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Use of Forest Associations by Bank Vole Population

[With 2 Tables & 5 Figs.]

Studies were made of a bank vole population on an island 4 ha in area by means of the *CMR* method. A total of 2233 individuals and 32,102 captures were obtained during the course of five seasons. It was found that this species more readily exploits the humid *Salici-Frangule-tum* and *Circaeo-Alnetum* associations than the dry *Tilio-Carpinetum stachyetosum silvaticae* and *Tilio-Carpinetum typicum*. When transfer from one habitat to another is easy exploitation of unpreferred associations increases with increasing population numbers, males exploiting the habitat more frequently than females. Old adults occupy preferred habitats in greatest numbers and thus reduce the young animals' chances of settling there. Reduction in numbers of cohort K_0, together with mortality and aging of the young cohorts, results in their moving to wetter associations.

1. INTRODUCTION

Earlier studies on a population of *Clethrionomys glareolus* (S c h r e b e r, 1780) showed that these animals prefer a moist habitat (W r a n g e l, 1939; T u r č e k, 1960; C h e ł k o w s k a, 1969) with an abundant supply of dead organic substances. During the course of studies on the secondary succession of a mountain forest stand maximum population density was found in the undergrowth and bush layer (G r o d z i ń s k i, 1959). G l i w i c z *et al.* (1967), in their studies on the bank vole population on the island, found that highly trappable individuals occupied humid habitats and those with lower trappability dry habitats. H s i a W u - P i n g (1964) found when examining variations in numbers (of

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C. rutilus, C. rufocanus, A. speciosus) in different biotopes that in years with high and very low population numbers the density of rodents is similar in different biotopes, while in years with average population numbers a high degree of density of the rodents was found only in humid habitats. The studies so far made on populations of the bank vole have thus shown which habitat this species prefers.

The purpose of the present study is to attempt to assess the degree of exploitation by a free-living population of *C. glareolus* of different plant associations under conditions formed by a habitat so mosaic-like in character that individuals were able to exploit more than one plant association simultaneously. Endeavour was also made to ascertain whether preferences shown for different biotopes vary in time and whether this depends on age, sex structure and population numbers.

This paper forms one of the cycle of studies on the bank vole carried out on material collected by a group of researchers of the Institute of Ecology, Polish Academy of Sciences. This material has been used, *inter alia*, for investigation of such problems as: variations in numbers (Gliwicz *et al.* 1968, Andrzejewski *et al.* in press), age structure (Gliwicz *et al.* 1968; Gliwicz, 1970), spatial structure (Mazurkiewicz, 1971), sex structure and reproduction (Bujalska, (1970), trappability (Gliwicz *et al.* 1968), and production (Petrusewicz *et al.* 1968, Petrusewicz *et al.* 1971), and part of the material from these studies was used for the present paper.

2. STUDY AREA, METHODS AND MATERIAL

The studies were carried out on an island 4 ha in extent, in Lake Bełdany (northern Poland 53°40′N, 21°35′E). The least distance of the island from the shore was 120 m, which prevented the rodents from migrating, and isolated the study population. The island is covered by a forest stand belonging to four phytosociological associations (Traczyk, 1965).

The *Tilio-Carpinetum typicum (T-Ct),* Traczyk (1962) (1.7 ha) association covers the central part of the island, which is highest and driest. The tree layer in this association is formed by *Pinus silvestris* L., *Carpinus betulus* L., *Tilia cordata* Mill. The herb layer is not dense (50%) and includes *Oxalis acetosella* L., *Aegopodium podagraria* L., *Asperula odorata* L. The soil is clayey and there is a considerable amount of small stones.

The lower parts of the island are occupied by the *Tilio-Carpienetum stachyetosum sylvaticae (T-Cs)* association (Traczyk 1962), (1.4 ha). *Alnus glutinosa* L. occurs in addition to the species of trees found in the above association. Species occuring in the herb layer include: *Stachys silvatica* L., *Athyrium filix-femina* (L), Roth., *Dryopteris filix-mass* (L), Schott. There is humus-like black sand on the soil surface. In the wet and peaty depressions on the island this association changes to *Circaeo-Alnetum (C-A)* Oberdorfer (1953) (0.3 ha). This association is characterized by far denser undergrowth (80%) in which the dominating species are *Urtica dioica* L. and *Circaea alpina* L. Soil there is black and peaty.

The *Salici-Frangueletum (S-F)* Malc. 1929 association (0.6 ha) forms a border round the island. The only tree species here is *Alnus glutinosa*, and the shrub species *Salix cinerea* L. and *Salix pentrandra* L. The herb leyer in which *Carex acutiformis* Ehrh. dominates is very dense (70%). Soil consists of more or less homogenous peat, covered by grass and sedge (Fig. 1).

The material used in this study was obtained during the period from 1966—1970. Five trapping series were carried out year ly from April to October (Table 1), with an interval of approx. 4 weeks between succesive series. Each of these series

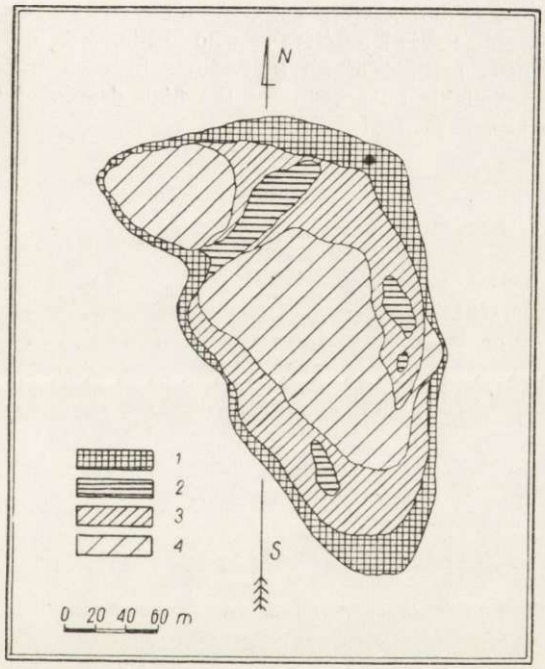


Fig. 1. Island in Lake Bełdany (after Traczyk, 1965).
1 — *Tilio-Carpinetum typicum* (*T—Ct*), 2 — *Circaeo-Alnetum* (*C—A*), 3 — *Tilio-Carpinetum stachyetosum sylvaticae* (*T—Cs*), 4 — *Salici-Franguletum* (*S—F*).

asted for 2 weeks in 1966 and 1967, and for ten days as from 1968. In 1969 and 1970 he first series were carried out at the beginning of May, and not in April, on ıccount of the late melting of ice on the lake.

The island was covered by a grid of live traps set on 159 sites, at intervals of 5 m. Two traps were set on each site in 1966 and 1967. In 1968 a pitfall of the ype used by Andrzejewski & Wrocławek (1963) was sunk into the ground on each site and baited, and in 1969 and 1970 3 traps and 1 pitfall. The study method was based mainly on the *CMR* method (Catch-Mark-Release).

The animals being marked with individual numbers by means of toe clipping. Traps were inspected twice daily at 7,00 and 19,00. Information obtained from the data recorded during the trapping period and used in this study consisted mainly of: number of individual, sex and trapping site. A total of 2,233 individuals were caught a total of 32,102 times.

3. MATERIAL FROM OTHER STUDIES USED IN THIS PAPER

The material used in this study has already formed the subject of other elaborations. Variations in numbers were accepted after Gliwicz *et al.* (1968) and Andrzejewski & Rajska (1972), who estimated numbers of rodents by the general census method of all individuals in each trapping series. These figures proved very reliable on account of the high degree of trappability of the population (Gliwicz *et al.* 1967).

Table 1

Times of successive trapping series.

1966	1967	1968	1969	1970
22—29.IV	15—29.IV	17.IV—1.V	1—10.V	5—14.V
2—16.VI	31.V—14.VI	1.VI—14.VI	5—14.VI	5.VI—15.VI
17—31.VII	16—30.VII	16.VII—29.VII	22—31.VII	22.VII—1.VIII
5—18.IX	31.VIII—14.IX	30.VIII—12.IX	7—16.IX	6.IX—16.IX
19.X—2.XI	16—30.X	14.X—25.X	24.X—2.XI	24.X—2.XI

Table 2

Percentage of sites in different associations.

	Area, ha	No. trapping sites	Percentage of sites
Salici-Franguletum	0.6	25	15.70
Circaeo-Alnetum	0.3	12	7.55
Tilio-Carpinetum stachyetosum sylvaticae	1.4	53	33.35
Tilio-Carpinetum typicum	1.7	69	43.40
Total	4.0	159	100.00

Data on the population's age structure were accepted after Gliwicz *et al.* (1968) and Gliwicz (1970). Bujalska *et al.* (1968) on the basis of the rodents' time of birth, differentiated several groups of individuals born at a given time, termed cohorts. The following cohorts were distinguished: cohort K_0 — individuals which had survived the winter (old adults), cohort K_1 — early spring generation, cohort K_2 — early summer generation, cohort K_3 — late summer generation and cohort K_4 — early autumn generation.

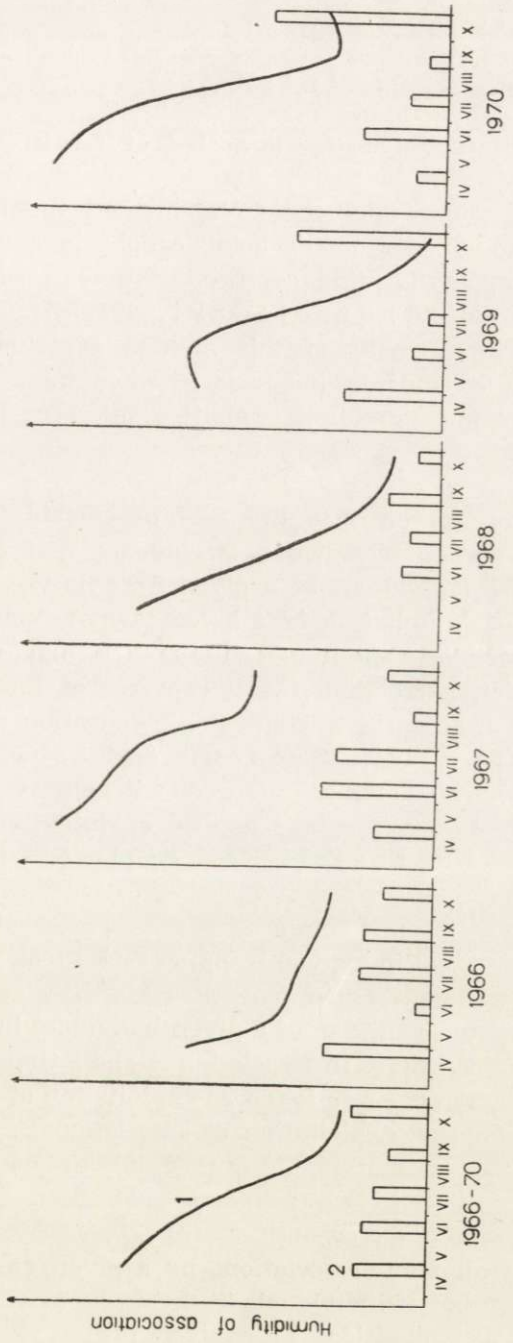


Fig. 2. Variations in humidity of associations.
1 — rainfall, 2 — water level.

Humidity indices for the habitat were elaborated on the basis of data obtained from the State Institute of Hydrology and Meteorology on fluctuations in water level in the lake and rainfall (Fig. 2).

4. RESULTS

4.1. Assumptions in Analysis of Material

When catching rodents by the *CMR* method the basic information is the fact of the given animal's being caught in a trap and the circumstances accompanying this capture — time, place, characteristics of the individual *etc.* (Andrzejewski, 1969). If therefore it is desired to estimate by means of this method exploitation of different plant associations by rodents, particularly when there is the possibility of one and the same individual exploiting different plant associations within one period, it is necessary to accept certain assumptions which enable further analysis of material to be made.

It was therefore taken that the fact of certain individuals being caught in a given plant association is evidence that this association is exploited by these individuals at a given time. It was further accepted that intensivity of exploitation of a given plant association by an individual is in proportion to the number of captures made of this individual in a given habitat, in relation to all captures of this individual. This assumption is often accepted in studies on penetration of the home range by rodents (Hayne, 1949; Calhoun & Casby, 1958; Mazurkiewicz, 1971). This assumption agrees with observations which show that frequency of visits to a trap depend on intensivity of penetration of a given habit (Andrzejewski, Fejgin & Liro, 1971).

The above assumption made it possible to calculate the number of individuals using different habitats in such a way, that when all captures of a given individual in a given trapping series took place in one plant association, it was taken as »exploiting« this association only. On the other hand if, out of y captures of a given individual in a given trapping series, it was saught x times in association A and z times in association B, then x/y of the individual was taken as exploitation of association A and z/y of the individual as exploitation of association B. The sum total of individuals and part of individuals caught only in the given association was termed »exploitation« of the given association by a given group of individuals (population, cohort). In the same way the sum total of »exploitation« of all plant associations by a given group of individuals is equal to the number of individuals in this group.

In addition to »exploitation« of a given plant association calculation was made of »visits« to a plant association. In this case all individuals

were counted, regardless of the number of their captures in the given association and trapping series. If therefore the individual was caught in two or more associations, then it was counted as »visiting« each of them.

The null hypothesis was also accepted, that both exploitation and visiting of different plant associations should be in proportion to the area which they occupy on the island. Hence both the area occupied by the different plant associations, and also exploitation and visiting were given in percentages of the total area of the island and the sum total of exploitation and visiting of the associations on the whole island. Conclusions were reached from comparing these percentages.

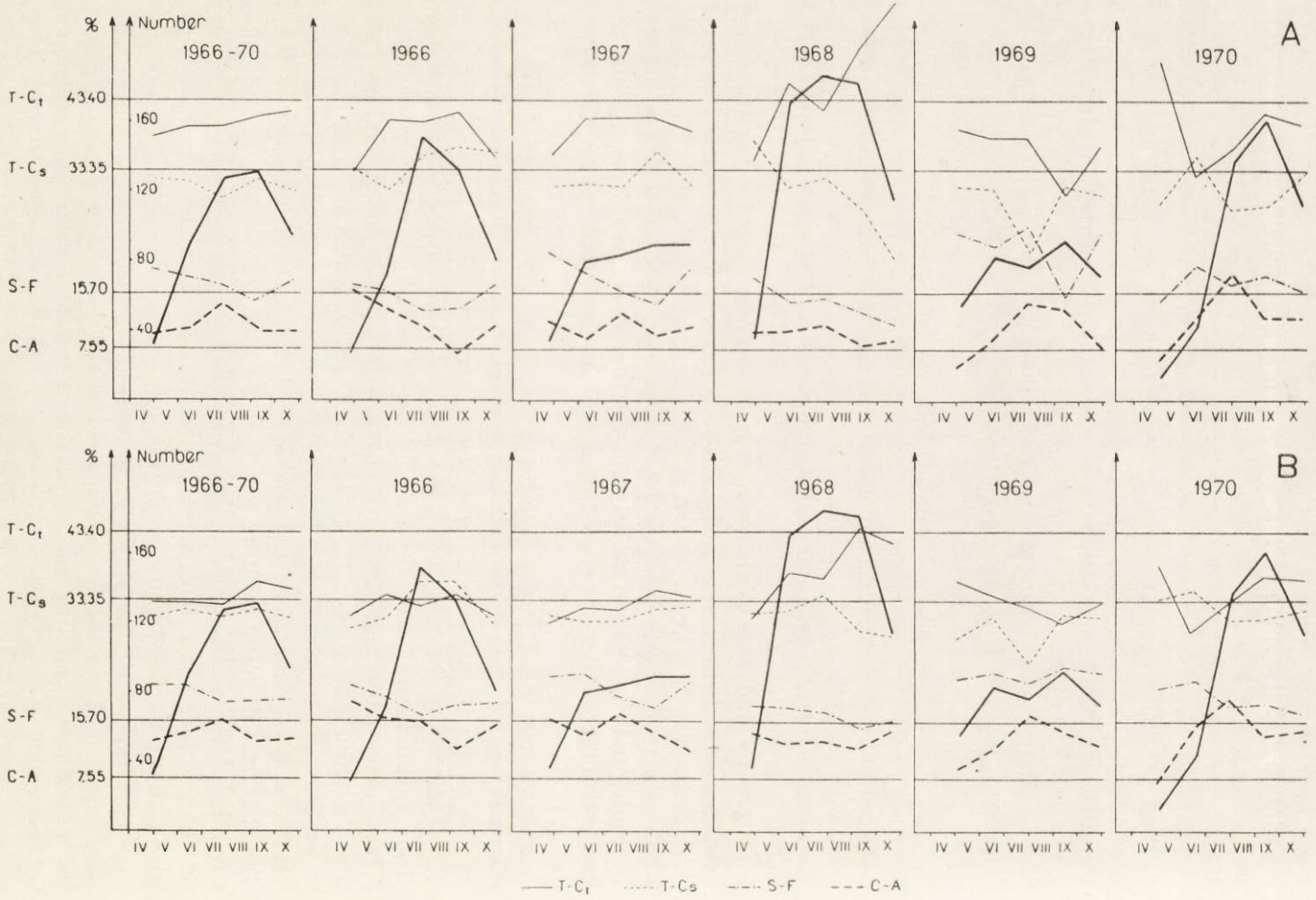
4.2. Exploitation of Different Habitats

Initial analysis of captures of males and females did not reveal differences in exploitation of the associations, which permitted of treating the sexes jointly. It was found that exploitation of humid habitats (*S—F* and *C—A*) is higher throughout the whole season and lower in dry habitas (*T—Cs* and *T—Ct*) than could have been expected from the percentage of the island area occupied by these associations (Fig. 3).

Exploitation of *Circaeo-Alnetum* increases from spring to July, and exhibits a tendency to decrease from August to October. The percentage of individuals exploiting *Salici-Franguletum* decreases from spring to the beginning of September and does not increase until the end of October (Fig. 3).

The wettest association — *Salici-Franguletum* — was exploited in 17 cases out of 25 to a greater degree than the percentage of the area of the island formed by this association. A distinct decrease in the interest shown by the bank voles in this association can be observed from June to September 1966, and also from mid-June to September 1968. These years (1966 and 1968) are characterized by high survival rate of the individuals in cohort K_0 (Gliwicz, 1970), which have the largest home ranges (Mazurkiewicz, 1971) and, as suggested by Gliwicz (1970), probably dominate over younger individuals. It is possible that the considerable numbers in cohort K_0 prevented the younger individuals from using the wet habitats occupied by the former. As a result animals in the younger age groups were obliged to resort to the driest association — *Tilio-Carpinetum typicum* (Fig. 3).

In the second of the wet associations — *Circaeo-Alnetum* — it was found that in 22 of the 25 trapping series the percentage of the number of individuals exploiting this association is greater than the percentage of the whole area of the island formed by this association. It was only


%
Number
1966-70
1966
1967
1968
1969
1970
A
B
T-Ct 43.40
T-Cs 33.35
S-F 15.70
C-A 7.55
160
120
80
40
IV V VI VII VIII IX X
T-Ct
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in spring 1969 and 1970 and in September 1966 that the percentage of individuals using this association was smaller than the percentage of the island area formed by this association (Fig. 3).

The great survival of individuals in cohort K_0 in 1966 resulted in exploitation of *Circaeo-Alnetum* in September of that year being lower than the percentage of total area formed by the association. The failure to make full use of this association in May 1969 was due to the large numbers of rodents then living in *Salici-Franguletum*. The low population numbers in spring 1970 might account for the incomplete use of *Circaeo-Alnetum* by bank voles at that time.

Exploitation of dry associations (*T—Cs* and *T—Ct*) during the season is lower than the value resulting from the percentage of these associations of the island area in 18 cases out of 25 for *T—Cs*, and in 21 cases out of 25 for *T—Ct* (Fig. 3). Exploitation of the driest association, *Tilio-Carpinetum typicum*, was lower, except for June and the period from August to October 1968, than the percentage of this association of the total area of the island (Fig. 3).

Exploitation of the second dry association (*Tilio-Carpinetum stachyetosum sylvaticae*) for the average of five years was lower throughout the whole season than the percentage of total area formed by this habitat. Its exploitation markedly increases above this level from July to October 1966, while at the same time there was a decrease in the exploitation of the wet associations *Salici-Franguletum* and *Circaeo-Alnetum*, as stated above.

Comparison was made of the exploitation of dry associations and variations in population numbers. It was found that the extent to which the two dry associations (*T—Cs* and *T—Ct*) are used by bank voles is in proportion to variations in numbers (Fig. 3). The only deviation from this pattern was in 1968, when the number of individuals exploiting *Tilio-Carpinetum typicum* increased, with simultaneous decrease in the numbers of these rodents in the other three associations during the period from July to October. It would, however, seem that population numbers do not affect exploatation of wet associations, which are always more intensively exploited by bank voles.

4.3. Visits to Forest Associations by Bank Voles

When the parcentage of the number of individuals visiting and exploiting an association were compared it was found that the values illustrat-

Fig. 3. — Numbers of individuals exploiting association, in per cent (A), and numbers of individuals visiting association, in per cent (B).
Heavy line — dynamics of numbers.

ing this would seem to exhibit variations of a similar character, but the numbers of individuals visiting wet associations are greater than the corresponding numbers of individuals exploiting them (Fig. 3). The reverse situation is found in dry associations. Thus in wet associations it is not only the bank voles living there which are caught, but also the individuals visiting there, which exploit dry associations. In dry associations it is mainly the individuals resident there which are caught.

4.4. Age of Individuals and Exploitation of Associations

4.4.1. Number of Associations Visited by Bank Voles

Differences between sexes, and also between cohorts, become clear when the number of associations visited by these rodents are considered (Fig. 4). It was found that individuals belonging to cohort K_0 visit more

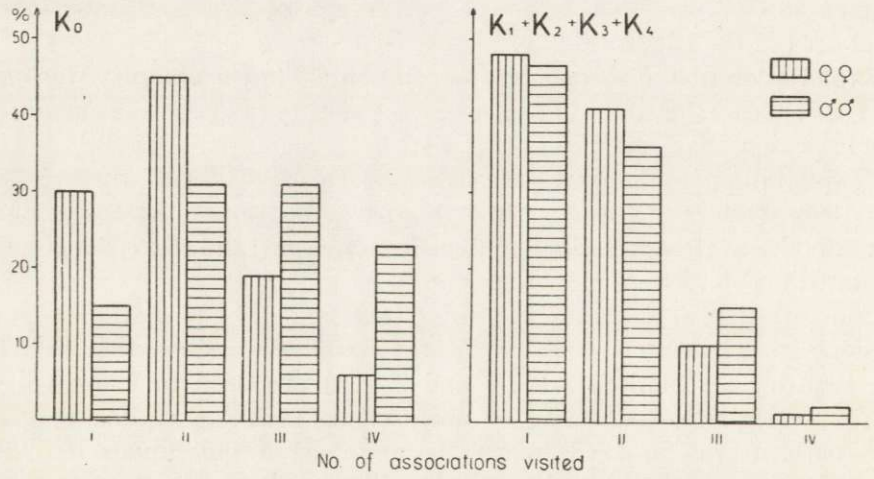

Fig. 4. Percentage of rodents caught in given number of associations.

associations than animals in the other cohorts. The majority of females in cohort K_0 are caught in two associations. The males of this cohort have the largest home ranges (Mazurkiewicz, 1971) and therefore their participation in all four associations is more balanced than that of females. The percentage of cohort K_0 males occurring in one association only is relatively low (15%). In the other cohorts (from K_1 to K_4) there are no such differences between males and females. The greater part of captures of both males and females take place in either one or two associations (Fig. 4). This is probably connected with the smaller

home range of individuals belonging to the younger age groups (Mazurkiewicz, 1971).

4.4.2. Exploitation and Visiting of Associations by Different Age Groups

It was found that the different age groups exploit the associations in an analogical way to that of the whole population, that is, they prefer wet associations (Fig. 5). A relation can, however, be observed to occur between the age of the individuals and exploitation of associations. The percentage of individuals exploiting wet associations (*S—F* and *C—A*) increases parallel to aging of the population. The percentage of individuals in the youngest cohort (K_4) is smallest in the exploitation of these associations, and that of old adults (K_0) the greatest. The reverse situation is found in dry associations (*T—Cs* and *T—Ct*). Simultaneously the bank voles are observed to pass from dry to wet associations as the age groups get older. This is connected with the mortality of old individuals (chiefly K_0) and to their place being taken by animals from the younger age classes (Fig. 5).

When exploitation and visiting of associations by different age groups are compared it was found that the numerical values illustrating this take a similar course, but in the case of individuals visiting associations they occur on a higher level. The behaviour of different age groups is therefore analogical, like that of the whole population taken jointly, since when the percentages of the number of individuals visiting and exploiting associations were compared it was observed that the numbers of individuals visiting moist associations (*S—F* and *C—A*) are greater than the corresponding numbers of individuals exploiting these associations. This confirms the supposition that it is not only the bank voles exploiting wet associations which are caught there, but also individuals entering them from dry associations. In the latter it is chiefly the individuals exploiting them which are caught in them.

In order to check whether changes in exploitation of moist associations by cohort K_0 and younger cohorts are similar in time, calculation was made of the correlation of exploitation of these associations by cohorts K_0 and K_1, and K_1 and K_2. Using Spaermann's sequence test it was found that there is correlation of exploitation ($r=0.679$) and visiting ($r=0.740$) of these associations by individuals of the young cohorts (K_1 and K_2). This is evidence of an absence of significant differences between these cohorts. Correlation was also found between the number of individuals belonging to cohorts K_0 and K_1 ($r=0.589$) visiting these associations, which shows that there are no differences between individuals of cohort

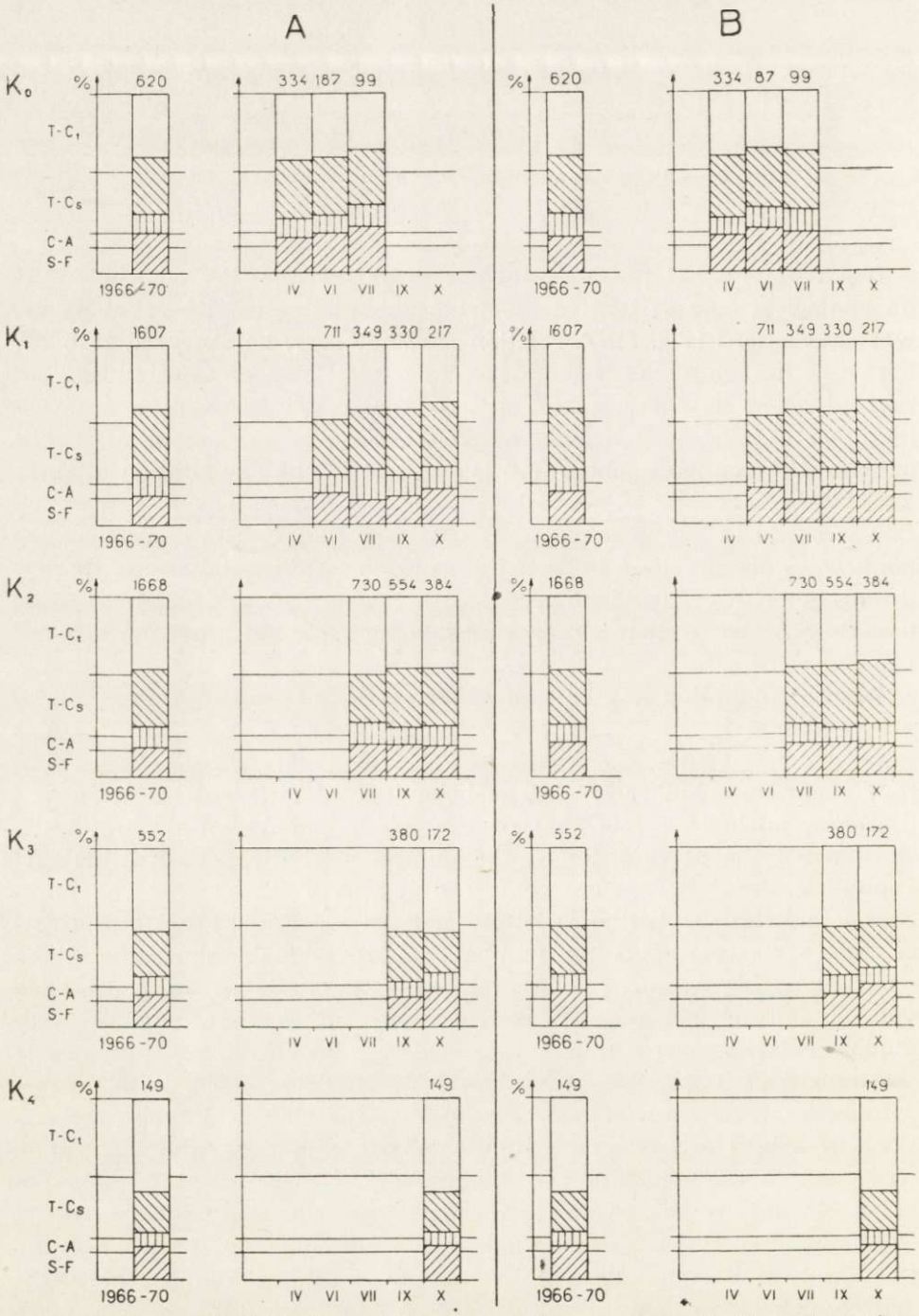

Fig. 5. Number of individuals exploiting association, in per cent (A), and number of individuals visiting association, in per cent (B).

Numbers above columns indicate number of individuals from which percentage value was calculated.

K_0 and those of cohort K_1 in intensity of visiting moist associations. Changes in exploitation of these associations by cohorts K_0 and K_1 exhibit correlation which is not statistically significant ($r=0.358$), which is evidence of the independence of changes in exploitation of these associations by individuals of these cohorts.

4.5. Humidity of an Association and Exploitation of Associations

In order to ascertain whether exploitation of different associations by bank voles depends on the humidity of the former, a diagram was made of changes in subsoil water level and amount of rainfall (Fig. 2). Subsoil water level depends on the water level in the lake surrounding the island. When the level of subsoil water is high (particularly in 1967) the wettest association — *Salici-Franguletum* — was partially under water.

Increase in the moisture of dry associations (*T—Cs* and *T—Ct*) raises the degree of their attraction for the bank vole. In 1967 population numbers were low and despite this the animals readily exploited dry associations. Subsoil water and rainfall were maintained on a very high level in that year (Fig. 2). It is possible that a rise in the lake water level and rainfall balance the contrasts in humidity between the different types of plant association on the island. The situation in 1969 was quite different. As in 1967, the population numbers were low, there was a drought and the level of subsoil water and rainfall was very low (Fig. 2). An increase in exploitation of moist habitats greater than that in the other years was observed, with simultaneous decrease in the exploitation of dry associations.

It would appear that the humidity of an association may be a factor conditioning its exploitation only when population numbers are low (1967 and 1969), whereas in years when population numbers are high (1966, 1968 and 1970), despite the drying up of dry associations from spring to autumn, an increase was observed in the exploitation of these associations by young individuals, parallel to increase in population numbers.

5. DISCUSSION

On the basis of the results obtained it was found that the preferences of bank voles for the plant associations occuring on the island differ. Humid associations (*S—F* and *C—A*) are greatly preferred and their exploitation was far higher than the value resulting from the percentage which they form of total island area. Exploitation of drier associa-

tions (*T*—*Cs* and *T*—*Ct*) was usually lower than would be indicated by their percentage of total area. The results obtained agree with data in literature showing that the bank vole likes a damp habitat with a large amount of dead organic substances in the ground (Wrangel, 1939; Turček, 1960; Chełkowska, 1969 and others).

It is possible that a decrease in the value of the percentage of exploitation and visiting of moist associations from April to September 1966 and over the whole season in 1968 was caused by the high survival of individuals in cohort K_0. In those years exploitation of those biotopes by individuals of the oldest cohort prevented their being occupied by individuals in the younger cohorts (Gliwicz, 1970). As individuals in cohort K_0 disappear, animals from the younger age groups are observed to move into these associations (Fig. 5).

In years distinguished by high population numbers of *C. glareolus* (1966, 1968 and 1970) both exploitation and visiting of different associations came close to an even distribution, corresponding to the percentages of total area formed by these associations, and gradual occupation by these animals of dry associations was observed. The spatial distribution of the population was more even at that time. Simultaneously increase in exploitation of dry associations was observed from spring to September. Exploitation of associations in years of low population numbers (1967 and 1969) depends to a great extent on the moisture of the association. When this is high (1967) their exploitation is nearly even, but with low moisture (1969) preference for moist associations is clearly marked (*S*—*F* and *C*—*A*). It would, however, seem that the most important factor deciding the spatial distribution of the population is its numbers. This finding is also confirmed by data in literature (Hsia Wu-Ping, 1964). Despite the reduction in the humidity of associations observed during the season animals belonging to the younger age groups were observed to move to dry habitats. Rodents exploiting moist associations are closely connected with the latter, and the animals are not observed to transfer to dry associations. Animals from dry associations also are readily caught in moist habitats. This may perhaps be connected with the bank vole's tendency to move to wetter habitats.

The different character of individuals in cohort K_0 from the other cohorts is also confirmed by other studies made on the island, relating to home ranges (Mazurkiewicz, 1971) and reproduction in the bank vole population (Bujalska, 1970). Old adults inhabit the most preferred habitats. The males of this cohort have the largest home ranges (Mazurkiewicz, 1971) and when conditions in an area are of a mosaic character these animals can be encountered in all associations. As the

numbers in cohort K_0 decrease over the season, bank voles from younger age groups may move to the preferred habitats.

The results presented thus permit of arranging factors inducing the bank voles to occupy different plant associations in the following order.

The first factor determining distribution is the humidity of a given plant association, which at the same time is probably to a great extent responsible for the food conditions available to the bank vole in the given association.

The second factor in this order is population density, increase in which causes the voles to occupy drier habitats, which are less favourable to them.

Finally the third factor is the age structure of the population, and in particular the percentage in this structure of the oldest age group — the old adults. This group, dominating over the younger individuals, occupies the optimum associations and prevents the younger cohorts from settling in them.

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WYKORZYSTANIE ZESPOŁÓW LEŚNYCH PRZEZ POPULACJĘ NORNICY RUDEJ

Streszczenie

Analizowany materiał uzyskano w latach 1966—1970 z badań populacji *Clethrionomys glareolus* (Schreber, 1780) zamieszkującej wyspę o powierzchni 4 ha na jeziorze Bełdany (północno-wschodnia Polska) (Fig. 1). Wyspa pokryta jest lasem należącym do czterech zespołów fitosocjologicznych: *Salici-Franguletum, Circaeo-Alnetum, Tilio-Carpinetum stachyetosum sylvaticae i Tilio-Carpinetum typicum* (Traczyk, 1965) (Fig. 1). Podział populacji nornicy na grupy jednowiekowe (kohorty) przyjęto za Bujalską (1968). Gliwicz *et al.* (1968) wyróżnili następu-

jące kohorty: przezimki (K_0), pokolenie wiosenne (K_1), wczesnoletnie (K_2), późnoletnie (K_3) i pokolenie jesienne (K_4).

Analiza uzyskanych wyników wykazała, że mając do wyboru cztery wyżej wymienione środowiska, nornica preferuje *Salici-Franguletum* i *Circaeo-Alnetum* (Fig. 3), które odznaczają się wyższą wilgotnością, bogatą szatą roślinną i dużą ilością martwych substancji organicznych w podłożu. W warunkach łatwego przenoszenia się z jednego środowiska do drugiego, wykorzystanie niepreferowanych środowisk zwiększa się ze wzrostem liczebności populacji (Fig. 3). Przezimki zajmują najliczniej środowiska preferowane, umniejszając w ten sposób szanse młodzieży w osiedlaniu się tam (Fig. 5). Zmniejszenie się liczebności kohorty K_0 osiadłej w środowiskach preferowanych, umożliwia osobnikom kohort młodszych przechodzenie do środowisk wilgotnych (Fig. 5).