

Joanna GLIWICZ

**Relation between Trappability and Age of Individuals
in a Population of the Bank Vole**

[With 6 Tables & 4 Figs.]

The trappability of a population of *Clethrionomys glareolus* (Schreber, 1780), the age structure of which is complex, exhibits a connection with the age of individuals. Differences in trappability between individuals of the same age are considerable at the beginning of their lives, then decrease, but later increase during the course of their lifetime. The correlation of number of captures of the same individuals in successive series of trappings increases slightly, which may constitute evidence that differences in trappability become permanent in character. Differences in trappability connected with sex are distinct in the case of overwintered individuals only. In the remaining age groups they are effaced by differences in the age of individuals and also in the maturation rate of males and females. In late autumn differences in trappability between individuals of different sex and of different age partly disappear. A discussion is given of the factors affecting the trappability of a population of complicated age structure, with particular emphasis on the role of the social structure.

1. INTRODUCTION

Investigations of animal populations made by means of the Catch-Mark-Release (CMR) method enable the same individuals to be caught several times over. The number of these captures within a definite period, that is, trappability, depends on two groups of factors. The first consists of purely methodical factors, such as the quality of trapping devices (traps, pitfalls *etc.*) and also the ratio of the number of these devices arranged in the study area to the numbers of the population living in this area. The second group consists of »population-produced« factors which determine the biological reaction of the animals to these devices, such as the distribution of animals in the area, their activity, relations between individuals, interest in bait *etc.* The factors cause the frequency of capture of animals to differ even when the intensity of the effect of the trapping devices is constant.

Trappability can be considered from two standpoints in ecological studies on small mammals. In the first case they supply material making it possible both to determine population numbers (Lincoln's index —

Lincoln, 1930, the CC method — Petruszewicz & Andrzejewski, 1962; Andrzejewski, 1969 etc.) and to calculate indices requiring information obtained several times over about the same animals (e. g. home range size, growth rate of the individual). In the second case trappability is in itself an index of differences between individuals (or groups of individuals) in respect of the biological reaction to traps. This reaction is conditioned by the animal's behaviour, which in turn depends on the individual's physiological and ecological situation.

In the present study trappability has been considered from the latter point of view, in particular an analysis has been made of the relation between the trappability of different individuals and their age and sex and factors indicated as responsible for the existence of this relation in a population of *Clethrionomys glareolus* (Schreber, 1780).

2. DESCRIPTION OF STUDY AREA, METHOD AND MATERIAL

The material contained in the present study was obtained from a two-year study period (1966 and 1967) of a population of *C. glareolus* living on an island 4 ha in extent situated in Lake Beidany (north Poland — N 53°40' E 21°35').

The island is covered with vegetation belonging to three phytosociological associations: *Salici-Franguletum* Malc., 1929; *Circeo-Alnetum* Oberdorfer, 1953; *Tilio-Carpinetum* Traczyk, 1902, with two sub-associations — *T.-C. typicum* and *T.-C. stachyetosum silvaticae* (Traczyk, 1965).

The minimum distance of the island from the shore of the lake is about 120 m, as a result of which the phenomenon of migration of individuals between the bank and the island does not take place. The rodents living on the island can thus be considered an isolated population.

Five series of captures using the CMR method were made at 6-week intervals in both years during the period from spring to autumn (April 15th — October 31st). A detailed description of the methods used on the island is to be found in studies by Andrzejewski, Petruszewicz & Waszkiewicz-Gliwicz (1967), Gliwicz *et al.* (1968). All the animals caught were marked with individual numbers by toe-clipping. Each series of trappings lasted 14 days. During the trapping period the island was covered by a grid (15 × 15 m) of live traps, arranged with two traps always on the same 159 sites. The traps were inspected twice daily (7⁰⁰, 19⁰⁰). Each series of trappings thus consisted of 8904 trap inspections (28 inspections × 159 trapping sites × 2 traps per site), which each time constituted the upper limit of the number of captures possible to obtain for all individuals in the population.

It was only in April 1966 that the trapping series lasted only 7 days. In order to obtain comparable results all data on trappability during this period were multiplied by 2.

In practice the number of captures obtained during one series of trappings varied within limits of 848 — 2412 in 1966, and 813 — 2165 in 1967, the lowest number being obtained in every case in April, and highest in September. All the individuals were caught during each series of captures (cf. — Andrzejewski, *et al.*, 1967), which made an exact assessment of their numbers possible.

The material used in this study has already formed the subject of other comprehensive elaborations. Using the data on disappearance of marked individuals during periods between successive series of captures (mortality) and arrival of unmarked individuals during the reproductive season (natality) as a basis, an accurate picture was obtained of dynamics of population numbers during the given periods (Fig. 1), based on five censuses of numbers (Gliwicz *et al.* 1968).

By analysing vaginal smears taken from females at each capture (Bujalska *et al.*, 1968; Bujalska *in litt.*) it was possible to determine the dynamics of numbers of pregnant females and on this basis to assess the average day of birth of individuals which were recorded for the first time in traps during each of the

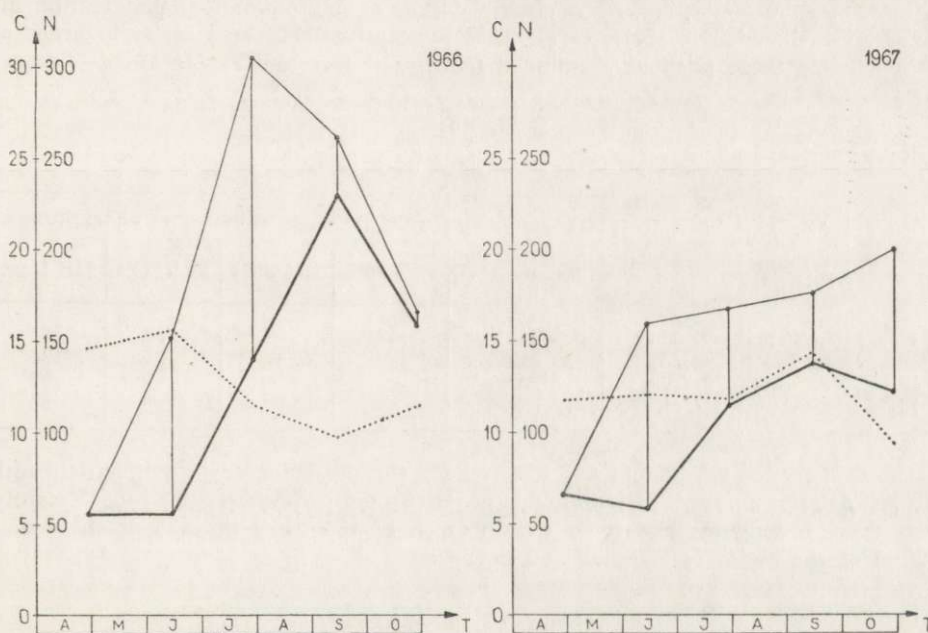


Fig. 1. Trappability of a population and its numbers: Thin line — dynamics of population numbers (N); thick line — dynamics of numbers of »fully-trappable« individuals; dotted line — effective trappability of a population (c).

trapping series. In this way it was possible to distinguish four groups of young individuals born within a relatively short time each year, the so-called cohorts: K_1 , K_2 , K_3 and K_4 and a group of older animals which had overwintered (K_0) and had been born the previous reproduction season.

All the unmarked young individuals caught during the June series of trappings were allocated to cohort K_1 , which included individuals born in April and May. Correspondingly individuals recorded for the first time during the July series of trappings, and born during the period from May to mid-June, were allocated to the second cohort (K_2), and consequently the period during which K_3 were born — recorded during the first half of September, was the second half of June, July and August. The period during which cohort K_4 was born — recorded in the

second half of October — was held to be the final day of births of K_3 , and on the other hand the end of the reproduction season on the island, and thus lasted from the end of August to the beginning of October¹).

A detailed analysis and description of cohorts (Table 1) has been made and published for 1966 (Bujalska *et al.*, 1968, Gliwicz *et al.*, 1968). The deviations from data given in Table 1 for the cohorts born in 1967 are relatively small.

The cohort is a group of individuals of more or less uniform age. Differences in the age of individuals belonging to one cohort may be at most 6 weeks. As the result of the application of this division of individuals each series of captures is a different successive series for each cohort, *e.g.* the September series of trappings is the third successive series for K_1 , the second for K_2 and the first for K_3 . It may thus be assumed, with a certain degree of approximation, that all the individuals included in a series of captures constituting the same series in order of sequence for these particular animals, are of uniform age (Table 1).

Table 1.
Description of cohort born in 1966.

Cohort	Period during which the cohorts are born	Average day of birth of the cohort	Age in consecutive series of trappings			
			16th June	31st July	18th Sept.	2nd Nov.
K_1	1 April—26 May	5 May	42	87	136	181
K_2	27 May—10 July	19 June	—	42	91	136
K_3	11 July—28 Aug.	2 Aug.	—	—	47	92
K_4	29 Aug.—1 Oct.	10 Sept.	—	—	—	53

In consequence we had at our disposal for the present study a population with strictly defined numbers of individuals of strictly defined age and also the certainty that these individuals had lived within reach of the traps throughout the whole period of the series of trappings.

3. ANALYSIS OF MATERIAL

3.1. General Remarks

It was accepted, after Petruszewicz & Andrzejewski (1962) and Andrzejewski (1969), that the index of trappability describing the study population during each series of trappings was the so-called real trappability expressed by the equation

$$c = \frac{C}{aN} \quad (1)$$

where c — real (effective) trappability, C — the total number of captures made during one series of trappings, a — number of times the

¹) There were very few animals in cohort K_4 in 1966 and it could not therefore be included in the analyses of trappability made.

trapping devices were set during this series, N — number of trappable individuals in the population.

As the number of times the trapping devices were set was the same in both years for each series of trappings ($a = \text{const.}$) this equation can be simplified as follows:

$$c = \frac{C}{N} \quad (2)$$

The real trappability of the study population during the given series of trappings will thus be the average number of captures per individual during this series. This equation was also used to calculate the trappability of individuals belonging to the given cohort.

Table 2.
Numbers of »fully-trappable« individuals.

Cohort	1966				
	22—29 April	2—16 June	17—31 July	5—18 Sept.	19 Oct. — 2 Nov.
K_0	56	38	21	6	—
K_1		18	78	50	31
K_2			41	164	111
K_3				10	15
	56	56	140	230	157
Cohort	1967				
	15—29 April	31 May — 14 June	16—30 July	31 Aug. — 14 Sept.	16—30 Oct.
K_0	68	36	12	8	—
K_1		22	89	54	36
K_2			12	54	38
K_3				22	33
K_4					15
	68	58	113	138	122

The index of trappability accepted as above makes some degree of selection of trapping material necessary. In further analysis of this material we shall take into consideration only captures of those individuals which could undoubtedly have been caught during the whole 14-day period of the series. In consequence some of the individuals from the youngest cohort for the given period of trapping, which grew up to trap age during this period and entered into the trappable part of the population during the time the series of trappings lasted, have been eliminated from these investigations. The number of captures recorded for them was therefore limited by the shorter period of contact between these individuals and traps.

In practice all those individuals from the youngest cohort which had not made their appearance in the area during the first two inspections of the traps were omitted from the analysis of captures. The reason for this was that the results obtained in the study by Gliwicz *et al.* (1968), showed that 75% of the individuals of a study population which are present in the area make their appearance after two inspections. Captures of those individuals which had not survived through the whole period of the given series of captures were also omitted from the material. As a result of these omissions values N and C included in equation (2) refer respectively to population numbers and number of captures of »fully-trappable« individuals (possessing chances of being caught from the first to the last trapping in the given series).

There are considerable differences between the numbers of these fully-trappable individuals (Table 2) and the numbers of the whole population in certain periods (Fig. 1).

In further consideration of the variations in trappability of different individuals within one cohort (section 3.3. and 3.4.) the number of captures of a given individual during one series of trappings was taken as a measure of this individual's trappability.

3.2. Age of the Cohort and Its Trappability

Calculation was made for each cohort of its effective trappability during each series of trappings in 1966 and 1967 (Table 3, Fig. 2). It was found in both years that the younger the cohort the smaller the values of trappability considered for each series of trappings of individuals belonging to different cohorts. An exception to this is October 1966, in which the trappability of individuals in all cohorts is balanced and September 1967, in which the trappability of cohort K_0 is relatively low.

On the other hand, when considering variations in trappability of the same cohort during successive series of captures, it is not found that trappability increases as the cohort grows up, *e. g.* in 1966 K_1 gives an average of 12.9 captures per individual in June but in July and September the trappability figures are lower, *i. e.* 11.6 and 11.1 captures per individual, despite the fact that the cohort is older. The probable reason for this is that in each of the periods observed (within one year) the trappability of individuals is determined under slightly different population density conditions (with a different ratio of number of traps to number of individuals) and under different phenological and climatic conditions which, as Kikkawa (1964) states, exert a very significant effect on trappability through variation in the interest taken by the rodents in the traps.

Table 3.

Effective trappability of cohorts and of whole population.

Cohort	1966				
	22-29 April	2-16 June	17-31 July	5-18 Sept.	19 Oct. - 2 Nov.
K_0	14.7	↑ 16.9	↑ 17.5	↑ 20.7	—
K_1		12.9	↑ 11.6	↑ 11.1	11.5
K_2			8.8	↑ 9.1	11.6
K_3				7.5	11.7
All population	14.7	15.6	11.7	9.8	11.6
Cohort	1967				
	15-29 April	31 May - 14 June	16-30 July	31 Aug. - 14 Sept.	16-30 Oct.
K_0	11.9	↑ 12.8	↑ 18.1	14.0	—
K_1		10.7	↑ 11.7	↑ 16.3	↑ 11.3
K_2			7.6	↑ 14.2	9.5
K_3				9.4	7.4
K_4					7.5
All population	11.9	12.0	11.9	14.3	9.2

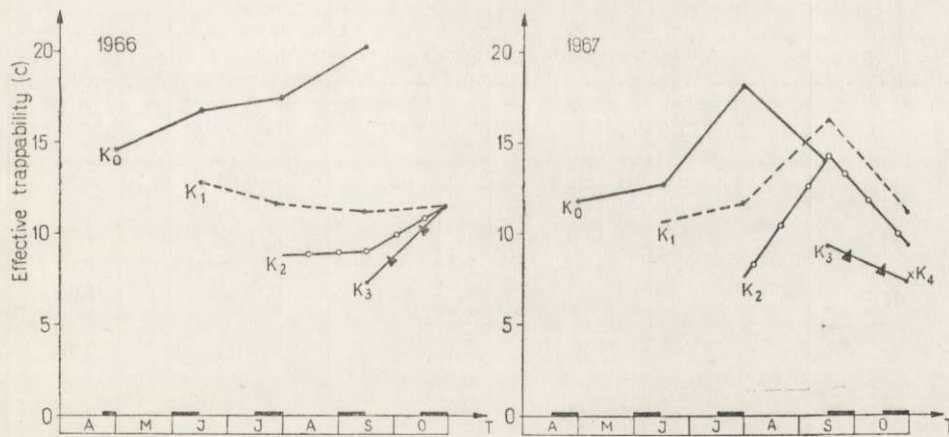


Fig. 2. Effective trappability of cohorts.

Therefore it is not possible, for the above reasons, to treat the curve taken by the trappability values of the cohorts during successive series of captures as a function exactly illustrating the dependence of trappability on age. In order, however, to ascertain this relation, it was assumed that factors irrespective of age determining the trappability

of the rodents in the study population affected all the age groups of individuals to a uniform degree. This assumption would appear to be even more justified by the fact that the trappability of individuals belonging to different cohorts is on the whole distributed similarly in relation to each other within a given period, regardless of general tendencies to decrease or increase in the trappability of the population (Fig. 2).

After accepting this assumption a relative comparison was made of variations in the trappability of each cohort in time, by means of checking whether the trappability of the given cohort in relation to the

Table 4.

Participation of different cohorts in the trappability of the whole population.

Cohort	1966				
	22—29 April	3—16 June	17—31 July	5—18 Sept.	19 Oct.— 2 Nov.
K ₀	1.00	↑ 1.08	↑ 1.50	↑ 2.11	—
K ₁		↓ 0.84	↓ 1.00	↓ 1.13	1.00
K ₂			↓ 0.75	↓ 0.96	1.00
K ₃				↓ 0.76	1.00
Cohort	1967				
	15—29 April	31 May — 14 June	16—30 July	31 Aug. — 14 Sept.	16—30 Oct.
K ₀	1.00	↑ 1.07	↑ 1.52	0.98	—
K ₁		↓ 0.88	↓ 1.00	↓ 1.14	↑ 1.25
K ₂			↓ 0.64	↓ 1.00	↓ 1.05
K ₃				↓ 0.66	↓ 0.82
K ₄					↓ 0.82

trappability of the whole population increases together with increasing age of this cohort. In other words a check was made to discover the distribution of index $\frac{c_k}{c_p}$ for the different series of captures, when c_k —

the effective trappability of the cohort in a given series of captures, and c_p — the trappability of the whole population during this same series

(Table 4). Variations in the index increase with increasing age of the cohort, as can be seen both (1) in a given moment of time for different cohorts (as also shown by Table 3) and (2) for a given cohort as it ages (horizontal arrows in Table 4).

The analyses made thus concurred in showing that there is a relation between trappability and age of individuals. Each cohort entering into the trappable part of the population is characterized by relatively low trappability, after which trappability increases with the increasing age of the cohort.

3.3. Differences in Respect of Trappability of Individuals of One Cohort

Even preliminary observations show that there are also differences in the trappability of individuals within one cohort. An attempt was therefore made to ascertain when differences in trappability of individuals begin to form within a cohort, that is, a group of individuals of uniform age.

In order to check how the differences in trappability of individuals in one cohort are distributed in different periods of their life, examination was made of the change in the variability index (I_v) of the distribution of number of captures of individuals in one cohort which take place with increase in the age of the cohort (Table 5).

As changes take place in the mean value of distribution of captures of individuals (\bar{x}) with increasing age of the cohort — that is, the effective trappability of the cohort, and also in the number of elements of this distribution (n) — that is the numbers of animals in the cohort, the variability index was calculated by means of the equation:

$$I_v = \frac{\sigma}{\sqrt{n \bar{x}}} \cdot 100$$

where: \bar{x} — mean value of distribution, n — number of elements of the distribution, σ — standard deviation, $\frac{\sigma}{\sqrt{n}}$ — mean error.

The values of the variability index exhibited fairly considerable differences in respect of trappability of individuals immediately after their entry into the trappable part of the population. During the second series of captures in succession for the given cohort, however, differences in individuals in this respect decrease, then increase consistently with increasing age of the cohort.

3.4. Perpetuation of Differences in Trappability between Individuals of One Cohort

The occurrence in a group of animals of uniform age — that is, a cohort — of individual differences in respect of trappability is evidence

that certain factors differentiating the individuals in the cohort are present in this group. If the factors responsible for differentiating individuals in respect of trappability are permanent in character, then it will always be the same individuals in the cohort which will be caught more often than others consistently less frequently caught.

A check was made to ascertain whether individual differences take on a more permanent character with increasing age of the cohort, which

Table 5.
Values of variability index (I_v)

Cohort	1966				
	22—29 April	2—16 June	17—31 July	5—18 Sept.	19 Oct. — 2 Nov.
K ₀	5.6	5.7	9.3	6.2	
K ₁		10.0	6.9	8.1	9.6
K ₂			7.3	4.3	4.3
K ₃				18.2	9.8
Cohort	1967				
	15—29 April	31 May — 14 June	16—30 July	31 Aug. — 14 Sept.	16—30 Oct.
K ₀	5.3	8.2	8.5	10.0	
K ₁		11.7	5.6	6.1	8.4
K ₂			10.4	6.1	8.6
K ₃				12.3	11.0
K ₄					12.4

should be expressed by the decrease in successive series of captures of the number of individuals changing from the more trappable group to the less trappable and *vice versa*.

For this purpose calculation was made of the values of correlation coefficients: (1) between the number of captures of all individuals during the series of captures which is the first for them, and the number of captures of these same individuals during the series which is the

second for them (r_1); (2) between the number of captures of individuals during the series of captures which are second and third for them (r_2); (3) between the number of captures made during the third and fourth series (r_3) (Table 6).

As a large number of correlated elements is desirable when making calculations of the correlation coefficient, captures of individuals of uniform age belonging to different cohorts were added together. The values of the correlation coefficients obtained (r_1 , r_2 , r_3) are statistically significant and form evidence of the relatively permanent character of differences in trappability.

Table 6.
Changes in the correlation coefficient (r) with change in age of individuals.

Successive series of trappings	I—II r_1	II—III r_2	III—IV r_3
Value of correlation coefficient	0.38	0.49	0.50

Material totalled in this way cannot be very exactly analysed. It is, however, possible to observe that between the first and second series of captures, the order in which individuals take their place in respect of trappability is slightly less permanent in character than that between the second and third series of captures (the difference between r_1 and r_2 is significant on the level of 0.1). No increased stability in the trappability order of individuals occurs, however, between the two subsequent trapping periods ($r_2 = r_3$).

3.5. Differences in Trappability of Males and Females

In order to examine the differences in trappability of individuals of differing sex calculation was made of the effective trappability of females and males within one cohort separately for different series of captures (Fig. 3).

In both years K_0 males exhibited the maximum trappability, the next in order being K_0 females. Of the individuals in the other cohorts females from cohort K_1 are distinguished by relatively high trappability in 1966 and in June 1967. It is difficult to find any regularity in the trappability of other individuals in 1966, but in 1967 among individuals in cohorts K_1 , K_2 and K_3 females and males of uniform age are caught similarly and age plays a far more important role than sex in differentiation as to trappability.

It would appear that differences in trappability connected with sex appear far later on in the cohort and overlap the differences connected with the individual's age. They may be due to the cohort's entering upon reproduction.

4. DISCUSSION

Problems connected with the trappability of rodent populations and the factors responsible for this trappability have frequently been described (Young, Neess & Emlen, 1950; Blair, 1951; Davis, 1955; Andrzejewski, Petruszewicz & Walkowa, 1959; Tanaka, 1956; 1963; 1964; Crowcroft & Jeffers, 1961; Petruszewicz & Andrzejewski, 1962; Ryszkowski, 1962; Andrzejewski, 1963; Kikkawa, 1964; Andrzejewski *et al.*,

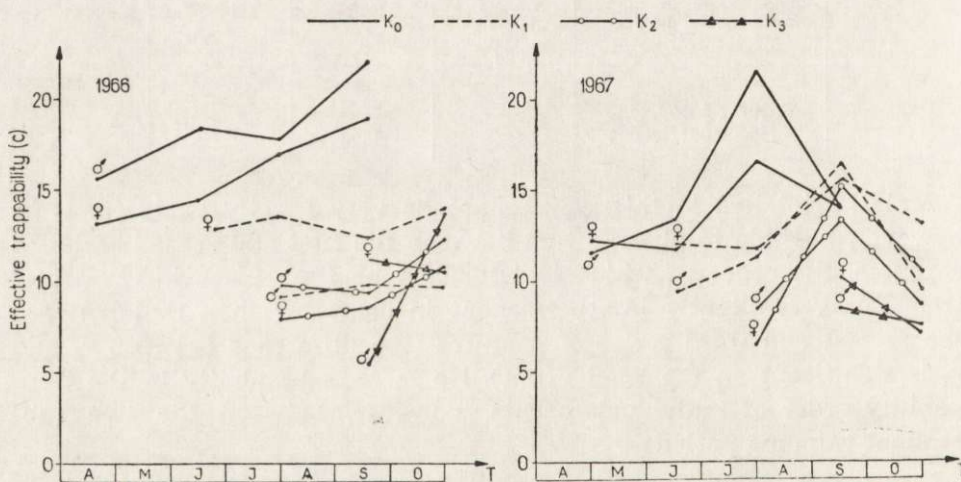


Fig. 3. Trappability of males and females in different cohorts.

1967; Andrzejewski, 1969 and others). A diagram is given showing a few chosen factors conditioning the trappability of a population, the thickness of the arrows indicating the strength of the effect of these factors (Fig. 4 A).

Factors exerting a strong direct influence on effective trappability of a population include: (1) an individual's chance of being caught, in its most general sense, expressed in the relation of the number of trapping devices to the population numbers and also (2) degree of interest in the traps exhibited by the population as a whole (Kikkawa, 1964). Both these factors vary during the reproduction season, the first as the result of variations in density (with a constant number of traps), the second

on account of variations in the animal's behaviour, climatic, phenological and food conditions.

The social structure constitutes a separate type of factor conditioning a population's trappability. Andrzejewski *et al.*, (1967) found that the most trappable individuals in a population have simultaneously the

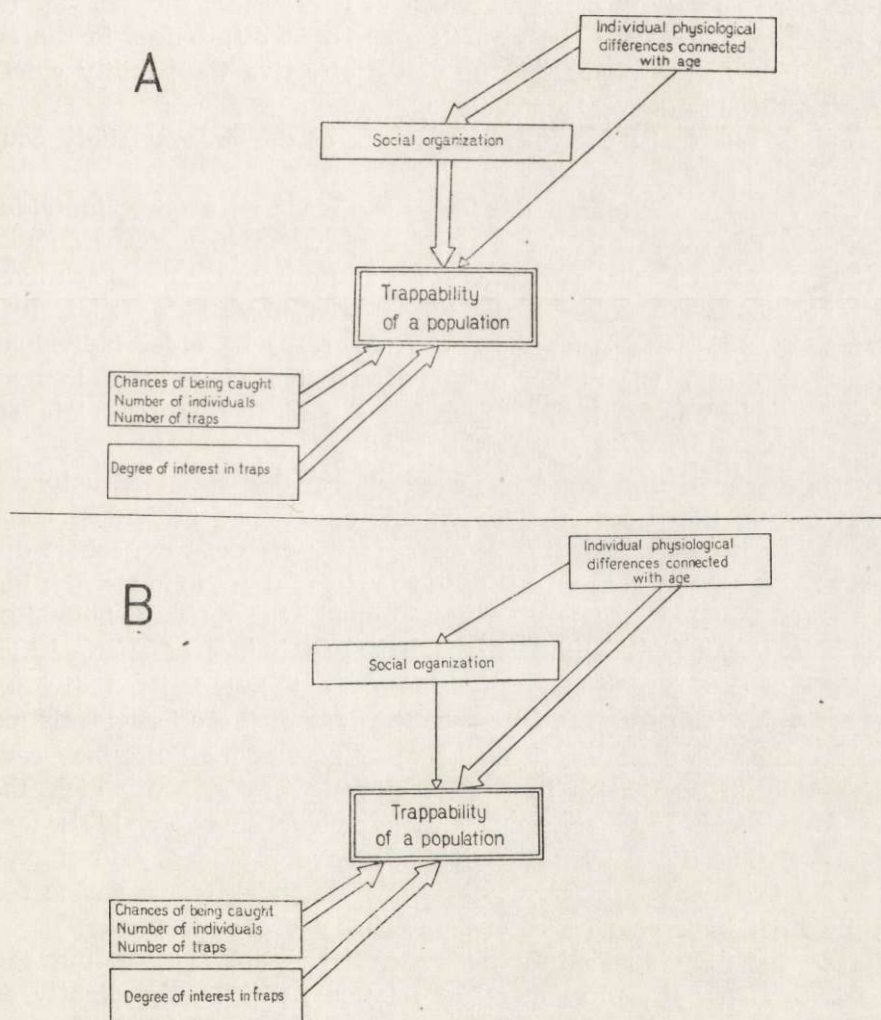


Fig. 4. Some factors conditioning trappability.

largest living areas, occupy phytosociological habitats preferred by rodents and also enter the traps earliest after they have been opened. All the above features can be considered characteristic of individuals dominating in the social structure of the population. The results of the experi-

ment made by Crowcroft & Jeffers (1961), showing that after overthrowing the social hierarchy in a population of *Mus musculus* Linnaeus, 1788 there is subsequent evening up of the trappability of individuals, also point to the strong effect exerted by the social structure on trappability. Both the studies cited refer to populations of a homogeneous age structure; it can, however, be assumed that the same applies to a population of varied age structure and that differences in the age of individuals in the population influence effective trappability chiefly indirectly, through the social structure.

Assuming this to be the case the results of the present study could be interpreted as follows:

1. The younger the cohort, the lower the place its average individual occupies in the social hierarchy of the population in comparison with individuals in older cohorts, and as a result its trappability is relatively lower. It moves a less extensive living area (Ryszkowski, 1962; Kikkawa, 1964), is driven away from traps by older individuals, particularly during the period of more intensive competition to reach the traps (Kikkawa, *l.c.*), approaches the traps relatively late and often finds them occupied (Tanaka, 1964).

2. In a group of uniform age, *i.e.* a cohort, the social structure is created during the life of the individuals and causes individual trappability differences between its members. In the case of each cohort during the series of captures which is the first for these animals, the high value of the index of variability in the number of captures of individuals is probably connected with trappability differences of another kind, directly due to the physiological differences between its individuals (thin arrow on the diagram). Differences in age of these individuals may be as much as 6 weeks, which in the early part of their life may cause considerable differentiation in respect of weight, distance which they move from the burrow *etc.* It is also known (Naumov, 1951; Rajska, 1970) that the youngest individuals have a tendency to clumped dispersion immediately after leaving the nest and in consequence reciprocally limit their chances of encountering a vacant trap.

During the individual's life these differences are effaced, but their place is taken by the forming social relations, which only slightly differentiate the cohort during the series of captures which is the second for it, and in subsequent series play an increasingly greater role. They probably determine the home range size priority in approaching the traps and also the reaction to pressure exerted by individuals of the older cohorts.

3. In accordance with what has been said in section 2, during the cohort's life the factors differentiating individuals in respect of trapp-

ability change from physiological to structural. As a result of these changes captures obtained during the first and second series of trappings for the cohort exhibit a lower correlation ($r = 0.38$) than captures made during the second and third series of captures ($r = 0.49$), when structural factors already exert a differentiating action on the population. The correlation between numbers of captures of individuals made during further series of captures does not increase and it may be considered that the influence of other age groups, particularly older groups occupying a higher place in the social structure of the population, interfere with the stabilization of the cohort's social structure.

4. The oldest group of individuals (K_0) exhibits differences in trappability connected with sex similar to those found by Ryszkowski (1962), Kikkawa (1964), Tanaka (1964). Among individuals in the remaining cohorts (K_1, K_2, K_3, K_4) it is not sex, but age and rate of maturation, which determine its trappability, and thus (in accordance with the original premise) the place occupied in the social hierarchy. Within one cohort sexually immature males and females, which form the majority in cohorts K_2 and K_3 , and the entirety in cohort K_4 (Bujalska, *in litt.*), are in principle uniformly trapped. Attainment of sexual maturity probably contributes to occupation of higher places in the social hierarchy (Beeman, 1947) and is perhaps the reason why females K_1 , in which maturation is rapid and occurs in a high percentage of these animals, form a group among the younger animals (particularly in 1966) distinguished by high trappability. Higher trappability of adult females in relation to immature females was found by Bujalska (1970). The maturation rate of males in the study population was not investigated, but it may be assumed that they mature later than females from the same cohort (Delost, 1955; Koškina, 1965) and therefore the trappability of K_1 males is far lower.

5. The cause of the observed disappearance of differences in trappability which occurred in the late autumn of 1966 among individuals of both sexes and of different age is probably the change in the character of the social structure after the reproduction season ends. This is manifested, *inter alia*, by the disappearance in the study population of differences in the size of home range (Mazurkiewicz, *in litt.*). It is well known also from literature (*e. g.* Getz, 1961) that individuals exhibit a tendency to clumped dispersion before the winter period. In 1967 no such evening up of trappability was observed, probably as the result of the reproduction season being prolonged (Bujalska, *in litt.*).

It would be possible to counter the diagram accepted at the beginning of the discussion by another diagram (Fig. 4 B), which assumes that age differences between individuals mainly affect trappability directly and

not through the social structure. Differences in trappability of individuals would then be conditioned by the differences in their physiology, physical condition, food requirements *etc.*, which would affect the activity of individuals in moving about the area.

The problem as to which of the diagrams is the correct one could be decided by a series of experiments carried out in populations of different density, and consisting in removing the most trappable individuals from the study populations (without any significant change in population numbers) and checking whether this causes a change in the trappability of the other individuals (in accordance with diagram A), or whether the trappability of other individuals remains unchanged (in accordance with diagram B). In the first case the result will be similar to the results obtained by Calhoun (1963) during removal of individuals.

It may be assumed as a start that in a dense population trappability will be ecologically conditioned through the social structure, and in populations with low density, if significant differences occur in trappability, they will be directly conditioned by physiological differences between individuals.

The relations described in this study between trappability and the age of individuals refer only to an isolated population, that is, to a situation in which the phenomenon of migration does not occur. The influence reciprocally exerted by settled and migrating individuals could possibly complicate the relations described above.

Acknowledgements: The author tenders her grateful thanks to Dr. R. Andrzejewski for his helpful advice and suggestions of which she was able to take advantage during the preparation of this study.

REFERENCES

1. Andrzejewski R., 1963: Processes of incoming, settlement and disappearance of individuals and variations in the numbers of small rodents. *Acta theriol.*, 7, 11: 169—213.
2. Andrzejewski R., 1969: Analiza wyników połowów drobnych ssaków metodą »kalendarza złowień« (Analysis of results of catches of small mammals by the »calendar of catches« method). *Polska Akad. Nauk, Inst. Ekol., Zesz. Nauk.*, 2: 1—104, Warszawa.
3. Andrzejewski R., Petruszewicz K. & Walkowa W., 1959: Preliminary report of results obtained with a living trap in a confined population of mice. *Bull. Acad. Pol. Sci. Cl. II*, 7: 367—370.
4. Andrzejewski R., Petruszewicz K. & Waszkiewicz-Gliwicz J., 1967: The trappability of *Clethrionomys glareolus* (Schreber, 1780) and other ecological parameters obtained by CMR capture method. *Ekol. pol. A*, 35: 709—725.
5. Beeman E., 1947: Effect of male hormone on aggressive behaviour in mice. *Physiol. Zool.*, 20: 373—404.

6. Blair W. F., 1951: Population structure, social behaviour and environmental relations in a natural population of the beach mouse (*Peromyscus polionotus leucocephalus*). Contr. Lab. Vertebr. Biol., Univ. Mich. 48: 1—47.
7. Bujalska C., 1970: Utrzymywanie stałości składników strukturalnych populacji, decydujących o reprodukcji u *Clethrionomys glareolus* (Schreber, 1780). Polska Akad. Nauk, Inst. Ekol., Zesz. Nauk., 3 (in print).
8. Bujalska G., Andrzejewski R. & Petruszewicz K., 1968: Productivity investigation of an island population of *Clethrionomys glareolus* (Schreber, 1780). II. Nataliy. Acta theriol., 13, 24: 415—425.
9. Calhoun J. B., 1963: Social use of space [In: »Physiological Mammalogy«, Eds W. V. Mayer and R. G. van Gelder] Academic Press, 1: 1—187. New York, London.
10. Crowcroft P. & Jeffers J., 1961: Variability in behaviour of wild house mice (*Mus musculus* L.) towards live traps. Proc. zool. Soc. Lond., 137: 573—582.
11. Davis D. E., 1955: Social interaction of rats as indicated by trapping procedures. Behaviour, 8: 335—343.
12. Delost P., 1955: Etude de la biologie sexuelle du campagnol des champs (*Microtus arvalis* P.). Arch. Anat. microsc. et Morph. exp., 44, 2: 150—190.
13. Getz L., 1961: Home range, territoriality and movement of the meadow vole (*M. pennsylvanicus*). J. Mammal., 42, 1: 24—35.
14. Gliwicz J., Andrzejewski R., Bujalska G. & Petruszewicz K., 1968: Productivity investigation of an island population of *Clethrionomys glareolus* (Schreber, 1780). I. Dynamics of cohorts. Acta theriol., 13, 23: 401—413.
15. Kikkawa J., 1964: Mobility, activity and distribution of small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. J. anim. Ecol., 33: 259—299.
16. Koškina T. V., 1965: Plotnost' populacii i ee značenie v regulacii čislennosti krasnoj polevki. Bull. Mosk. Obšč. Isp. Prir., Biol., 70, 1: 5—18.
17. Lincoln F. C., 1930: Calculating waterfowl abundance on the basis of banding returns. Circ. USDA, 118: 1—4.
18. Naumov N. P., 1951: Novyj metod izučenia ekologii melkih lesnyh gryzunov. Fauna i ekologija gryzunov. Materialy po gryzunam, 4: 3—21.
19. Petruszewicz K. & Andrzejewski R., 1962: Natural history of a free-living population of house mice (*Mus musculus* L.) with particular reference to grouping within the population. Ekol. pol., A., 10, 5: 85—122.
20. Rajska E., 1970: Some aspects of space organisation of an island population of *Clethrionomys glareolus* (Schreber, 1780). (in prep.).
21. Ryszkowski L., 1962: Differences in trapping frequency of coypu. Bull. Acad. Pol. Sci. Cl. II, 10, 3: 91—93.
22. Tanaka R., 1956: On differential response to live traps of marked and unmarked small mammals. Annot. Zool. Jap., 29: 44—51.
23. Tanaka R., 1963: On the problem of trap-response types of small mammals populations. Res. Popul. Ecol., 5, 2: 139—146.
24. Tanaka R., 1963: Recent status of rat infestation in the southwest coastal region of Shikoku and comments on census trapping of rat population. Bull. Konchi Wom. Univ., Nat. Sci., 8: 1—8.

25. Traczyk H., 1965: Roślinność »Wyspy Dzikiej Jabłoni« na Jeziorze Beldąńskim. (The vegetation of »The Wild Apple-Tree Island« of the Lake Beldąńskie). *Fragm. flor. geobot.*, 11, 4: 541—545.
26. Young H., Neess J. & Emlen J., 1952: Heterogeneity of trap response in population of house mice. *J. Wild. Mgmt.*, 16: 169—180.

Received, November 11, 1969.

Institute of Ecology,
Polish Academy of Sciences,
Warszawa, Nowy Świat 72.

Joanna GLIWICZ

ZALEŻNOŚĆ POMIĘDZY ŁOWNOŚCIĄ A WIEKIEM OSOBNIKÓW
W POPULACJI *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780)

Streszczenie

Badano łowność osobników izolowanej, naturalnej populacji *Clethrionomys glareolus* (Schreber, 1780). Materiał stanowiły złowienia zrealizowane w okresie 2 lat w czasie 10 serii połowów (2 × 5 serii) przeprowadzonych metodą CMR, w trakcie sezonu rozrodczego (Ryc. 1). Jako wskaźnik łowności charakteryzujący badaną populację w czasie każdej serii połowów przyjęto tak zwaną łowność realną wyrażającą się wzorem: $c = \frac{C}{N}$, gdzie N — liczba osobników populacji będących na powierzchni przez cały okres jednej serii połowów (Tabela 2), C — liczba złowien zrealizowanych przez te osobniki. Analogicznie obliczono łowność realną kohort tj. jednowiekowych grup osobników (Tabela 1).

Stwierdzono, że istnieje związek łowności poszczególnych osobników populacji z ich wiekiem (Ryc. 2, Tabele 3 i 4). Obserwuje się też zróżnicowanie osobników pod względem łowności w grupie jednowiekowej tj. kohorcie. Wraz z wiekiem kohorty następuje zmiana stopnia zróżnicowania wśród jej osobników; bardzo młode osobniki wykazują duże zróżnicowanie potem jego stopień maleje, by następnie znów zacząć konsekwentnie wzrastać (Tabela 5). Stwierdzono także nieznaczną tendencję do utrwalania się zróżnicowania osobników kohorty wraz z ich wiekiem, o czym świadczy niewielki wzrost korelacji liczby złowien tych osobników w kolejnych seriach połowu (Tabela 6). Zróżnicowanie w łowności osobników, związane z ich płcią jest często zacierane przez różnice w wieku osobników należących do różnych kohort, a także przez różnice wynikające z tempa dojrzewania samców i samic. W okresie późniejszym w 1966 roku (Ryc. 2, 3) nastąpił zanik zróżnicowania łowności wśród osobników różnej płci i w różnym wieku.

Przeprowadzono interpretację wyników przyjmując, że według zaproponowanego schematu (Ryc. 4 A) zróżnicowanie wiekowe osobników określa ich miejsce w strukturze socjalnej populacji i pośrednio, poprzez tę strukturę, wpływa na łowność osobników. Schematowi temu przeciwstawiono inny (Ryc. 4 B), wg którego łowność osobników i całej populacji może być bezpośrednio warunkowana fizjologicznymi właściwościami osobników związanymi z ich wiekiem.