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**Reproduction Stabilizing Elements in an Island Population
of *Clethrionomys glareolus* (Schreber, 1780)**

[With 11 Tables & 12 Figs.]

During three years of studies on the reproduction of an island population of *C. glareolus* it was found that the numbers of adult females stabilized in the summer months independently of population numbers and of immature females. It was suggested that the factor stabilizing numbers of adult females is their territorial tendency. This was verified by examining the spatial distribution, overlapping of home ranges, and home range utilization by adult and immature females. The numbers of pregnant females were always lower than the numbers of adult females and variations in their abundance was different in successive years. The individual days of pregnancy, and therefore the number of young born, was nevertheless constant on a yearly basis. This is the result of the inversely proportional relation between the value of this index in old adults and in females born the current year. Social contact between young and adult females, with only the latter showing territorial tendencies, is discussed. Intrapopulation mechanisms influence the number of females attaining reproductive status, thus affecting the reproductive capacity of the entire population. An hypothetical scheme of population stabilizing mechanisms is suggested on the basis of the results.

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1. INTRODUCTION

Variations in reproduction are of fundamental importance in regulating the density of small rodents. Intensive reproduction characterizes populations with low or increasing density, while populations with high or decreasing density experience low reproduction (Hamilton, 1937; Hoffman, 1958; Naumov & Nikolskij, 1962; Sviridenko, 1967 and others). One population factor studied in detail is the influence of male social structure on variation in reproduction of laboratory mouse population (Petrusewicz, 1957, 1960, 1963, 1966).

Also many authors (Chitty, 1952, 1960; Clarke, 1955; Kalela, 1957; Zejda, 1961, 1967; Koškina, 1965; Jewell, 1966) have drawn attention to the inhibition of puberty in females in very dense populations.

The number of reproducing females, which rarely approaches the number of sexually mature females, indicates that reproduction is limited in some populations of the red-backed vole, *C. glareolus*. Pregnant females in a population of *C. glareolus* examined by Sviridenko (1967) varied in successive years from 20 to 60%. Bujalska & Ryszkowski (1966) found seasonal variations in the number of pregnant females within limits of 10 to 50%, and Bujalska, Andrzejewski & Petrusewicz (1968) from 20 to 96%.

There is less variation in other reproductive indices in red-backed vole populations, e.g. in the number of individuals born in a unit of time (the average number of young in a litter and duration of gestation). The average number of young per litter varies slightly over the season from 4.4 to 5.2 (Zejda, 1966), or from 4.0 to 5.6 young (Sviridenko, 1967). The duration of gestation also varies within relatively narrow limits: 17.5 days (Wrangel, 1940), 17 to 18 days (Popov, 1960), 18 to 25 days (most often 20 days) (Drożdż, 1963), 22 days (Bujalska & Ryszkowski, 1966).

Variation in the number of pregnant animals would therefore seem a parameter of prime importance in red-backed vole reproduction.

The present study is an attempt to define some population processes affecting the abundance of adult and pregnant females in a population of the red-backed vole, *Clethrionomys glareolus* (Schreber, 1780). The population studied lived on an island in a lake and consequently, owing to the elimination of migration (Andrzejewski, Petrusewicz & Waszkiewicz-Gliwicz, 1967), dynamics of population numbers were limited to the function of reproduction and mortality.

2. STUDY AREA AND METHODS OF COLLECTING INFORMATION

2.1. Description of Area

The island, known as »Crab Apple Island«, is four hectares in area, and is situated in lake Beldany (northeast Poland). It is covered by mixed forest in which three phytosociological associations are distinguished, according to Traczyk (1965): the fringe area — *Salici-Franguletum* Malc. 1929 (Fig. 1); the central part — *Tilio-Carpinetum* Traczyk 1962 (Fig. 1) occurring in two sub-associations as *Tilio-Carpinetum typicum* and *Tilio-Carpinetum stachyetosum sylvaticae*, and in the depressions of the area — *Circaeo-Alnetum* Oberdorfer, 1953. *Tilio-Carpinetum* occupies 78, *Salici-Franguletum* 15 and *Circaeo-Alnetum* 7% of the total area of the island.

In addition to *C. glareolus* two other species of rodents live on the island: *Apodemus flavicollis* (Melchior, 1834) and *Microtus agrestis* (Linnaeus, 1761). During the study period the populations of these two species were comprised of only a few individuals which were caught during the course of the year. *Sorex araneus* Linnaeus, 1758, *Sorex minutus* Linnaeus, 1766 and *Talpa europea* Linnaeus, 1758 constituted the insectivore fauna. No carnivores were observed on the island during the study period.

2.2. Scope of Information Collected

A total number of 159 trap sites were evenly distributed at intervals of 15 m over the entire island. In 1966 and 1967 two live-traps, baited with oat grains, were placed at each site and inspected at 7.00 and 19.00 daily. In 1963 live-traps were replaced by pitfalls sunk into the ground (Andrzejewski & Wroclawek, 1963). Bait (also oat grains) was offered at the site for a period of three hours after each inspection. During this time the pitfalls were covered. As the pitfalls were also examined twice daily (7.00 and 19.00) they were therefore left open for a shorter time than were the live traps, i.e., 18 hr per day. This change in trapping method limited comparison of some variables — such as trappability or size of home range — with data from 1966 and 1967.

Information obtained by the catch-mark-release method made it possible to arrive at an accurate estimate of population numbers, since all the individuals thought to be living on the island were registered (Andrzejewski et al., 1967). Records were kept of time of capture, sex, and body weight. The reproductive condition of females was also assessed (see 2.4). Since every individual was marked all the information collected — compared by the »calendar of captures« method of Petrusiewicz & Andrzejewski (1962) and Andrzejewski (1969) served to define variations in the ecological characters of the different groups of voles.

2.3. Study Periods

Five censuses were made each year, beginning in mid-April and ending the last of October or beginning of November. Each census lasted 14 days (28 trap inspections), except for April 1966, in which trapping lasted only one week. Intervals between censuses were about one month. The fifth census (end of October or beginning of November) always occurred when all females were in winter anoestrus, hence analyses of their reproductive condition and related parameters were limited to the April, June, July and September censuses.

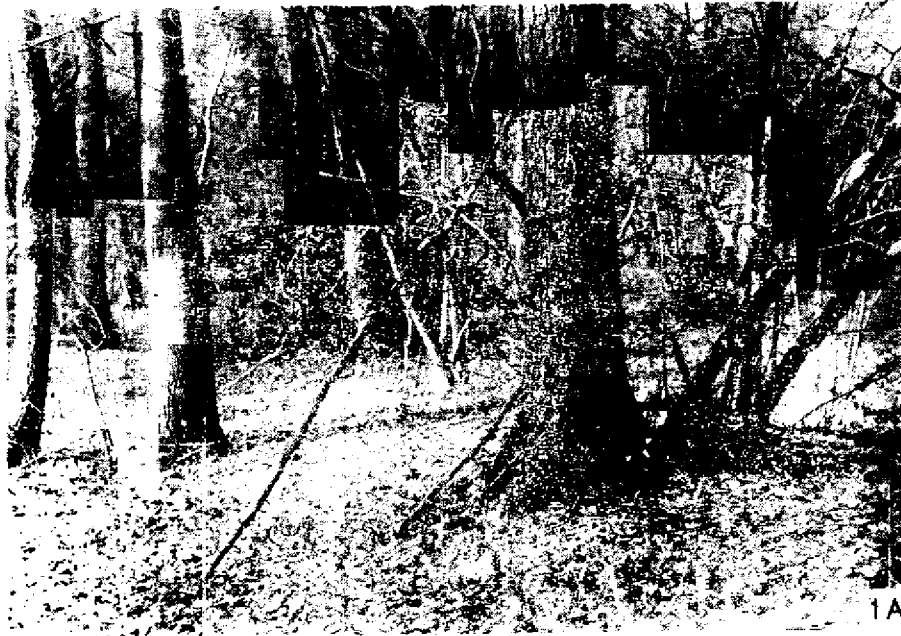


Fig. 1. Dominating forest associations of the study area. A — *Tilio-Carpinetum*
B — *Salici-Franguletum*.

All the information on population numbers and groups of individuals distinguished for each census was elaborated according to »general census« principles. A total of 5,116 captures of adult females, 4,958 vaginal smears, and 3,387 captures of immature females were analyzed during 1966—1968 (Table 1).

Four age groups, termed »cohorts«, were distinguished among the individuals born in the given current year (Gliwicz, Andrzejewski, Bujalska & Petruszewicz, 1968). Individuals recorded for the first time in the June census, and produced solely by old adults, i.e., cohort K_0 , were termed the spring cohort (K_1). Young animals which appeared for the first time in the July census were called the early summer cohort (K_2), those in the September census — the late summer cohort (K_3), and those in the October census — the autumn cohort (K_4).

It was assumed that young red-backed voles were trappable soon after leaving the nest at the age of 21 days (Kowalski, 1964). Individuals recorded for the first time in any census (e.g., June) therefore were born at least 21 days before the final trapping day in this census. Individuals born one day later could, however, not have been caught until the subsequent census (July): they thus formed part of the next cohort. The beginning and end of the birth period of each cohort was determined in this way (Table 2).

Division of age classes into cohorts thus makes it possible to compare the ecological characteristics of females born at different times of the year. Justification for this division is provided by previous studies which demonstrated that cohorts differ from each other in respect to such ecological indices as mortality (Gliwicz *et al.*, 1968), reproduction (Bujalska *et al.*, 1968; Gliwicz *et al.*, 1968), and biomass production (Petruszewicz *et al.*, 1968). Cohorts K_1 and K_2 correspond to the spring generation distinguished by Schwarz, Pokrowski, Istchenko, Olenjev, Ovtschinnikova & Pjastolova (1963), and cohorts K_3 and K_4 — to the autumn generation.

2.4. Determination of Female Reproductive Condition

Vaginal smears were taken from each female having a patent vagina by gently swabbing the vagina with a small, cotton-tipped stick and transferring the adhering material to a glass slide¹⁾. The smears were stained with methyl blue in the laboratory. This technique is sufficiently accurate for distinguishing the vaginal phases of animals with a short oestrous cycle (Nalbandov, 1966). It has been used in field studies by Larina & Golikova (1960), Bujalska & Ryszkowski (1966) and Bujalska *et al.* (1968) where no symptoms of permanent oestrus were induced as a result in rats (Wade & Doisy, 1935).

The day on which oestrus was first observed in adolescent females was taken as the time of attainment of puberty by that vole²⁾. This criterion is more accurate than estimating puberty by the date of vaginal opening. In 42 observed cases, oestrus was found simultaneous with opening of the vagina 34 times. In one case oestrus followed vaginal opening by 8.5 days and in seven cases oestrus (or any other phase of the cycle) was not observed during next 4.5 to 11.5 days.

¹⁾ The possibility that pseudopregnancy could be induced in oestrus voles by use of a rod such as this cannot be ignored. Such induction has been demonstrated in other rodents (see Nalbandov, 1966) and would therefore affect the duration of the cycle. Mechanical induction of pseudopregnancy has, however, not been reported in *Clethrionomys*.

²⁾ This applies to females which attained puberty during the time covered by the given census.

Table 1.
Numerical comparison of data collected.

Females	Number of:	Last date of censuses												Σ
		1966				1967				1968				
		29 IV	16 VI	31 VII	18 IX	29 IV	14 VI	30 VII	14 IX	1 V	14 VI	30 VII	14 IX	
Adult	Individuals	24	61	58	58	37	58	63	57	40	61	38	57	612
	Captures	145	593	684	572	454	523	650	819	170	174	133	249	5166
	Smears	145	575	680	529	435	512	640	793	164	156	120	209	4958
Immature	Individuals	0	12	99	66	0	24	15	21	0	122	151	122	632
	Captures	0	49	529	547	0	108	125	208	0	470	805	546	3387

Field methods used by different authors for diagnosing pregnancy (except autopsy) are obviously enlarged abdomen (Kalela, 1957), palpation of embryos (Negus, Gould & Chipman, 1961) and detection of pubic symphysis relaxation before parturition (Krebs, 1966). Indirect methods based on assessment of the number of lactating females (Davis, 1953) have also been used. Some of the above-mentioned methods establish only advanced gestation, and consequently females in the initial stages of gestation escape observation (e.g., in *C. rufocanus* gestation is not apparent until the 15th day (Kalela, 1957).

Several methods were used parallel with each other in this study in order to distinguish pregnant females. This permitted diagnosis of unadvanced pregnancies. A female was considered pregnant when the following were found:

1. Presence of vaginal plug.
2. Occurrence of bloody exudate originating from the placenta visible in the smear even to the naked eye.
3. Obvious abdominal swelling or distinct and systematic increase in body weight. These observations distinguished advanced pregnancies, 2 to 6 days before parturition.

Table 2.
Periods of births of cohorts.

Cohorts	1966	1967	1968
K ₁	1 IV — 26 V	25 III — 24 V	30 III — 24 V
K ₂	27 V — 10 VII	25 V — 9 VII	25 V — 8 VII
K ₃	11 VII — 28 VIII	10 VII — 24 VIII	9 VII — 22 VIII
K ₄	29 VIII — 1 X	25 VIII — 10 X	23 VIII — 1 X

4. Parturition in the trap.
5. Plucked fur around the teats, indicating lactation. This criterion, like the preceding one, permitted establishing recent pregnancy.
6. Absence of oestrous cycle in an adult female for at least 8 successive days, i.e. during a period equal to the average cycle length in *C. glareolus* (Larina & Golikova, 1960).
7. Smooth, structureless form of mucus in the smear, frequently with a few leukocytes. This type of mucus was observed in 361 smears in 1966 and 1967, 90% of which occurred during pregnancy and the remaining 10% occurred chiefly during diestrus. This index was used in 1968, when the small number of female recaptures (Table 1) reduced chances of diagnosing gestation by other methods. This method was used for the first time in the present studies.

The methods used for diagnosing puberty and pregnancy made it possible to distinguish the following categories of females: sexually immature, sexually mature, and pregnant. In each census two further categories were distinguished among sexually mature females, depending on the time of puberty. Females which attained puberty in the preceding census were termed early matured females, and those which reached puberty during the present census or after completion of the previous census were termed adolescent.

3. ABUNDANCE OF ADULT FEMALES AND FACTORS LIMITING ABUNDANCE

3.1. Abundance of Adult and Immature Females

In April the population consisted solely of old adults. Analysis of vaginal smears showed that all the females had attained puberty. This was therefore the number of females which survived the winter and which determined the abundance of adult females in April — varying in successive years from 24 to 40 individuals.

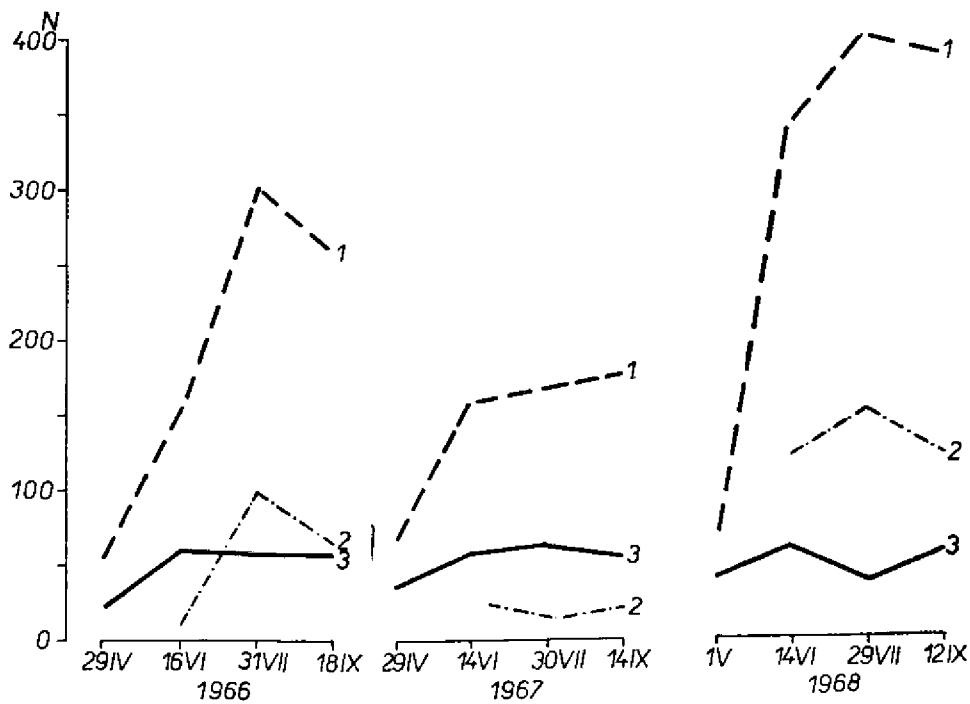


Fig. 2. Variations in number of the population and categories of females distinguished.

1 — population, 2 — immature females, 3 — adult females. The dates of last day of censuses are given on the x axis.

The abundance of adult females in the June, July, and September censuses was relatively constant in the study years varying from 57 to 63 individuals (Fig. 2). In these censuses the presence of immature females permitted maintaining the numbers of adult females on a constant level. An exception to this is the period in July 1968, when only 38 females were recorded and five of them (belonging to cohort K_1 and reaching puberty in June) were in anestrus as indicated by closed vaginae.

During the period from June to September the stabilized numbers of adult females were accompanied by considerable variations in numbers of immature females and variations in number of population as a whole (Fig. 2). It can therefore be concluded that numbers of adult females do not depend on these variables.

3.2. Factors Limiting Abundance of Adult Females

Examination was made of the age structure of females reaching puberty in July in the successive study years (only females from cohort K_1 could attain puberty in June). In July 1966 females from cohort K_2 predominated among adolescents despite the presence of immature females from cohort K_1 (Tab. 3), whereas it was primarily females from cohort K_1 which attained puberty in the July censuses of 1967 and 1968. Analysis of the age structure of females attaining puberty in September 1966 and

Table 3.

Age structure of adolescent females in successive months and years (number N and their percentage among females in given cohort).

Cohort	1966		1967		1968	
	July	Sept.	July	Sept.	July	Sept.
K_1	N 6	0	18	0	6	26
	% 75	0	100	0	6.2	30.2
K_2	N 10	26	12	12	1	7
	% 9.3	34.6	44.5	92.4	1.6	18.9
K_3	N 0	2	0	4	0	2
	% 0	11.1	0	16.7	0	5.9

1967 showed that they were mainly females from cohort K_2 which attained puberty. In September 1968, however, adolescent females belonged mainly to cohort K_1 . This shows that inhibition of puberty was not due to the youth of the females.

Examination was then made of whether there was a connection between body weight and attainment of puberty. For this purpose body weight during the first days of puberty was determined³⁾.

It was found that females from a given cohort which attained puberty in earlier censuses are distinguished by slightly lower body weight than that of females attaining puberty in later censuses (Tab. 4). This phenomenon is usually repeated in each cohort and shows that attainment of

³⁾ In order to eliminate the possibility of error when weight was examined only once consecutive weights of a female (which attained puberty during that census) were taken for analysis, beginning with first oestrus.

a certain weight is not automatically accompanied by attainment of puberty ⁴⁾.

The above results justify searching for the causes of limitation of the number of adolescent and adult females, not in individual characters (such as age and weight), but in population phenomena. According to Naumov (1951), Tanaka (1953) and Kořkina (1965) the home ranges of adult females of *C. glareolus*, *C. rufocanus* and *C. rutilus* are separate or only partly overlap. Naumov (1951) and Kořkina (1965) term this phenomenon territoriality, and Tanaka (1953) territorial tendency. Territorial tendency in adult females of *C. rufocanus* occurred during the breeding season when population density was low. Adult males did not exhibit territorial tendency during this period (Tanaka, 1953).

Table 4.
Mean weight of females at time of attaining puberty (given in grams).

Year	Cohort	Months		
		VI	VII	IX
1966	K ₁	14.0±2.7	19.6±2.5	17.0*
	K ₂	—	14.3±4.3	16.5±2.6
	K ₃	—	—	16.5*
1967	K ₁	15.5±2.2	17.2±3.0	—
	K ₂	—	17.3±2.2	17.1±3.2
	K ₃	—	—	17.5±1.9
1968	K ₁	16.0±1.1	18.0*	—

* Standard deviations were not calculated when sample size was very small.

Kořkina (1965) suggests that the territoriality of adult females may limit numbers of adult females by delaying puberty in young females. The mechanism of this process may be explained by the studies of Christian, Lloyd & Davis (1965) who found that increased number of social contact inhibits attainment of puberty through changes in the pituitary—adrenal—gonad system («stress»).

Therefore, if increased home range overlapping is accompanied by increased number of contacts, then the abundance of adult females living on a given area should be limited by area of the home ranges and the degree of overlapping tolerated.

⁴⁾ Females from cohort K₁ attain puberty in June with lower body weight than females from cohort K₂ in July and from cohort K₃ in September. This may show that it is primarily only the heaviest females which attain puberty in cohorts K₂ and K₃.

The data were analyzed to establish whether stabilized numbers of adult females can result from their territorial tendency. The spatial requirements of adult and immature females were determined for this purpose. If the limiting factor of numbers of adult females was in fact their spatial requirement, than the requirement should be different for adult females (with constant numbers) and immature females (with varying numbers).

Differences in the spatial requirements of these categories of females were defined by means of the following indices:

1. Index of spatial distribution. In order to determine the distribution of females on the island, lists were made of the number of females caught on each trap site. Distributions of this kind were made for adult and immature females for each census in 1966 and 1967. The measure of difference between empirical distribution and Poisson's distribution (this distribution takes place with random distribution of individuals over an area — Cole, 1946) used was the index of variation $v = \frac{\sigma^2}{\bar{x}}$ where σ is standard deviation and \bar{x} the mean number of females caught at a site. When $V = 1$, distribution is random, values $V < 1$ indicates uniform distribution and $V > 1$ its clumped character. In order to verify the hypothesis as to significance of the difference between the two distributions (empirical and theoretical) the statistic

$$t = \frac{v-1}{\sqrt{\frac{2}{s}}}$$

was used, where S expresses the number of all trap sites on the island. This statistic has Student's distribution with $n-1$ degrees of freedom (Greig-Smith, 1957).

Verification made in this way showed that in five cases the spatial distribution of adult females differs significantly from random distribution and is uniform. In the other three cases the distribution of females did not in fact differ from the random, but two of them were close to uniform distribution (Tab. 5). The distribution of immature females, on the other hand, significantly differed in three cases from random, and was clumped. In the other three cases the distribution of females in this category did not differ from random but two of them were close to clumped distribution (Tab. 5). Adult females thus have a tendency toward even, and immature toward clumped, distribution in space.

Uniform spatial distribution of adult females would appear to indicate their tendency of mutual avoidance, whereas the clumped distribution of immature females indicates close social tolerance. Analysis of the degree to which their home ranges overlap supports these conclusions.

2. Degree of overlapping of home ranges. This is the function of the extent of the home range and abundance of individuals. As the numbers of females has been determined (section 3.1., Fig. 2) it is possible to define the extent of the home range.

The measure of the extent of the home range has been given using the method suggested by Wierzbowska (in litt.); extent of the home range was expressed by the number of trap sites (r) contained in this area. This extent was defined by using the correlation between expected value $E(X)$ of the number of revealed trap sites and number of captures of an individual (k) and parameter r :

$$E(X) = r \left[1 - \left(\frac{r-1}{r} \right)^k \right]$$

Home range area was estimated on the basis of the first five captures of an individual in a given census ($k = 5$). This value was determined

Table 5.
Variations in index of spatial distribution of adult and immature females.

Females	Indices	Dates of last day of successive censuses							
		1966				1967			
		29 IV	16 VI	31 VII	18 IX	29 IV	14 VI	30 VII	14 IX
Adult	V	0.79	0.69	0.65	1.02	0.58	0.74	0.83	0.50
	t	1.875	2.729	3.084	0.178	3.776	2.311	1.511	4.453
Immature	V	—	1.37	1.12	0.88	—	1.83	1.13	1.32
	t	—	3.315	1.075	1.067	—	7.431	1.173	2.809

$V = 1$ — random distribution

$V < 1$ — uniform distribution

$V > 1$ — clumped distribution

$t > 1.97$ — distribution significantly different from random.

for adult females in all censuses in 1966 and 1967, but only during the July and September censuses for immature females⁵⁾. The extent of the home range was expressed in square meters (one trap site corresponds to 225 m²). The findings (Tab. 6) show that the extent of the home ranges of adult and immature females is similar and relatively constant.

The degree to which home ranges overlap was examined in each census for adult females and for immature females, by means of the index

$$Z = \frac{rN}{S'}$$

where r — measure of the extent of the home range, expressed by the number of trap sites; N — number of females; S' — number of trap sites

⁵⁾ In June the amount of material was insufficient.

on which ($x = 1, 2, 3 \dots m$) females were caught in a given census: this defines the extent of the area occupied by a given category of females. S' is an empirical value depending on duration of observations (only after a certain period can a female reveal all the trap sites within the limits of her range). If the extent of home range varies within the limits of the values observed in the present material, then according to W i e r z b o w s k a (in litt.) after 8 captures the individual reveals all the sites in its home range. As the mean number of captures of adult females was 12.4 for 1966 and 1967, and of immature females 6.6 (Table 1), then the duration of the census 14 days is sufficient to accurately estimate the area occupied by adult females, while the area occupied by immature females may be slightly underestimated.

If the home ranges of females in a given category are completely separated, then $rN = S'$ and therefore index $Z = 1$. If the home range of each female is completely covered by the home range of another female, i.e., the degree of overlapping of home ranges is 100% — then $Z = 2$. The

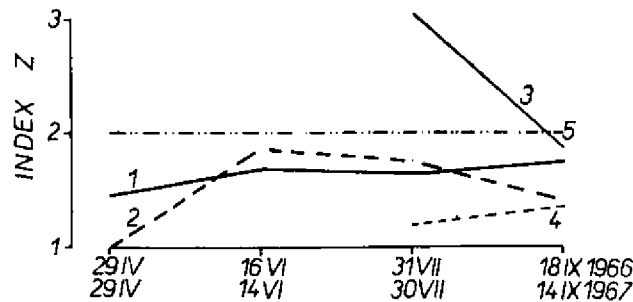


Fig. 3. Comparison of extent of variations in home range overlapping index (Z) of adult and immature females. 1 — adult females 1966, 2 — adult females 1967, 3 — immature females 1966, 4 — immature females 1967, 5 — value of index indicating total overlapping of home ranges. The dates of last day of censuses given on x axis.

value of index Z may be higher than 2; if $Z = 3$ then home ranges three females overlap, etc. Index Z would take on maximum value if the home ranges of all females in a given category completely overlapped each other. Then $S' = r$, and therefore $Z = N$.

The results obtained show (Fig. 3) that the degree of overlapping of home ranges of adult females in June, July and September, i.e. during the period of stable numbers of these females — is relatively constant and varies from 1.40 to 1.86. In April index Z varies within the limits of 0 to 1.45 (Fig. 3). Complete overlapping of home ranges was therefore never found. Immature females are, however, distinguished by variable values of the index of overlapping of home ranges (Fig. 3). In 1966, when the numbers of immature females were higher than in 1967, this index

assumes higher values so that treble overlapping of home ranges takes place.

This result thus confirms the assumptions advanced above and indicates that adult females, contrary to immature females, exhibit a constant tendency to separate their home ranges.

Investigations were continued to establish whether there are differences in the way the home range is used by adult and immature females.

Table 6.

Comparison of extent of home range of adult and immature females assessed on basis of number of trap sites (r) situated within home range (extent of home range expressed in square metres given in brackets).

Females	1966				1967			
	IV	VI	VII	IX	IV	VI	VII	IX
Adult	3.76 (846)	3.59 (808)	3.99 (898)	3.52 (792)	2.86 (643)	3.99 (898)	3.70 (832)	3.54 (796)
Immature	—	—	3.03 (682)	3.48 (783)	—	—	4.29 (965)	3.88 (873)

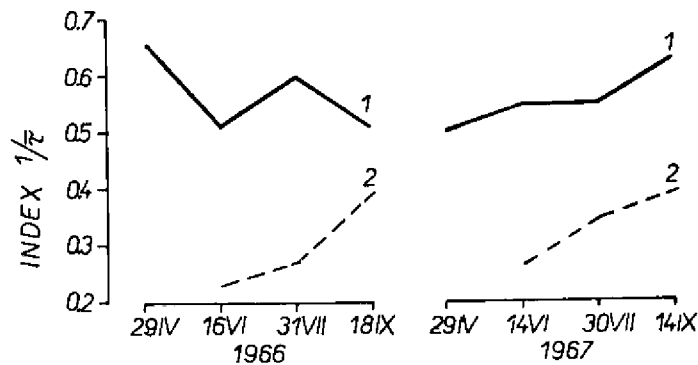


Fig. 4. Comparison of trappability index $1/\bar{\tau}$ of adult and immature females. 1 — adult females, 2 — immature females. The dates of last day of censuses given on x axis.

3. Home range utilization. Conclusions were drawn as to the way in which adult and immature females use the home range on the basis of frequency of visits to traps situated within the range. The general index of frequency of visits to traps by an individual (termed »trappability«) was defined on the basis of the average interval between consecutive captures of the same individual (τ) (Petrusiewicz & Andrzejewski, 1962; Adamczyk & Ryszkowski, 1965; Trojan & Wojciechowska, 1967). τ is here the interval between two consecutive captures. Trappability index was expressed as $1/\bar{\tau}$ (Grüm, 1959).

Calculations show that adult females are characterized by far higher trappability than immature females (Fig. 4), which indicates their greater activity. Trappability differences of the two categories of females are significant, since values of standard deviations calculated for τ , in no case overlapped. In view of these results, the limited overlapping of the home ranges of adult females, unlike that of immature females, may be the result of a constant tendency to reduce the number of mutual contacts. If this tendency toward social isolation is the case, then reduction of individual contacts should apply to adult females and not to immatures.

4. Intensity of contacts. Intensity of contacts was defined indirectly by investigating whether the presence of a female in the given trap site limited the number of captures of other females. For this purpose comparison was made of the empirical number of captures (M_x) at trap sites where one ($x = 1$), two ($x = 2$) and three or more ($x \geq 3$) females were caught at a given site with the number of captures calculated theoretically (M'_x), assuming that this number is proportionate to the number of females (x) at given trap site (and thus assuming that the increase in number of females at the trap site does not affect their trappability). The theoretical number of captures was calculated by means of the equation:

$$M'_x = \frac{S_x}{\sum_{x=1}^m S_x} \sum_{x=1}^m M_x$$

where: S_x — number of females occurring singly ($x = 1$), in twos ($x = 2$), threes ($x = 3$) etc. on the trap site.

$\sum_{x=1}^m S_x$ — sum of numbers of females occurring singly, in two or threes on the trap site ⁶⁾.

$\frac{S_x}{\sum_{x=1}^m S_x}$ — defines the percentage of females occurring singly, in twos or threes etc. of the total number of females.

$\sum_{x=1}^m M_x$ — joint number of captures on all trap sites.

For the purpose of statistical verification of the hypothesis as to the constancy of the mean number of captures, comparison was made of the empirical sequence M_x and theoretical sequence M'_x by means of test χ^2 accepting a confidence level $\alpha = 0.05$ (Tab. 7).

Results show that the trappability of immature females does not depend on the number of females caught on a given trap site. Mature females, on the other hand, are caught less frequently than random on trap site at which more than one female occurs ($x = 2, x \geq 3$; Fig. 5). This

⁶⁾ $\sum_{x=1}^m S_x$ is always greater than the numbers of females (N) in a given category, because each female was recorded on several trap sites and was thus counted several times.

Table 7.
Comparison of agreement of sequences M'_x and M_x (explanations in text) by means of test χ^2

Fe- males	Date of last day of census	M'_x M_x	Number of females recorded on trap site							d.f.	χ^2 emp.
			1	2	3	4	5	6	7		
Adult	16 VI 1966	M'_x M_x	155 178	237 256	181 148	20 11				2	14.990*
	31 VII 1966	M'_x M_x	195 227	310 297	95 84	56 52	28 24			3	7.900*
	18 IX 1966	M'_x M_x	168 173	176 183	115 118	99 72	14 26			3	18.140*
	29 IV 1967	M'_x M_x	256 239	188 201	10 14				X	1	3.630
	14 VI 1967	M'_x M_x	145 175	222 216	126 98	30 34				2	13.120*
	30 VII 1967	M'_x M_x	125 157	215 213	206 188	68 63	36 29			3	11.500*
	14 IX 1967	M'_x M_x	219 250	379 347	180 187	41 35				2	8.220*
Immature	16 VI 1966	M'_x M_x	32.1 31	6.8 7	10.1 11					1	0.124
	31 VII 1966	M'_x M_x	70.3 70	158.8 163	136.0 145	93.7 70	36.0 43	21.7 27	12.5 11	5	9.529
	18 IX 1966	M'_x M_x	119 112	232 223	109 103	87 109				2	5.531
	14 VI 1967	M'_x M_x	43.0 39	12.6 14	33.3 40	19.1 15				2	2.755
	30 VII 1967	M'_x M_x	67.8 66	41.6 41	15.6 18					1	0.426
	14 IX 1967	M'_x M_x	89.8 98	69.1 68	27.7 25	18.4 14				2	1.733

* Differences between sequences M'_x and M_x statistically significant, d.f. — number of degrees of freedom.

agrees with the tendency found above for clumped distribution of immature females and the tendency toward even distribution of adult females.

It would not appear that the differences obtained in respect to the way the home range is used by adult and immature females were due to blocking of traps. The possibility of traps being blocked should vary depending on the numbers of the whole population. It was not found, however, that variations in the numbers of the population caused significant variations in trappability of females. In July 1966 for example the population number was twice that those of July 1967 (Fig. 2) yet in both these censuses the number of captures per adult female decreased with increase in the number of females in this category at the trap site. The

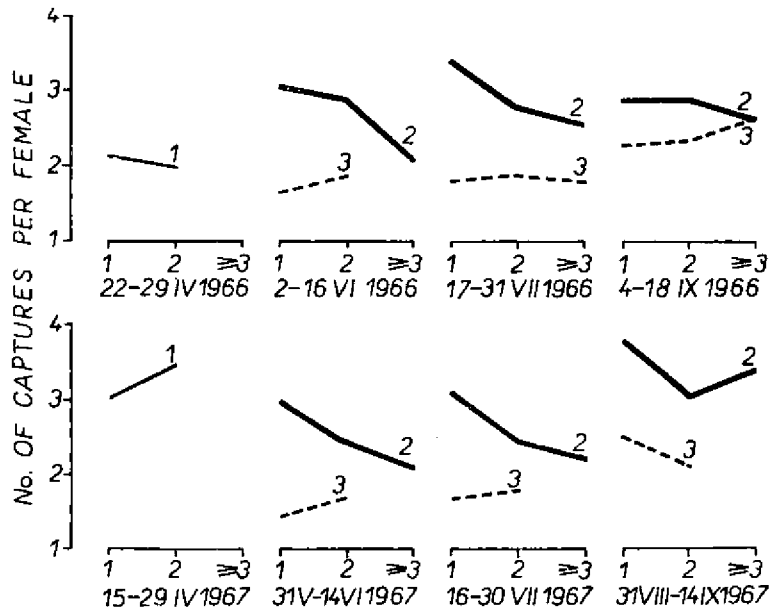


Fig. 5. Variations in number of captures per given female, which accompanies increase in number of females recorded on trap site. 1 — adult females, variations statistically insignificant, 2 — adult females, variations statistically significant, 3 — immature females, variations statistically insignificant. Number of females recorded on trap site given on x axis.

number of captures of immature females, on the other hand, was independent of the number of females meeting on a given trap site (Fig. 5).

The above interpretations indicate that adult females — contrary to immature females — reciprocally limit the possibility of extensive invasion of the whole home range.

As the numbers of adult females did not change in the June, July and September censuses, it is obvious that only as many females attained puberty as adult females died. If the hypothesis as to the important role

of territorial tendency in limiting numbers of adult females is correct, then the number of adolescent females should depend on the extent of the area not penetrated by females which reached puberty earlier. A check was therefore made to see whether the number of adolescent females was proportional to the number of trap sites unvisited by females which attained puberty earlier.

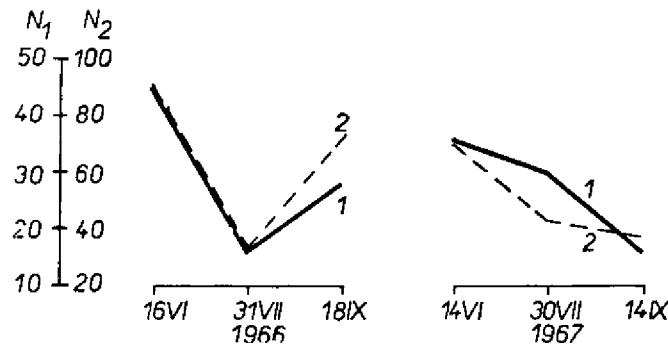


Fig. 6. Comparison of number of adolescent females with number of trap sites not visited by females which matured earlier. 1 — number of females, 2 — number of trap sites. The dates of last day of censuses given on x axis.

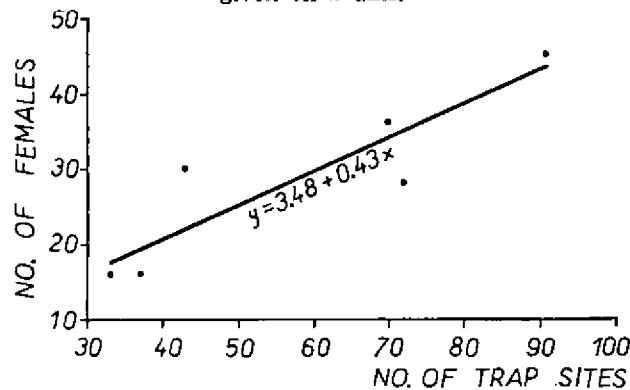


Fig. 7. Relation between number of adolescent females and number of trap sites not visited by females which matured earlier.

The greatest number of adolescent females was found in June 1966, when low numbers of old adults resulted in a large number of trap sites not being visited by them (Fig. 6). The smallest number of »free« trap sites was recorded in July 1966. This was accompanied by a small number of currently adolescent females. When comparison was made in this way of data from the June, July and September censuses for 1966 and 1967, direct relation was found between the number of adolescent females and the number of trap sites not visited by females which had previously attained puberty (Fig. 6). More accurate analysis showed that the relation

between the number of adolescent females (y) and the number of free trap sites (x) is a simple relation of the type $y = 3.48 + 0.43 x$ (Fig. 7).

This relation confirms the hypothesis that the territorial tendency characterizing adult females limits their abundance.

The analyses made indicate a territorial tendency among adult females in the population of *C. glareolus* studied. This tendency is illustrated by the following results:

1. Uniform, or a tendency toward uniform distribution of adult females as opposed to the clumped, or tendency toward clumped distribution of immature females.

2. Mutual overlapping of home ranges of adult females is never complete, while the home ranges of immature females can completely overlap (even home ranges of three females can completely overlap each other).

3. In addition it may be assumed that adult females — contrary to immature females — mutually limit major home range trespassing.

4. A consequence of territorial tendency — as has been shown — is to render attainment of puberty by a female dependent on the presence of a »free« place not currently visited by any adult female.

The above discussion points to limitation of the reproductive potentialities of the study population, resulting from limitation of the numbers of females physiologically capable of reproduction, *i.e.* sexually mature females. The factor limiting the numbers of mature females would appear to be their territorial tendency.

4. REPRODUCTION IN THE STUDY POPULATION

4.1. Variations in Abundance of Pregnant Females

The dynamics of abundance of pregnant females was described on the basis of a knowledge of the beginning and end of the reproductive season and the abundance of these females in successive censuses.

The beginning and end of the reproductive season — lying outside the observation period — were determined indirectly. The start of the season was defined by subtracting the length of gestation, *i.e.* 22 days (B u j a l s k a & R y s z k o w s k i, 1966) from the date of the first spring births (April 23rd 1966, April 16th 1967, April 21st 1968). October 1st was taken as end of the reproduction season in 1966 and 1968 (A s d e l l, 1964). Justification for the choice of this date was the observations made on October 14th 1966 and October 14th 1968, when all the females had already reached winter anoestrus. Termination of the reproductive season must therefore have taken place between the final day of the September censuses and October 14th. In 1967 the reproductive season was longer, and in addition to its earlier beginning, was indicated by the considerable number of pregnant females in September and the presence of recent

weanlings as late as the end of October. In that year the cessation of the breeding season was determined by subtracting 21 days from the final day of October censuses, that is, the age at which red-backed voles could earliest trapped. Similar prolongation of the reproduction season was recorded by Bergstedt (1965) in a population of *C. glareolus* in year with low population numbers.

The start of the reproductive season of females from cohorts K_1 and K_2 was determined in a similar way, i.e., subtracting length of gestation from the date of the first observed parturition of a female in the given cohort. In these absence of such observations, the mean time between the

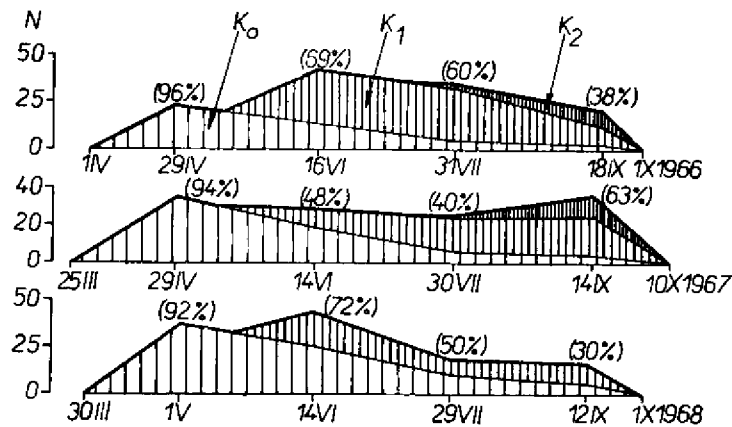


Fig. 8. Variations in abundance of pregnant females. The dates of beginning and end of breeding season and the dates of last day of censuses given on x axis. Percentage of pregnant females given in brackets.

last observed pregnancy (of the first pregnant females in the given cohort) and the first observation of absence of gestation in the female examined (and thus observation of one of the phases of the oestrus cycle or signs of lactation). Dates of first births determined in this way are as follows: K_1 — June 7th 1966, June 4th 1967, June 9th 1968, K_2 — July 31st 1966 and July 30th 1967.

It was found that the abundance of pregnant females varies during the reproduction season (Fig. 8) and is not proportionate to the abundance of adult females (variable percentage of pregnant females among the total number of adult females). The frequency of numbers of pregnant females is also different. In 1966 and 1968 the maximum number of pregnant females were recorded in June, and the lowest in September (Fig. 8). A bimodal curve of abundance of pregnant females characterized 1967, namely peaks in April and September (Fig. 8). In July 1968 there was considerable reduction of the numbers of adult females (Fig. 2), accom-

panied by reduction in the numbers of pregnant females. Reduction in the numbers of pregnant females in this month could thus be due to inhibition of puberty, and anestrus observed in some of the adults. A similar phenomenon was observed by Koškina (1965) in a high density year of *C. rufocanus*. This phenomenon was also accompanied by manifestations of population overcrowding.

For the purposes of a general description of reproduction in the study population, the total number of individual days of pregnant females (\bar{N}_pT) was defined for each year. The number of individuals born during the year (with an accepted constant length of gestation and litter size subject to very little variation) is directly proportionate to the value \bar{N}_pT (Bujalska, 1967; Bujalska *et al.*, 1968).

It was found that \bar{N}_pT — despite seasonal variations in the numbers of pregnant females — is an almost stable value on a yearly scale (Tab. 4).

4.2. Contribution of Cohorts K_1 and K_2 to Maintenance of a Constant Value of Reproduction

It was chiefly females of cohort K_1 which reproduced in 1966, and in 1967 and 1968 females of cohort K_0 (Fig. 8). The higher value \bar{N}_pT calculated for females of cohort K_0 was accompanied by the lower value of \bar{N}_pT for females from cohorts K_1 and K_2 . In 1968 when value \bar{N}_pT characterizing reproduction of cohort K_0 was particularly high, females from cohort K_2 did not reproduce at all (Tab. 8).

A check was made to see if the above relations are connected with the numbers of adult females in each of the cohorts. It was found that the percentage of pregnant voles among adult females from cohort K_2 is high, although it always decreases from April to July (Fig. 9). The small number of females in this cohort which survive to autumn made it impossible to calculate the percentage of pregnant females in September. In the September censuses, however, females from cohort K_0 continued to reproduce intensively (in 1966 and 1968 all the females which survived were pregnant, while in 1967 four out of six females were pregnant). The percentage of pregnant females among adult females from cohorts K_1 and K_2 varied considerably in successive censuses (Fig. 9). The labile character of participation of young females in reproduction has been recorded by Davis & Hall (1951) and Koškina (1965).

The above analysis indicates that the reproduction of cohort K_0 is determined primarily by the number of adult females (since the percentage of pregnancy females is high and varies only slightly). On the other hand the wide variations in percentage of pregnant females from cohorts K_1 and K_2 suggests that other factors exert an influence here.

In view of the foregoing, the correlation between value \bar{N}_pT of females in cohort K_0 and the mean percentage of pregnant females among adult females from cohort K_1 and K_2 for the given year was examined. It was found that the increase in value \bar{N}_pT of cohort K_0 is always accompanied by reduction in the average percentage of pregnant females in cohort K_1 and in general (except for 1967) reduction in the average percentage of pregnant females in cohort K_2 (Tab. 9).

Table 8.

Comparison — on yearly scale — of number of individual days (\bar{N}_pT) of pregnant females in each cohort.

Cohorts	Year		
	1966	1967	1968
K_0	1859	2697	3260
K_1	2665	1843	1364
K_2	341	383	0
Σ	4865	4923	4624

Table 9.

Comparison of yearly data referring to value individual days (N_pT) of females from cohort K_0 and percentage of pregnant females from cohorts K_1 and K_2 .

Cohorts	Year		
	1966	1967	1968
K_0	1859	2697	3260
K_1 (%)	58.7	45.3	38.5
K_2 (%)	30.0	37.5	0.0

It follows from this that increase or decrease in the average percentage of pregnant females from cohorts K_1 and K_2 is a factor supplementing value \bar{N}_pT of the population on a yearly basis. In view of the considerable abundance of adult females in cohort K_1 and their low numbers in cohort K_2 , it is mainly the first of these cohorts which is responsible for bringing \bar{N}_pT up to a constant value.

4.3. Analysis of Variations in Abundance of Pregnant Females

The numbers of pregnant females in April were almost equal to the numbers of adult females (Fig. 8). In the other censuses (June, July and

September), however, these numbers differed from those of adult females, the percentage of pregnant females varying greatly (Fig. 8).

A check was made to see whether indices of distribution, home range overlapping and the home range utilization was characteristic of adult females and whether these fluctuated in agreement with variations in the percentage of pregnant females. The results obtained (Tab. 10) do not justify concluding whether the factor which probably limits the numbers of adult females (degree of overlapping of home ranges and the number of social contacts involved by this) also affects variations in the percentage of pregnant females.

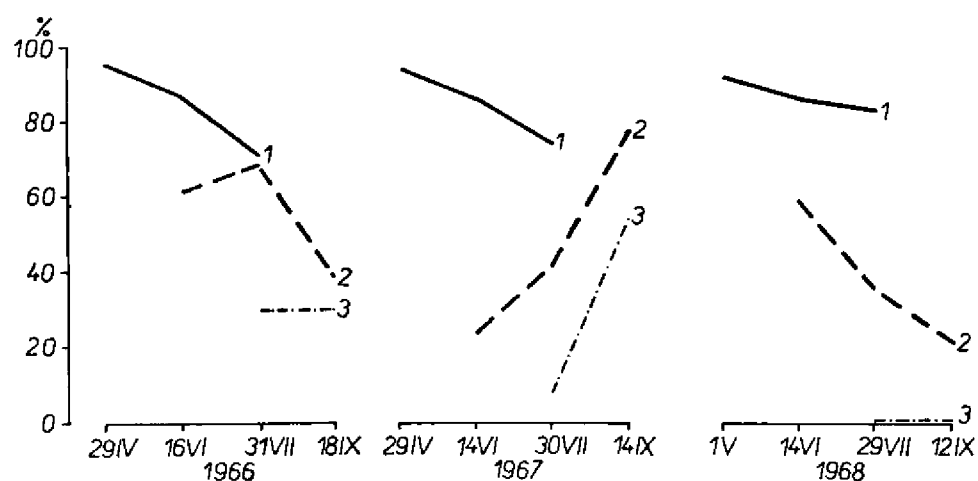


Fig. 9. Variations in percentage of pregnant among adult females from cohorts K_0 , K_1 , and K_2 . 1 — cohort K_0 , 2 — cohort K_1 , 3 — cohort K_2 . The dates of last day of censuses given on x axis.

Investigations were made to see whether female reproductivity in the current year's cohorts is connected with variations in the oestrous cycle, i.e., whether percentage of pregnant females from a given cohort and number of oestrous cycles per adult female, and average duration of oestrous are correlated.

In order to eliminate incorrect assessment of the duration of oestrus, investigations were made to determine whether the capture intervals for a given female erroneously caused successive observations of oestrus to be allocated the same, or different oestrous cycles. Intervals between successive observations of a particular phase (24, 36 and 48 hours) were considered. Depending upon their duration the percentage of cases was calculated in which two successive captures during the oestrus phase at intervals of 24, 36, 48 and more hours were not separated by a different

phase of the oestrous cycle. This percentage indicates the probability of oestrus existing during the interval between captures. It is high for the 24-hour interval, i.e. 0.91 and decreases considerably when the interval is 36 hours (0.55) (Tab. 11).

Table 10.

Comparison of variations in indices characterizing the spatial requirements of adult females, in view of the increasing percentage of pregnant females.

Indices	Dates of final day of successive censuses					
	18 IX 1966	30 VII 1967	14 VI 1967	31 VII 1966	14 IX 1967	16 VI 1966
Percent of pregnant females	38	40	48	60	63	69
Distribution characters	random	random	uniform	uniform	uniform	uniform
Home ranges overlapping index	1.744	1.752	1.866	1.664	1.401	1.697
Trappability index	0.510	0.549	0.545	0.598	0.629	0.510
Variation in number of captures with increase in number of females on trap site	decrease	decrease	decrease	decrease	decrease	decrease

Table 11.

Variations in chances of occurrence of oestrus (P_e), and not another phase of the cycle, depending on length of interval (expressed by number of hours) between two successive observations of oestrus in the same female.

Number of hours	Number of cases		P_e
	Not separated by the another phase of the cycle	Separated by the another phase of the cycle	
24	52	5	0.912
36	10	8	0.555
48	5	8	0.384
60	8	12	0.400
72	4	8	0.333
84	2	4	0.357
96	3	5	
108	1	6	0.083
120	0	5	
132	3	6	0.214
144	0	2	
156	0	1	
192	0	2	

On this basis it was accepted that two successive observations of oestrus separated by an interval of not more than 24 hours are observations of the same oestrous cycle.

Investigation was next made to discover whether there is connection between the percentage of pregnant females in a given cohort and frequency of occurrence of the oestrous cycle. This frequency is defined by the number of oestrous cycles not resulting in fertilization per unfertilized female in the given census. When cohort K_1 was taken as an example (the small amount of material made analysis of cohort K_2 impossible) it was found (Fig. 10) that in 1966 and during the period from June to July 1967 there is a positive relation between these variables, whereas during

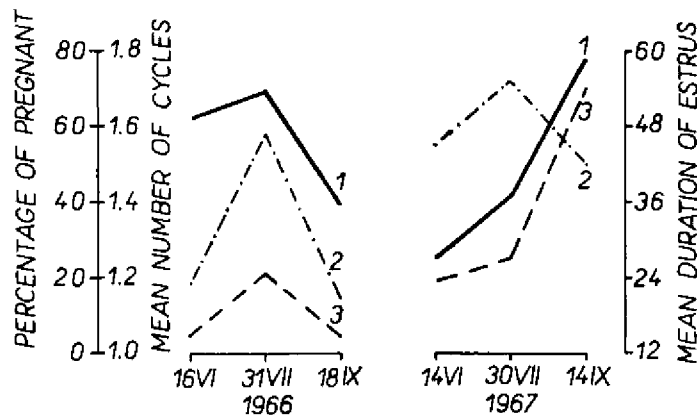


Fig. 10. Relation between percentage of pregnant females from cohort K_1 and variations in estrous cycle.

1 — percentage of pregnant females, 2 — mean number of estrous cycles per female during 14 days, 3 — mean duration of estrus (in hours). The dates of last day of censuses given on x axis.

the period from July to September 1967 this relation does not occur. This result does not justify finding a relation between the percentage of pregnant females among the adult females in cohort K_1 and the number of oestrous cycles occurring per unfertilized female.

In searching for the mechanism responsible for establishing the value $\bar{N}_p T$ during the reproductive season, comparison was made of the percentage of pregnant females from cohort K_1 and the average duration of oestrus in unfertilized females in this cohort. Duration of oestrus was measured by the number of successive observations (interval between observations was 12 hours) during which this phase of the cycle was found in a female.

The relation between the percentage of pregnant females and average duration of oestrus is positive in both years (Fig. 10), and thus shows that prolongation of the mean duration of oestrus contributes to increas-

ed likelihood of the being fertilized. Therefore variations described in the oestrous cycle forms one of the links in the process modifying the reproduction of cohort K_1 . This cohort brings the reproduction of the population up to a constant value $\bar{N}_p T$ in each of the study years.

The arguments forwarded so far indicate that:

1. Reproduction (its estimate being $\bar{N}_p T$) in the study population was lower than that potentially possible defined by the numbers of adult females. Values $\bar{N}_p T$ was stable over the yearly cycle, since the decrease in reproduction of females in cohort K_0 was always accompanied by an increase in reproduction of females in cohorts K_1 and K_2 . This points to the important role of cohort K_1 and K_0 in keeping the reproduction of the population up to a constant value.

2. Increase in reproduction of cohorts K_1 and K_2 was characterized by increased percentage of pregnant animals among the adult females in this cohort.

3. An important element in the process modifying reproduction of cohort K_1 (and probably K_2) is duration of oestrus (increase in duration of oestrus was accompanied by increase in the percentage of pregnant females).

5. DISCUSSION

Numerous studies on populations of small rodents living under natural conditions have revealed a negative correlation between the percentage of adult females and population numbers (Chitty, 1952; Kalela, 1957; Zejda, 1961, 1967; Newson, 1963; Jewell, 1966). A similar relation was also found in laboratory populations (Christian, 1956; Lidicker, 1965). This phenomenon was interpreted as the result of the action of density dependent factors.

The results of this study show that this correlation does not necessarily reflect a causal relation between the percentage of adult females and population numbers, but only a simple arithmetical relation. If the numbers of adult females are stabilized and population numbers vary — as was the case in the present studies — then the automatic consequence of the above facts is the inversely proportional relation between the percentage of adult females among all females and population numbers (Fig. 11). The numbers of adult females were stabilized as the result of the action of a factor independent of population density, namely the territorial tendency in this category of females, which would appear to be connected with the permissible number of social contacts. The numbers of adult females, independent of population numbers, also indicates that contacts between adult females played a significant role here, and not contacts between adult females and the other categories of individuals

(males and immature females). In the latter case numbers of adult females would in fact vary together with population density.

These studies point to the existence of an intrapopulation mechanism limiting the increase of population numbers as a result of limitation of

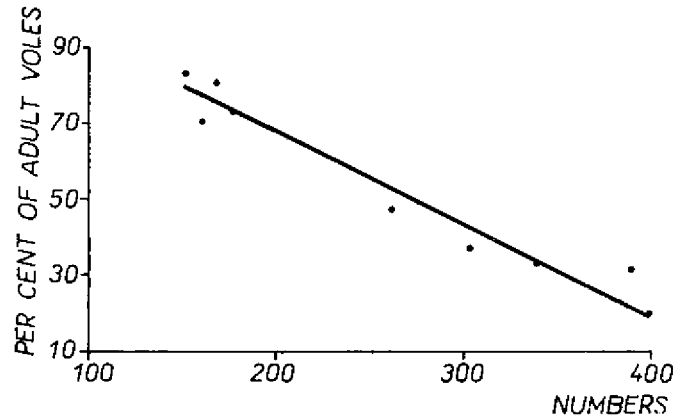


Fig. 11. Decrease in percentage of adult females which accompanies increase in population numbers.

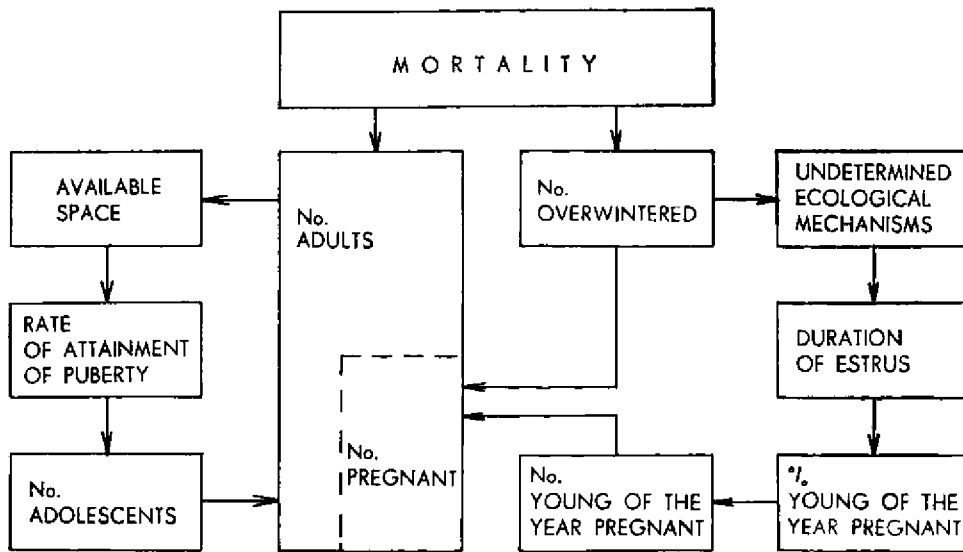


Fig. 12. Schematic representation of stabilizing effects on female reproductivity in an island population.

the numbers of females capable of reproduction. According to the assumptions made by many authors (Leopold, 1933; Calhoun, 1952; Kalela, 1957; Lidicker, 1962; Koškina, 1965) intrapopulation regulating mechanisms limit quantitative growth of the population. Consequently the population does not attain density allowed by the carrying

capacity of the habitat, but stabilizes at a lower density. The present studies show that limitation of increase in abundance of the population of red-backed voles is not of a density dependent nature, but depends on population structure. This agrees with opinions expressed by Petruszewicz (1966), who considered that regulation of numbers does not necessarily have to be a process dependent on density, but dependent on structure. The elements of population structure distinguished in the present studies are spatial structure and adequate physiological (adult and immature females) structure in relation to regulation of the numbers of adult females and age structure (old females and young of the year females) in relation to regulation of the number of pregnant females.

The above analyses show that there are two levels of stabilization of reproduction in the population investigated (Fig. 12). The first level is due to inhibition of attainment of puberty by all the young females (reproductive potential depends on numbers of mature females) on the basis their territorial tendency. The second level is limitation of actual reproduction of the population to a constant value of $\bar{N}_p T$ on a yearly scale. This value never reaches the potential value because there is a reciprocal relations between $\bar{N}_p T$ in overwintered females and females born during the current year. Unfortunately, ecological mechanisms responsible for the stabilisation of actual reproduction have not been distinguished yet.

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ELEMENTY STABILIZACJI ROZRODCZOŚCI W IZOLOWANEJ POPULACJI
NORNICY RUDEJ, *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780)

Streszczenie

W ciągu trzech lat badań nad rozrodczością żyjącej na wyspie (4 ha) populacji *C. glareolus* stwierdzono, że liczebność samic dojrzałych charakteryzowała się dużym stopniem stałości (57—63 samic — Ryc. 2). Jedynie we wczesnych miesiącach wiosennych liczebność samic dojrzałych zmieniała się w szerszym zakresie gdyż była uzależniona od liczebności samic, które przeżyły zimę.

Ustabilizowanej liczebności samic dojrzałych towarzyszyły znaczne zmiany liczebności populacji (160—399 osobników) oraz liczebności samic niedojrzałych (15—151 osobników (Ryc. 2).

Wysunięto hipotezę, że czynnikiem stabilizującym liczebność dojrzałych samic jest ich tendencja terytorialna. Hipotezę tę weryfikowano badając rozmieszczenie przestrzenne (Tabela 5), wskaźnik zachodzenia na siebie areałów osobniczych (Ryc. 3) oraz sposób wykorzystania areałów przez samice dojrzałe i niedojrzałe (Tabela 7, Ryc. 4—5). Zbadano również zależność między liczbą dojrzewających samic a rozległością wolnej przestrzeni, niepenetrowanej przez samice wcześniej dojrzałe (Ryc. 6—7). Wyniki potwierdzają wysuniętą hipotezę.

Liczebność samic ciężarnych była znacznie niższa od liczebności samic dojrzałych (17—44 osobników) a zmiany ich liczebności różne w kolejnych latach badań (Ryc. 8). Nie mniej jednak, w skali rocznej, wartość wskaźnika osobnikodni samic ciężarnych (a tym samym i liczba urodzonych) była prawie stała (4 865, 4 923, 4 624). Wynikało to z odwrotnie proporcjonalnej zależności między wartością wskaźnika u przezimków i samic tegorocznych (Tabela 9). Im więcej rozmnażało się przezimków, tym niższy był procent rozmnażających się samic tegorocznych. Zmiany procentu ciężarnych tegorocznych związane były ze zmianami czasu trwania estrus (Ryc. 10).