e., plot 3 for M. scabrinodis and plot 4 for L. flavus (Fig. 6). The distribution of foragers varied considerably and it was generally clumped, but not frequently statistically significant.


Fig. 6. Distribution pattern of Myrmica scabrinodis (1) in plot 3 and Lasius flavus (2) in plot 4, expressed by the index $I$ at successive catches $t$


Fig. 7. Distribution of foraging individuals I of Myrmica scabrinodis and Lasius flavus at cumulative catches $T$ in plots 1-4

To analyse the changes in the distribution of foragers throughout the season, the index $I$ is also calculated for cumulative catches (Fig. 7). The distribution of the sums of individuals caught in the same trap at successive catches in plots 1,2 and 4 shows that clumping tends to decrease significantly with time (Table VI). In plot 3, where the number of M. scabrinodis was the highest, the disappearance of the clumped distribution was not observed, and starting from the third catch clumping significantly increased in the cumulative catches ( $\rho=0.70000$, $N=9,0.05>P>0.01$ ). The clumped distribution of L. flavus foragers, calculated for the cumulative catches, does not show any characteristic trend throughout the season, except for plot 3 where it considerably increased with time (Table VI).

Table VI. Changes in the distribution of foragers, expressed by the Spearman rank correlation coefficient $\rho$
Significance od the coefficient is indicated as in Table V

| Species | Plots |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 |
| Myrmica scabrinodis <br> Lasius flavus | $-0.7381^{*}$ | $-0.8886^{* *}$ | 0.0727 | $-0.7455^{* *}$ |

The distribution pattern of foragers was correlated with their numbers and species diversity. The correlation is calculated only for the catches in which more than 25 individuals were captured. They were too scarce to analyse the situation in each of the plots separately. Therefore, the data for all the plots were cumulated, and the results were used to characterize the species.

There is a highly significant negative correlation between the clumped distribution and density of M. scabrinodis foragers $(\rho=-0.7034, N=20, P .<0.01)$. L. flavus has a clumped distribution independent of the number of individuals searching the area:

Clumped distribution of M. scabrinodis foragers is significantly positively correlated with the species diversity of all foraging ants ( $\rho=0.4195, N=20,0.05>P>0.01$ ). Thus, the aggregation of M. scabrinodis foragers increases with increasing species diversity. Similar tendency was also observed in L. flavus but the correlation was not significant.

## 4. DISCUSSION

The ant species observed in the meadow under study are typical components of grassland ecosystems and they were also found in other mountain meadows, e.g., in the Sudeten (Banert and Pisarski 1972), the Pieniny (Koehler 1951) or the Bieszczady (Parapura and Pisarski 1971).

Because the study area was covered with a relatively uniform plant community, the occurrence of only 11 ant species is fully justified.

Phytosociological studies carried out in the plots confirmed their great similarity. Therefore, almost identical ant species composition in the whole area under study seemed to be evident. Nevertheless, more detailed tests revealed the differences both between the plots and within the plots.

Species diversity of foraging ants shows a large amplitude over the season and from plot to plot, despite of a great number of samples and two-day long catches (Fig. 4). Seasonal changes in ant activity are so pronounced that a period considerably longer than two-days should be taken into account to compare the species diversity of ants caught in the plots. Only the index of diversity based on the total number of individuals caught throughout the season provides a proper estimate of foragers searching the area (Table IV). The species diversity of foragers caught over the season is also an effect of habitat conditions, and it can be regarded as an approximate index of habitat diversity (R.H. Mac Arthur and J.W. Mac Arthur 1961). The diversity interpreted in this way may be used to determine the differences between the plots, which can not be detected by habitat analyses.

The changes in the numbers of ants caught (Fig. 2) reflect to a high degree the activity of foragers, and they do not result from the changes in the size of worker populations described by Brian (1965) or Wilson (1972). It is indicated by the correlation between the number of individuals caught and temperature (Table III). Such correlation was found only in M. scabrinodis, and it shows that there are differences in the behaviour between this species and L. flavus. Activity of the majority of invertebrate prey increases with temperature, and so does the activity of predators. L. flavus, the ant living more underground than M. scabrinodis, is not so strongly controlled by the instantaneous ambient temperature. Predation in this species is likely to result from protein requirements by the ants in the nest, and it is not so much influenced by actual food supply in the habitat as the predation of the genus Myrmica. Certainly, temperature is not the only factor stimulating the activity of foragers. Food requirements of the colony, available food supply ( $\mathrm{P} \mathrm{e}_{\mathrm{t}} \mathrm{al}$ 1968), the effect of other
individuals of the same or different species (De Bruyn and Mabelis 1972) or social structure of the colony ( Pisarski 1973 ) are not of less importance, but it is more difficult to estimate them. Their effect on the activity of M. lobicornis and L.flavus is probably more pronounced than the effect of temperature.

The observed joint occurrence of M. scabrinodis and L. flavus foragers (Table V) can result from similar habitat requirements or from interspecies interactions. The occurrence of the two species was positively correlated in the major part of the study area. They exclude each other only in the plot with the highest species diversity of foragers and with the lowest density of both the species. It can be suggested that M. scabrinodis and L. flavus exclude each other in the habitats of highly mosaic structure, which are not fully utilized. In a uniform habitat these two species can be separated due to the differences in the time of searching the area. Such repartition of commonly used areas was observed in other species (Stebaev and Reznikova 1972).

Kaczmarek (1953) suggests that there is a competition between ant species of similar body size. According to the criteria used by this author, M. scabrinodis and L. flavus should be included into one group of competing species. The competition is so more probable that both these species feed on similar food such as honeydew of aphids that live on roots, and they are non-specific predators (Pontin 1961, Brian, Hibble and Stradlina 1965). If the amount of available food resources has a considerable effect on the numbers of ants in the population ( P e tal 1968,1972 ), the competition between M. scabrinodis and L. flavus for food can be a limiting factor for both of them.

The collected materials do not support the fact observed by Waloff and Blackith (1962) that M. scabrinodis and L. flavus predate on each other. The foragers of M. scabrinodis, the more predatory species, can readily locate the mounds of $L$. flavus. If the predation really took place, the distribution of both these species should be closely correlated, particularly at lower prey densities. But in fact, M. scabrinodis and L. flavus exclude each other at their low densities. It can be suggested that M. scabrinodis is not much interested in such potential prey. as L. flavus.

Field observations of the nests of M. scabrinodis and many other species seem to show that the nest cannot exceed an optimum size. An increase in the size of the nest is followed by an increase in the security of its inhabitants and in the possibility of maintaining a greater number of females, which secures the persistence of the nest. But the increase in the nest size cannot be unlimited. Larger colonies need more food and, in consequence, foragers must cover larger distances when searching for food, which requisite much energy, and exposes foragers to predators. In larger colonies the effectiveness of foragers decreases, which is followed by an increase in demand for their work. When the colony reaches a definite size, further increase in the number of ants becomes highly uneconomical. Further production that would exceed the mortality rate is possible only when the divided colony occupies a new area. If the whole habitat is already occupied by other colonies, and the foundation of new colonies or the moving of old ones is not possible, we can probably say about typical nest territories. When the carrying capacity of the habitat is reached, the strategy of an ant nest should be changed to secure further expansion of the species. The possibility of continuous reproduction can be effected due to the production of sexuals. Although the chance of establishing a new nest by a winged female is very small, it increases considerably when she finds a new, unoccupied habitat. The occurrence of nests and their numbers, therefore, depend on many factors. The most important factor seems to be the carrying capacity of the habitat, and the degree to what it is filled. Also the interactions between the colonies of the same or different species are of great importance (Y as uno 1964, 1965).

The situation is a little different in the case of $L$. flavus mounds. These ants are smaller than M. scabrinodis, and they construct much more complicated nests. They nurse aphids on the roots of plants in their nests to exploit honeydew or to prey on them (P on t in 1961). They also store food collected on the ground surface. This double-way utilization of feeding grounds enable this species to built nests dozen times larger than those of M. scabrinodis (Brian 1965). The tendency to construct larger nests may also result from smaller defensive capacity in a less predatory speeies such as L. flavus, as compared with ants of the genus Myrmica. Specialization ensuring the efficient utilization of foraging grounds, and difficulties in moving the nest, which is large and of complicated structure, could account for a high stability of the nest. The nest of this type can probably be propagated mainly due to fertilized females.

The proportion of sexuals to the production of the colony is higher in larger nests ( Brian 1965). It seems that large nests are safer, but their production per individual can be considerably less efficient than in smaller nests. The proportion of sexuals can also increase in all nests during the years scarce in food ( P eq $\mathrm{ta} \mid 1968$ ), but this is a result of the emigration of a part of the colony under unfavourable conditions.

Many literature data and also the authors' results seem to support the suggestions presented above.

A decrease in the aggregation of M. scabrinodis foragers combined with an increase in their activity (Table V) is possible when the searched area is being enlarged. The area used throughout the season can also be changed according to the needs and possibilities of the nest. In plot 3, where the number of M. scabrinodis nests was the highest, and the density of foragers disproportionately higher, aggregation tended to increase in the cumulative catches. It was an effect of searching still the same area, therefore one can suppose that carrying capacity of the habitat was completely filled. If it is the case, the competition between the colonies of the same species reached the maximum, and it is shown by a very high density of the foragers (Fig. 2). In the other plots estimates of aggregation based on cumulative catches tended to decrease throughout the season (Table VI). It was the effect of the changes in the size of foraging area as a result of moving the nest or its partition. Changes in the location of the nest or its part can be related not only with the level of its social organization but also with the changes in habitat conditions or in the reserve of the carrying capacity of the habitat over the season. Frequent changes in nest location and rapid response of ants to the changes in available food supply were observed by Pet al (1968) in Myrmica laevinodis.

The location of L. flavus mounds is very stable so these ants must search still the same foraging area. In such situation aggregation does not decrease in cumulative catches (Fig. 7).

The increase in aggregation of M. scabrinodis foragers, combined with increasing species diversity of all ants searching the area, is mainly an effect of the relationships described above. This species was the most frequently caught, and the increase in its density accounted for a decrease in the proportion of other ant species. As a result, the species diversity decreased. Because at lower densities of foragers, a smaller area is used, their aggregation increased. These two relationships can suggest a correlation between the species diversity and the distribution of foraging ants, which does not exist in fact. It is probable, however, that the species diversity, which reflects habitat diversity (R. H. Mac Arthur and J. W. Mac Arthur 1961), and is an effect of interspecific interactions, determines the distribution of the species both in space and in time.

Comparison of the two most frequently caught ant species shows that $M$. scabrinodis is less specialized than L. flavus.Higher specialization enables the ants to occupy for a longer time the same nest characterized by the conditions largely independent of the external environment
(Jakubczyk, Czerwiński and Pętal 1972). In addition, the colonies of L. flavus reach higher numbers of individuals per nest at a smaller area used by the nest. Such responses of the nest as changes in the production rate and quality, moving the total colony or its part to another area, or the changes in the distribution of foragers searching the area, are more frequently observed in M. scabrinodis, i e., in the species more dependent on instantaneous environmental conditions. Many adaptations acquired by this species, and the strategy of the functioning of its colonies seem to depend on abiotic factors and on the defensive capacity of the inhabitants.

We wish to thank Dr. A. Łomnicki for valuable suggestions concerning the way of data processing and thorough revision of the manuscript. Grateful acknowledgement is extended to: J. Baryła, M. Sc., for phytosociological characteristics of the study area, D. Syrek, M Sc., and B. Janusz, M. Sc., for their assistance in the field work.

## 5. SUMMARY

The materials collected in a mountain meadow of the Silesian Beskid range, during the growing season of 1973, were used to estimate the density of ant nests (Table II), and seasonal activity of foraging ants caught in the Barber traps (Fig. 2). A total of 11 species were recorded, six of which had their nests in the plots (Table II). Both the number of nests and foraging individuals were the highest for three species: Myrmica scabrinodis, M. lobicornis and Lasius flavus. Only the activity of M. scabrinodis was significantly correlated with temperature (Table III).

The species diversity of ants captured at successive catches considerably varied throughout the season, thus the occurrence of foragers over the season was considered to compare the plots. There are differences between the plots in the correlation of M. scabrinodis occurrence with $L$. flavus occurrence (Table V). They are probably related to the mosaic structure of the habitat. Competition for food between the two species can increase in the uniform habitat.

The size of both the colonies and the populations of $M$ scabrinodis and $L$. flavus is diseussed. It seems to depend on the carrying capacity of the habitat and on the degree to what it is filled. The colony may be divided or move in the whole, the rate and quality of production can be changed or forager's activity may be modified. These are the reactions of ant nests to the changes in environmental conditions. They depend on the actual situation within the nest, and are probably related with the defensive capacity and safety of the colony.

Generally, the foraging ants have a clumped distribution. M. scabrinodis foragers are usually dispersed at their low densities, and they tend to aggregate with an increase in the density of all ants searching the area.

## 6. POLISH SUMMARY (STRESZCZENIE)

Zebrany w ciạgu całego sezonu wegetacyjnego 1973 r. material, na polanie górskiej w Beskidzie Śląskim, posłużył do oceny zagęszczenia mrowisk (tab. II) i sezonowej aktywności furażerujących mrówek, odławianych w pułapki Barbera (fig. 2). Na polanie stwierdzono 11 gatunków mrówek, przy czym 6 spośród tych gatunków posiadało gniazda na badanych powierzchniach (tab. II). Tak pod względem liczby gniazd jak i liczby furażerujących osobników dominowaly trzy gatunki: Myrmica scabrinodis, M. lobicornis i Lasius flavus. Jedynie akty wność Myrmica scabrinodis zależała istotnie od temperatury (tab. III).

Różnorodność gatunkowa chwytanych w poszczególnych odlowach mrówek wykazuje dużą zmiennosć w sezonie i dlatego porównując powierzchnię należy brać pod uwagę występowanie furaźerów w czasie całego sezonu. Wspólwystępowanie furażerów Myrmica scabrinodis i Lasius flavus jest różnie skorelowane na powierzchniach (tab. V) i zależy prawdopodobnie od mozaiki zajmowanego siedliska. Konkurencja o pokarm obu gatunków może nasilać się w jednorodnym srodowisku.

Wpracy dyskutowana jest liczebność społeczeństw i wielkość populacji gatunków Myrmica scabrinodis i Lasius flavus, które - jak się wydaje - są zależne od pojemności i stopnia wypelnienia siedliska. Mrowisko może zostać podzielone lub przeniesść się w calości, zmienić wielkosś i jakosć produkcji, lub przystosować działanie furażerów w terenie. Są to reakcje, wynikające z aktualnej sytuacji spoleczeństwa mrowiska, na zmieniające się warunki środowiska. Różne zachowanie Myrmica scabrinodis i Lasius flavus jest prawdopodobnie zależne od możliwości obronnych i bezpieczeństwa gniazda.

Rozmieszczenie furażerujących mrówek jest z reguły skupiskowe. Furażery Myrmica scabrinodis rozpraszają siẹ przy większym zagęszczeniu osobników tego gatunku, skupiają się natomiast wraz ze wzrostem róznorodności gatunkowej wszystkich penetrujących teren mrówek.

## 7. REFERENCES

1. Banert P., Pisarski B. 1972 - Mrówki (Formicidae) Sudetów - Fragm. faun. 18: 345-360.
2. Brian M. V. 1965 - Social insect populations - Academic Press, London-New York, 213 pp.
3. Brian M. V., Hibble J., Stradlina D. J. 1965 - Ant pattern and density in a Southern English heath - J. Anim. Ecol. 34: 545-555.
4. Celler L. 1972 - U̇̇ytki zielone w powiecie żywieckim -Wiad. melior. łąkar. 3: 90-92.
5. De Bruyn G. J., Mabelis A. A. 1972 - Predation and aggression as possible regulatory mechanisms in Formica -Ekol. pol. 20: 93-101.
6. Dobrzańska J. 1958 - Partition of foraging grounds and modes of conveying information among ants - Acta Biol. exp., Vars. 18: 55-67.
7. Gaspar C. 1972 - Actions des Fourmis du genre Lasius dans l'ecosysteme prairie - Ekol. pol. 20: 145-152.
8. Guilford J. P. 1964-Podstawowe metody statystyczne w psychologii i pedagogice - PWN, Warszawa, 570 pp .
9. Jakubczyk H., Czerwiński Z., Pętal J. 1972-Ants as agents of the soil habitat changes - Ekol. pol. 20: 153-162.
10. Kaczmarek W. 1953 - Badania nad zespołami mrówek lénnych - Ekol. pol. 1: 69-96.
11. Kajak A., Breymeyer A., Pętal J., Olechowicz E. 1972 - The influence of ants on the meadow inverte brates - Ekol. pol. 20: 163-172.
12. Koehler W. 1951 - Fauna mrówek Pienińskiego Parku Narodowego - PWRiL, Warszawa, 55 pp.
13. Lloyd M., Zar J. H., Karr J. R. 1968 - On the calculation of information-theoretical measures of diversity - Am.Midl. Nat. 79: 257-272.
14. MacArthur R. H., MacArthur J. W. 1961 - On bird species diversity - Ecology, 42: 594-598.
15. Parapura E., Pisarski B. 1971 - Mrówki (Hymenoptera, Formicidae) Bieszczadów - Fragm. faun. 17: 320-356.
16. Pętal J. 1968 - Woływ zasobności pokarmowej środowiska na rozwój populacji Myrmica laevinodis Nyl. (Formicidae) - Ekol. pol. B, 14: 287-296.
17. Petal J. 1972 - Methods of investigating of the productivity of ants - Ekol. pol: 20: 9-22.
18. Petal J., Pisarski B. 1966 - Metody ilosciowe w badaniach myrmekologicznych - Ekol. pol. B, 12: 363-376.
19. Pisarski B. 1973 - Struktura spoteczna Formica (C.) exsecta Nyl. (Hymenoptera: Formicidae) i jej wplyw na morfologię, ekologię i etologię gatunku - Instytut Zoologiczny PAN, Warszawa, 134 pp .
20. Pont in A. J. 1961 - Population stabilization and competition between the ants Lasius flavus (F.) and L. niger (L.) - J. Anim. Ecol. 30: 47-54.
21. Southwood T. R. E. 1966 - Ecological methods - Methuen and Co., London, 391 pp.
22. Stebaev I. V., Reznikova J. I. 1972 - Two interaction types of ants living in steppe ecosystem in South Siberia, USSR - Ekol. pol. 20: 103-109.
23. Waloff N., Blackith R.E. 1962 - The growth and distribution of the mounds of Lasius flavus Fabricius (Hym., Formicidae) in Silwood Park, Berkshire - J. Anim. Ecol. 31: 421-437.
24. Wilson E. 0.1972 - The insect societies - The Belknap Press of Harvard University 1 ress, Cambridge-Massachusetts-London, 548 pp .
25. Witkowski Z. 1970 - Zagadnienia różnorodności gatunkowej w badaniach biocenotycznych Wiad. ekol. 16: 117-132.
26. Yasuno M. 1964 - The study of the ant population in the grassland at the Mt. Hakkôda. II. The distribution pattern of ant nests at the Kayano grassland - Sci. Rep. Tôhoku Univ. Ser. 4, Biol. 30: 43-55.
27. Yasuno M. 1965 - Territory of ants in the Kayano grassland at Mt. Hakkôda - Sci. Rep. Tôhoku Univ. Ser. 4, Biol. 31: 195-206.

Paper prepared by H. Dominas

AUTHORS' ADDRESSES:
Mgr Michal Woyciechowski
Zakład Ochrony Przyrody PAN
ul. Lubicz 46
31-512 Kraków
Mgr Alicja Miszta
Instytut Botaniki
Uniwersytetu Śląskiego
ui. Jagiellońska 28
40-032 Katowice
Poland.

