ACTA THERIOLOGICA

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Shape, Size and Distribution of Home Ranges
of *Clethrionomys glareolus* (Schreber, 1780)

[With 10 Tables & 11 Figs]

Analysis was made of material obtained in 1966 and 1967 from studies of a free-living population with known dynamics of numbers and age structure. It was found that there is a relation between the examined features of the home range: shape, size, location in the study area degree of overlapping and shift from the phenological time of the annual cycle, population numbers and social moment of entry of a cohort (a group of individuals of identical age). Due to the high level of numbers the location of home ranges in the area was more random and the ranges shifted to a lesser extent. The degree of elongation and the size of the home range decreased independently of dynamics of population numbers. The size and shape of the home range of the various cohorts depended on the time of their entry into the population: the later the cohort's entry into the population, the smaller and rounder the home ranges of its individuals. Within the cohorts analysed, males were found to possess larger home ranges than females.

1. INTRODUCTION

The space around established home of an animal, over which it moves in connection with its normal vital activities such as obtaining food, reproduction and care of progeny, is defined by the concept of the home range, as given by B u r t (1943). Definition of the size of this space, and examination of its relation to different habitat, biocenotic and population factors, has become the subject of a whole section of ecological literature. This was due to the interest in the relation between the size of the home range as a specific character of the species and the spatial organization of the population connected with it (interrelations in space between individuals) and other aspects of population organization (B r o w n, 1966), dynamics of its numbers (N a u m o v, 1956; G e t z, 1961; R y s z k o w s k i, 1961), competition (A n d r z e j e w s k i & O l s z e w s k i, 1963; D o m i n a s & T a r w i d, 1964; C a l - h o u n, 1963), epizootics (K a r a s e v a, 1956).

Considerable methodological difficulty is encountered in studies on the size of the home range and spatial organization of a population. Examination of methods hither to used shows that there are two approaches to this problem — the cartographical approach and that based on a statistical model.

The first of these attempts is based on the accumulation information in order to form the most reliable representation possible of the extent of the individuals' movements and on this basis to define the size of their home ranges. Ranges defined in this way are then further analysed. This method of approach is used when elaborating the results of the Catch-Mark-Release (CMR) method, using a suitable grid of traps, defining the so-called »minimum area« (D a l k e & S i m e, 1938; M o h r, 1947). The method defines the area of a minimum convex polygon covering 100% of the capture sites of an individual; it was used by many researchers (B l a i r, 1940a; B u r t, 1943; L a y n e, 1954; S t i c k a l, 1954; R e i c h - s t e i n, 1962; T a s t, 1966; R a d d a, 1968 and others). Home range is similarly defined from material collected by methods based on direct observations of animals (S o l d a t o v a, 1962) and on recording of the traces they leave (H o w a r d, 1949; D a v i s, 1953; J u s t i c e, 1961; S h e p p e, 1967; K u l i k & F a t e e v, 1969) or by methods based on the application of radioisotopes (G o d f r e y, 1953, 1954a, 1954b; M i l l e r, 1957; K a y, 1961) or on radiolocation (L e M u n y a n, W h i t e & N e b e r t, 1959; C o n c h r a n & R e x f o r d, 1963; S i n i f f & T e s t e r, 1965; S t o r m, 1965; T e s t e r & S i n i f f, 1963).

The second methodological approach aims at creating a model of the home range by means of which, using collected information on the animal's movements and in turn statistical analysis, an objective measure can be obtained of the size of the home range. The collected data for statistical definition of home range size consists of the material normally collected by means of the CMR method in various trapping devices arranged in defined areas.

»Observed range length« and »Adjusted range length« methods define the maximum distance covered by an individual during the study period (C h i t t y, 1937; G o d f r e y, 1954a; B r o w n, 1956).

A different method for statistical definition of the home range was suggested by A d a m c z y k et al. (1966), basing estimation of its size on the relation between the probability of visits by an individual of defined catch points located within its home range and home range size.

H a y n e (1949) showed that it is possible to define the centre of an individual's activity as the arithmetical mean of all of its capture sites, and to define home

range area on the basis of degree of probability of an individual's capture. He also found decrease in this probability as distance increased from the centre.

Using Hayne's statistical concept (1949) as a basis, Dice & Clark (1953) and Calhoun & Casby (1958) elaborated a theoretical model of the home range. They accepted a circular home range, Dice & Clark (1953) defining the distribution of probability of an individual's capture along the radius of the area as Pearson's type III, while Calhoun & Casby (1958) as the bivariate normal distribution over the area of the circle.

Many authors (Godfrey, 1954a; Tanaka, 1963a; Mohr, 1965) draw attention to the inadequacy of a circle to express the real shape of the home range of small mammals in the field conditions. Observations of maps of home ranges found in many studies, chiefly analysing home range size, such as those by Naumov (1951), Karaseva (1956), Reichstein (1959, 1962), Tast (1966), leads to the assumption that in the majority of cases the home range is elongated in shape.

These data, and also the methodical considerations discussed above for accurate estimation of home range size, formed a basis for modification of the model proposed by Calhoun & Casby (1958). The proposed modification (Mazurkiewicz, 1969) is a generalization, accepting an elliptic shape for the home range and treating the circular shape as a special case. The elliptic model of the home range has also been propesed by Jennrich & Turner (1969) for *Cnemidophorus tigris*.

The purpose of the present study was to check empirically the suitability of the methodological model of the home range proposed by Mazurkiewicz, 1969 and, by using it, to trace changes in the size and shape of the home range and the way in which individuals are distributed over the study area depending on age and sex structure and dynamics of population numbers of *Clethrionomys glareolus* (Schreber, 1780).

2. AREA, METHOD, MATERIAL

The basis for the analysis was formed by materials obtained in 1966 and 1967 from studies of a population of *C. glareolus* inhabiting an island of 4 ha area, located on Lake Bełdany (northern Poland, 53°40′N, 21°35′E).

The island is covered by forest belonging to 4 phytosociological associations. The humid coastal belt is covered by the *Salici-Frangulatum* Malc., 1929 association, the central part of the island (the driest) by *Tilio-Carpinetum typicum* Traczyk 1962, and in certain parts passes into the sub-association *Tilio-Carpinetum stachyetosum silvaticae* and in the wet depressions of the island into *Circaeo-Alnetum* Oberdorfer, 1953 (Fig. 1), (Traczyk, 1965). Minimum distance between island and the lake shore is approx. 120 m.

The island creates conditions of isolation for the population living on it. This isolation, with absence of phenomena of emigration and immigration, greatly facilitates determination of certain population parameters, such a variations in numbers, mortality, reproduction and age structure. The data either published or in

course of preparation, on general dynamics of population numbers on the island, the participation of the cohorts differentiated in the population dynamics the mortality of the cohorts and their role in reproduction. (B u j a l s k a *et al.*, 1968; G l i- w i c z *et al.*, 1968; P e t r u s e w i c z *et al.*, *in litt.*) have been used in this study as the background for the analysis of home ranges made.

The methods used for collecting data were based on the Catch-Mark-Release (*CMR*) principle.

During the whole cycle of studies the island was covered by a grid of 159 catch points, distributed chequerwise at intervals of 15 m. Two live traps were placed at each trap station.
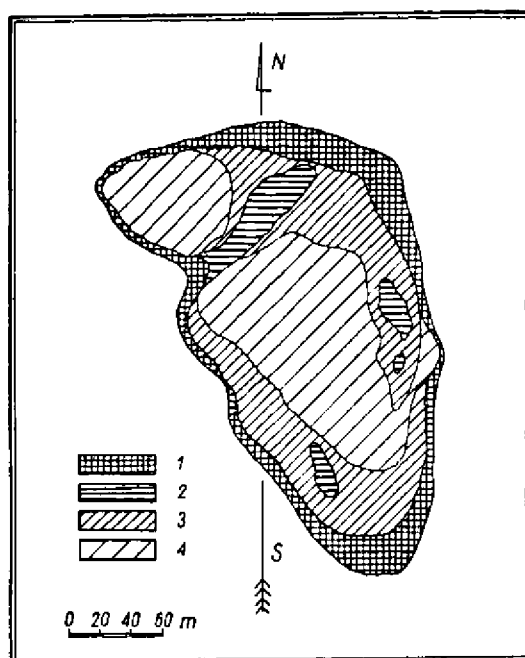

Fig. 1. Distribution of forest associations on »Crab Apple Island«.
1 — *Salici-Franguletum*, 2 — *Circaeo-Alnetum*, 3 — *Tilio-Carpinetum stachyeto-sum silvaticae*, 4 — *Tilio-Carpinetum typicum* (after T r a c z y k, 1965).

Five series of trappings were made from spring to autumn each year (total 10 series), at approximately one-monthly intervals. Each series of trappings lasted 14 days, with the exception of April 1966, when this period was 7 days only.

Traps were inspected twice daily, at 7,00 and 19,00, in every trapping series. The trapped individual was removed from the trap its number (the animals had been marked by toe-clipping), and weight, sex and trapping site recorded.

The material collected consisted of a total of 8334 captures of 939 individuals in 1966, and 7213 captures of 785 individuals in 1967 (Table 1).

G l i w i c z *et al.* (1968) and P e t r u s e w i c z *et al.* (*in litt.*) described the method of general census of the numbers of individuals on the island in successive trapping series (five times each year). The following findings argue in favour of the accu-

racy of the numbers given. In the first place, the 14-day period of trapping makes it possible to record all the individuals on the island, since there was not a single case of an individual missing out one trapping series and then making its appearance in the following series (A n d r z e j e w s k i *et al.* 1967). In the second place, capture and removal of marked individuals in previous trapping series was very rapid, so that 95% of the individuals had been recorded during the first three days of the given trapping period. Finally, individuals recorded for the first time weighed so little that it could be assumed that they had not yet reached trappable age during earlier censuses (G l i w i c z *et al.*, 1968).

Table 1

Distribution of individuals depending on number of captures in successive censuses.

Year	Month	No. of captures	K_0 ♀♀	K_0 ♂♂	K_1 ♀♀	K_1 ♂♂	K_2 ♀♀	K_2 ♂♂	K_3 ♀♀	K_3 ♂♂	K_4 ♀♀	K_4 ♂♂
	April	1—4	5	3								
		5—14	19	29								
	June	—	—	—	23	43						
		16	16	22	34	13						
	July	1—4	—	—	6	11	34	27				
		5—28	8	12	35	28	71	72				
	Sept.	1—4	—	—	6	7	20	36	4	10		
		5—28	3	3	18	20	59	49	14	13		
	Nov.	1—4	—	—	2	4	5	3	3	—	1	1
		5—28	1	—	12	14	53	60	10	3	2	2
	April	1—4	1	4								
		5—28	36	27								
	June	1—4	1	—	28	25						
		5—28	21	14	32	39						
	July	1—4	—	—	6	6	11	21				
		5—28	8	4	37	39	16	19				
	Sept.	1—4	—	—	2	5	3	3	4	19		
		5—28	5	2	25	23	16	29	20	19		
	Nov.	1—4	—	—	2	4	2	7	7	7	26	42
		5—28	2	—	15	16	12	17	9	11	9	14

On the basis of the analysis of the above material, G l i w i c z *et al.* (*l.c.*) divided all the individuals in the population into several age groups (cohorts):

Cohort K_0 — individuals which had lived through a winter (old adults), aged from 6 to 11 months the following spring

Cohort K_1 — early spring generation born between April 23rd and May 26th

Cohort K_2 — early summer generation, born between May 27th and July 10th

Cohort K_3 — late summer generation, born between July 11th and August 28th

Cohort K_4 — early autumn generation born between August 28th and October 1st.

The number variations of the distinguished cohorts (Fig. 2) formed a basis for analysing relations between the population's age structure and the parameters of is spatial structure. Calculations were made using a ZAM-21 alpha computer.

3. MODEL OF HOME RANGE

Initial analysis of the shape of the home range of *C. glareolus* (M a-
z u r k i e w i c z, 1969) confirmed the results given by M o h r (1965),
G o d f r e y (1954a) and others on the elongated shape of the home
range, both in an isolated (island) and open area. These results justified
acceptance of a model assuming no circular home range.

Capture sites for each individual living in the studied population,
were defined by the CMR method by two numbers (abscissa and ordi-
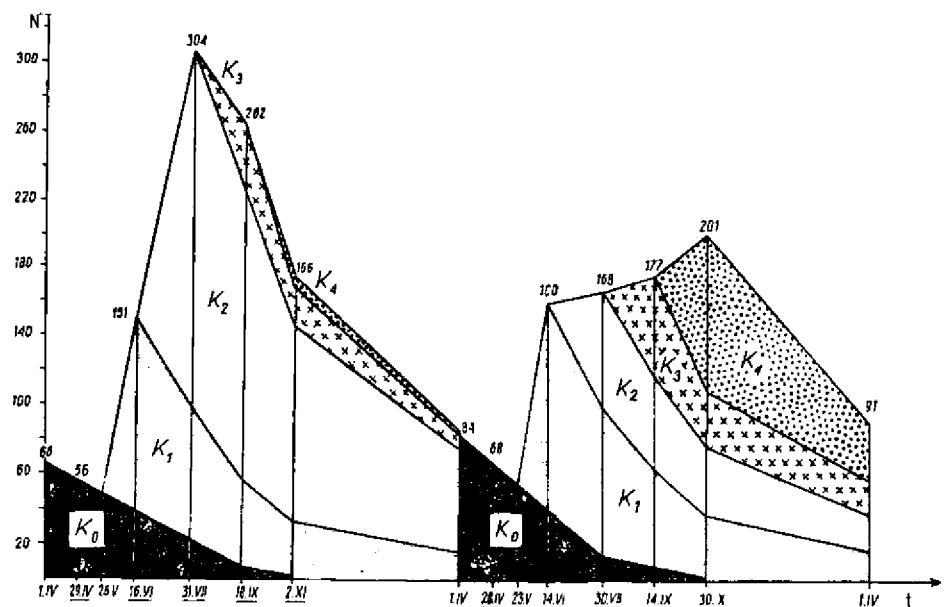nate) indicating respectively the number and position in the row of

Fig. 2. Population dynamics in 1966 and 1967.
K_0—K_4 — cohorts. Axis x — time (dates of general census underlined). Axis y —
numerousness of individuals (after G l i w i c z *et al.* 1968, and P e t r u s e w i c z
et al. in litt.).

traps. All capture sites of a given individual can be described statistically
by giving five parameters: the mean abscissa, the mean ordinate, devia-
tion from mean abscissa, deviation from mean ordinate, covariance of
deviations. The first two parameters indicate the co-ordinates of the
statistical centre of the individual's home range, the last three indicate
the way in which capture sites are distributed around this centrum.
These five statistical parameters approximately define the way in which
the individual makes use of the area and permits defining, also approxi-
mately, the animal's home range.

Statistical elaboration of coordinates of catch points, such as the one of C a l h o u n & C a s b y's (1958), is limited only to three parameters, the first two of which are identical with those given above, while the third replaces the remaining three. This third is the distance of trap points from the statistical centre of the range. C a l h o u n & C a s b y (*l.c.*) do not thus make use of part of the information provided by recording capture sites; in particular they do not take into consideration the fact that an individual living in the area may prefer one (or several) direction of movement over the area, but treat all directions equally. This consequently leads to acceptance of the circular model of the home range. From the statistical point of view, the limitation inherent in C a l h o u n & C a s b y's (1958) method is that it fails to take into account the fact that deviation from the mean along the rows of traps may not be of the same value as deviation across the rows and that covariance of deviations may not be equal to zero.

In order to utilize the five above-mentioned statistical parameters the following assumptions were accepted as a working hypothesis: (1) an individual moving about the area prefers one particular direction, (2) probability of revelation of trapping sites by an individual is subject to the rules of two-dimensional normal distribution, (3) the boundary of a home range is a closed curve connecting sites in an area of uniform probability *) of encountering an individual and closing the defined distribution of percentages of all captures.

In order to check the reliability of assumptions (2) and (3) the ellipses corresponding to home ranges of 50 individuals chosen at random were drawn. If the distribution of captures of an individual should contain 63.2% of captures in the area corresponded to the two-dimensional normal distribution. The real number of captures within the defined ellipses were then counted, combining 5 individuals in each group.

It was found by means of the χ^2 test that the figure obtained did not differ significantly from the theoretical value of 63.2% (Table 3). Although this finding is not sufficient proof of the normality of the distribution, there are no grounds for rejecting this hypothesis and it is justifiable to use the normal distribution when describing the home range. Assuming that distribution of likelihood of encountering an individual within its own home range is a normal distribution, then it is possible to describe the way in which the area is used by an individual. Distribution of probability of encounter of an individual within the home range creates an area similar in shape to a »bilaterally flattened bell«, with its apex above the geometrical centre. Ellipses with a common centre and uniform

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*) Strictly speaking: density of probability.

degree of flattening correspond to the curves on the surface of a uniform probability of encountering an individual. If the circular home range is accepted, the area obtained is similar in shape to a »bell« with circles instead of ellipses.

On the basis of the assumptions accepted, simple statistical elaboration leads to the determination of the home range boundary which is an ellipse with its centre in the geometrical centre, with axis deflected to the lines of rows at a certain angle φ and with a given degree of flat-

Table 2

Numerousness, number of captures and average number of captures of observed males and females.

Year	Month	Sex	N	No. of captures	No. of captures of individual	Per cent of population
1966	April	♂♂	29	265	9.0	85.7
		♀♀	19	146	7.7	
	June	♂♂	35	521	14.9	55.9
		♀♀	50	590	11.8	
	July	♂♂	100	1085	10.9	67.8
		♀♀	106	1225	11.6	
	Sept.	♂♂	81	890	11.0	65.6
		♀♀	91	1072	11.8	
	Nov.	♂♂	67	758	11.3	85.5
		♀♀	75	984	13.1	
1967	April	♂♂	27	342	12.7	92.6
		♀♀	36	451	12.5	
	June	♂♂	53	544	10.3	62 5
		♀♀	53	594	11.2	
	July	♂♂	58	717	12.4	64.3
		♀♀	53	641	12.1	
	Sept.	♂♂	71	1021	14.4	76.3
		♀♀	64	933	14.6	
	Nov.	♂♂	58	583	10.1	51.2
		♀♀	45	523	11.6	

tening. A home range model of this kind is called an elliptic model. Both angle φ and flattening of the ellipse can be easily calculated from the five statistical parameters given (cf. Appendix). Angle φ defines the direction of movement preferred by an individual, and the flattening of the ellipses (ratio of axes) the degree of preference for this direction.

Home range defined in this way has a definite shape and location in the area but an undefined size, dimensions of the ellipse forming the boundary of the home range depend on what percentage of all captures

it is to contain. Depending on the assumed percentage the boundary ellipse will be greater or smaller, but will retain a constant centre, direction of main axes and flattening. With the determination of a certain percentage of captures (in the present study — 95%) which, in accordance with the assumed normality of distribution is to be enclosed within the elliptical area, we can define the absolute sizes of the ellipses for the

Table 3

Comparison of the percentage of captures in elliptic home ranges with theoretical value 63.2% (according to noraml distribution).

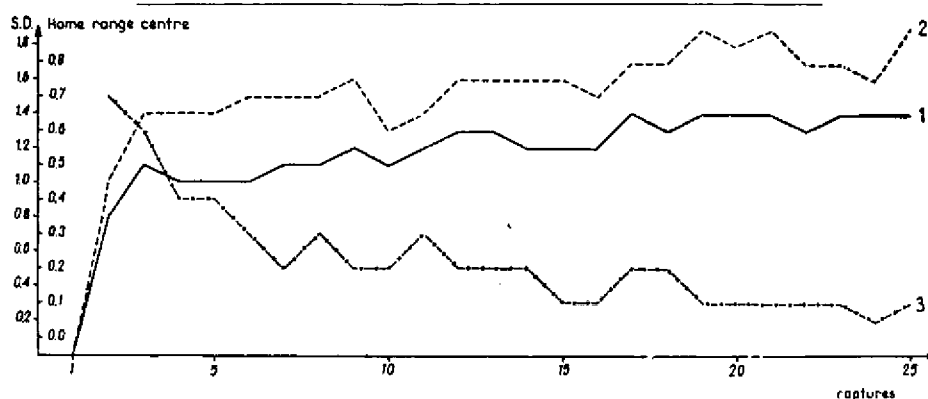| Groups	Pecentage of captures		χ^2
	Empirical	Theoretical	
1	64.3		0.019
2	67.1		0.240
3	61.8		0.031
4	66.3	63.2	0.152
5	69.2		0.569
6	68.2		0.396
7	68.6		0.461
8	66.7		0.193
9	74.6		2.050
10	59.4		0.228
			4.339

Fig. 3. Number of captures and estimated size of home range.
1 — standard deviation along axis x, 2 — standard deviation along axis y, 3 — shift in centre of home range.

given individuals. By comparing these sizes conclusions can be reached on the reciprocal relation of the real home ranges of these individuals.

Thus the parameters of the ellipses obtained from the calculated five statistical parameters provide a convenient method for investigating size and reciprocal distribution of home ranges of different individuals, pre-

ferred direction of the individual's movements and the intensity of this preference.

4. NUMBER OF CAPTURES AND ESTIMATED HOME RANGE SIZE

In order to find out how the number of captures of an individual affects the estimate of the size of its home range, we chose 50 individuals, males and females, characterized by a high number of captures (from 14 to 26 captures in one trapping series) and presence in several series of trappings. Calculation was made for each individual of the geometrical centre of its home range and standard deviation of distances of successive captures from this centre along each of the axes of the co-ordinates of the trapping grid, starting from two captures, and then adding one consecutive capture up to the total number of captures of the given individual. Calculation was made of the average shift in the geometrical centre of the home range and average standard deviation of distance of captures from this centre each time a capture was added (Fig. 3).
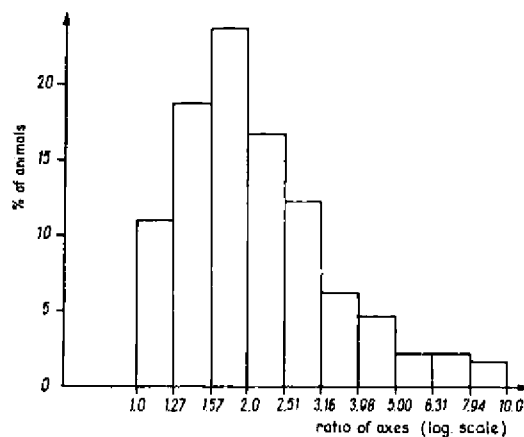

Fig. 4. Distribution of all individuals depending of degree of elongation of home range measured by the ratio of axes of elliptic home ranges.

It was found that the average shift in the geometrical centre of home ranges is slight and gradually decreases with increase in number of captures. It is not until the 19th repeat capture that it is established on a definite level. Standard deviations of distance of capture from the centre, however, increase sharply up to 3 captures, then continuously, but very slightly, increase up to the maximum number of captures.

Several authors (B l a i r, 1942; H a y n e, 1950; S t i c k e l, 1954) consider that reliable size of the home area is obtained only after the individual has been caught 10 times. The above results show that error in estimating home range size (calculated on the basis of standard deviations) does not significantly increase when a minimum number of 5 capture is

accepted (in one trapping series) as qualifying an individual for collective analysis. In this way analysis included in different trapping series from 51.2 to 92.6% of individuals of the study population and the mean number of captures varied from 7.7 to 14.6 for females and from 9.0 to 14.9 for males (Table 2). Reduction of the material concerned primarily the youngest individuals in a given trapping series, which were caught for the first time towards the end of the study period (Table 1).

5. SHAPE OF HOME RANGE

The shape of the home range was characterized by the degree to which the ellipse was flattened, accepting as an index the ratio of length of the main axes of the ellipses. In this way a numerical index was obtained
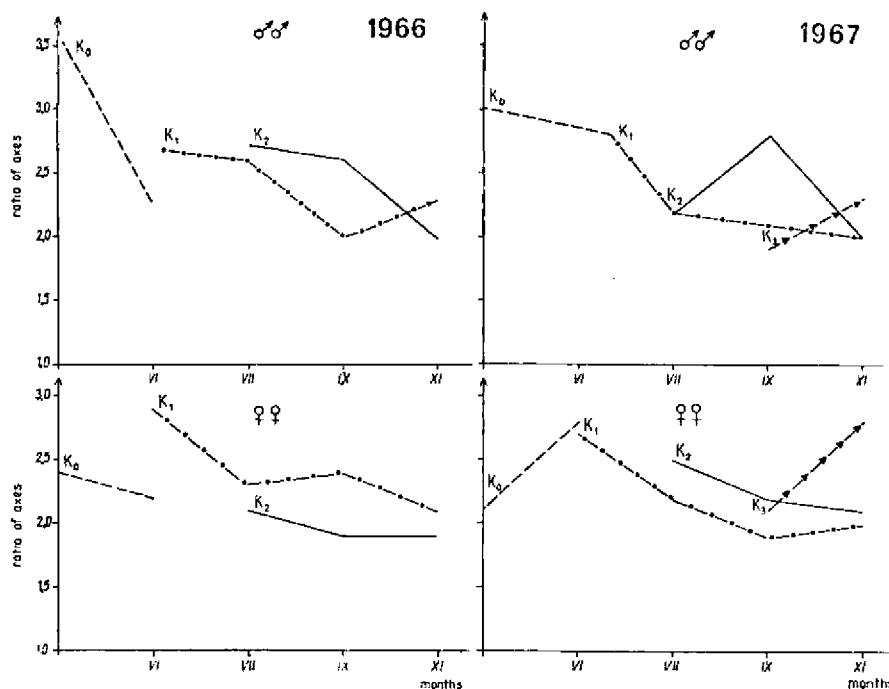

Fig. 5. Average elongation of home range of males and females.

for each individual defining how many times longer one axis of the elliptic home range was than the other. A histogram (Fig. 4) of the degree of elongation of the home range was made for all the individuals examined, and mean elongation of the home range calculated for females and males in each trapping series (Fig. 5). The coefficient of variations in elongation of the home range within the cohorts occurring in the given trapping series are given in Table 4.

5.1. Elliptic Shape of Home Range

Analysis of the shape of the home range in successive trapping series showed that in the majority of individuals it was similar in shape to a more or less flattened ellipse, on an average with one axis 2.51 times longer than the other. Out of the 1157 analyses, 30% of the individuals had an almost circular home range (with axis ratio 1—1.57), 40% of the individuals had a home range with axis ratio of 1.57—2.51, 30% of the individuals had a more elongated home range up to an axis ratio of 10.00 (Fig. 4).

Table 4

Coefficient of variation in elongation of home ranges of individuals belonging to different cohorts.

Cohort	Sex	1966					1967				
		April	June	July	Sept.	Oct.	April	June	July	Sept.	Oct.
K_0	♂♂	12.7	6.4				11.2	9.7			
	♀♀	12.1	8.6				5.4	13.8			
K_1	♂♂		16.9	11.1	10.1	17.3		16.5	7.7	8.0	15.2
	♀♀		7.6	9.9	14.5	9.6		10.3	8.5	5.7	9.1
K_2	♂♂			10.3	8.0	8.9			13.0	12.4	5.9
	♀♀			9.3	4.7	7.4			24.4	10.4	12.6
K_3	♂♂	·								10.3	12.0
	♀♀									10.6	22.4

The above data show that the elliptic model of the home range is a more accurate simulation of the actual distribution of captures of an individual in the study area than a model assuming the home range to be round.

5.2. Changes in Shape of the Home Range of Different Cohorts

The shape of the home range for individuals belonging to different cohorts was traced (measured by the ratio of axis lengths of the ellipse) at various times of the annual cycle, defined by the trapping periods (Fig. 5).

It was found that the shape of the home range for individuals belonging to different cohorts exhibits irregular changes in time with a distinct tendency to rounding of the home range from spring to autumn.

The most elongated home ranges are those of cohort K_0 males in spring (April). During this time a difference is observed in the degree of elongation of the home range between males and females. From June the degree of elongation of the home range is similar for females and males

in both cohort K_0 and also in cohorts K_1, K_2 and K_3 successively entering the population.

The home range of cohort K_1 individuals, whether females or males, is most elongated at the time this cohort enters the population (June). The course taken by seasonal variations in degree of elongation of the home range is similar in both study years for this group of individuals (Fig. 5). The shape of the home range of cohort K_2, entering the population in July, is similar to that of the cohort K_1 during this period. The home range of individuals belonging to cohort K_3 exhibits a tendency to elongation from the time this cohort enters the population till autumn (Fig. 5).

Analysis was made of the differentiation of females and males in respect of the shape of their home ranges within the different cohort in successive trapping series, using the variation coefficient (ratio of error in mean to the mean). It was found that the different cohorts do not form a uniform group in respect of home range shape. The degree of differentiation of the individuals in the cohorts varies in time, but such variations do not exhibit any regularities (Table 4).

Comparison of the home range shape for individuals in the different cohorts at the same age showed that its shape is not connected with this particular age.

Concluding it can be said that the home range is elliptic in shape, with average axis ratio of 2.5; maximum elongation is found in the home ranges cohort K_0 males (old adults) in spring; during this season differences occur between the shape of the home range of males (axis ratio 3.0—3.6) and of females (axis ratio 2.1—2.4). No correlations were found between the age of individuals and degree of elongation of their home range. The home range of individuals of the whole population tends gradually to become rounder from spring to autumn.

6. SIZE OF HOME RANGE

The size of the home range was defined by the area of an ellipse containing 95% of captures of an individual and expressed in units related to one catch point (1 = 225 m²). Calculation was made of the average size of the home range for males and females in the different cohorts appearing in the given trapping series (Fig. 6). Differentiation in home range size within the cohorts was defined by means of the variation coefficient (Table 5). Assuming that males and females in the different cohorts excluded from analysis have home ranges equal to the mean home range of individuals analysed in the given groups, calculation was made of the total sum of home ranges, average home range and

degree to which they overlap for the whole population in successive trapping series (Table 6).

6.1. Changes in Size of Home Range of Different Cohorts

The largest home ranges are those of males belonging to cohort K_0, particularly in June (Fig. 6). The males of each successive cohort entering the population always have smaller home ranges than those of males in the previous cohort which has already entered the population.
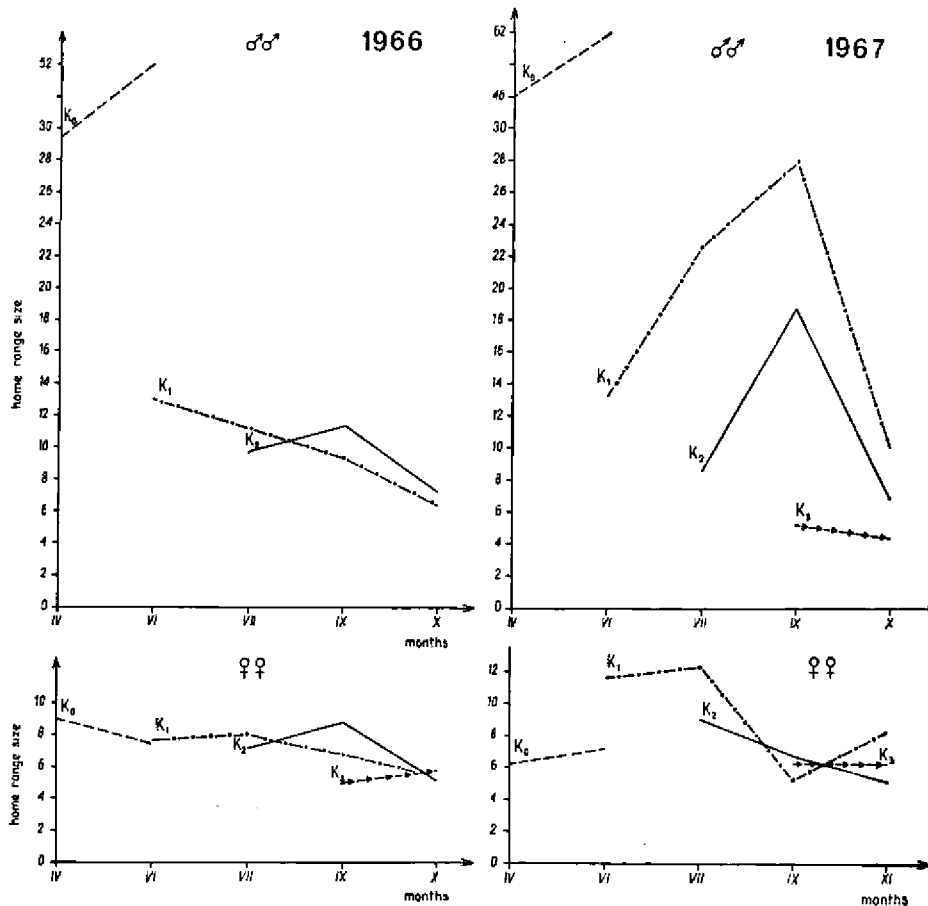

Fig. 6. Mean size of home range of males and females in 1966 and 1967
$(1 = 225 \ m^2)$.

The different course taken by variations in the size of home ranges of males belonging to different cohorts in 1966 and 1967 is probably connected with different population numbers in July and September

(Fig. 2). In 1967 the level of numbers is far lower in these months, which enables individuals to extend their home ranges. The second factor probably contributing to increase in size of home range of males in cohorts K_1 and K_2 up to September is the prolonged reproduction season (B u-jalska in litt.). The size of home ranges in cohort K_3 males (which probably do not participate in reproduction) is maintained on a similar low level in September and November.

The size of home ranges for females belonging to cohort K_0 varies very little from April to June (Fig. 6). The home range of cohort K_1 females at the time of their entry into the population is larger or the same as that of cohort K_0 during this period. The home range of females belonging to cohorts K_2 and K_3 is smaller at the time of entry of these cohorts into the population in relation to the home ranges of females

Table 5

Coefficient of variation in home range size of individuals belonging to different cohorts.

Cohort	Sex	1966					1967				
		April	June	July	Sept.	Oct.	April	June	July	Sept.	Oct.
K_0	♂♂	9.8	11.6				9.9	19.4			
	♀♀	34.0	3.7				62.9	14.5			
K_1	♂♂		32.9	13.2	12.2	21.2		17.5	16.8	17.4	18.9
	♀♀		16.9	10.7	15.2	16.7		14.2	24.7	9.7	12.9
K_2	♂♂			49.4	17.3	18.4			29.0	21.9	41.1
	♀♀			19.3	20.0	11.8			35.8	16.5	12.1
K_3	♂♂				34.0	36.3				12.2	9.8
	♀♀				12.0	7.9				36.1	24.6

which had entered the population earlier (home range of cohort K_2 in relation to that of cohort K_3, home range of cohort K_3 in relation to that of cohort K_2).

In the autumn, in November, there is a decrease in the size of home range of both females and males (Fig. 6). When the whole of the material is analysed the average size of the home area was found to be different for females and males. In cohort K_0, K_1 and K_2 the males' home ranges are greater than those of females, the greatest difference occurring in cohort K_0. In cohort K_3 the females' home range is slightly greater than that of males.

Very considerable differences were found between females and males in respect of size of the home range within the different cohorts (Table 5). These differences are greater than the differences between individuals

discussed in the previous section, in respect of shape of home range (Table 4). As in the case of shape of the home range, variations in time do not exhibit any regularities.

6.2. Seasonal Changes in Mean Size of Home Range and Degree of Overlapping

The mean size of the home range calculated for the whole population exhibited a tendency to decrease from April to November, in a similar way in both study years (Table 6). The inverse relation between mean size of home range and level of population numbers occurs in April and June 1966 and 1967, and the following months of 1967. In 1966, however, the mean home range decreased with decreasing populations numbers from July to November 1966.

Table 6

Numerousness, sum total od home ranges, average home range and degree to which they overlap in successive censuses

Year	Month	No of individuals studied	Total number of population	Sum of home ranges	Mean home range	'Degree of overlapping
1966	April	48	56	1154.4	20.6	7.3
	June	85	152	2425.6	15.9	15.2
	July	206	304	3202.6	10.5	20.1
	Sept.	172	262	2501.8	9.5	15.7
	Nov.	142	166	1482.0	8.3	9.3
1967	April	63	68	1648.6	24.2	10.4
	June	100	160	2565.0	16.1	16.1
	July	108	168	2626.0	15.0	15.9
	Sept.	135	177	2010.3	11.2	12.6
	Nov.	103	201	1433.6	7.1	9.0

The degree of overlapping of home ranges (ratio of total sum of home ranges to number of catch points — in the area) is the function of size of home ranges and population numbers. In 1966 it exhibits a positive relation to level of numbers in consecutive trapping series. In 1967 both population numbers and average size of home range, and also the degree to which they overlap, exhibit slight differences in June and July. Increase in numbers up to November is connected with reduction of the average home range size and degree of overlapping of home ranges.

To sum up it may be said that: females belonging to cohort K_0 (old adults) have the largest home ranges; home ranges of males are larger than those of females. The greatest difference occurs in cohort K_0. The later the cohort enters the population the smaller the home ranges of

the individuals forming the cohort (except for females in cohort K_1). In autumn the home range and its differentiation between cohorts, and also between males and females within the cohorts, decreases. The mean size of the home range decreases from spring to autumn irrespective of differences in the level of numbers in different months of the two years. The level of numbers and mean size of the home range determine the degree of overlapping of home ranges.

7. DISTRIBUTION OF INDIVIDUALS IN THE AREA AND ITS VARIATIONS IN TIME

7.1. Distribution of the Geometrical Centres of Home Ranges in the Area

Using the studies made by F i t c h (1947) and B r a n t (1962) as a basis, the distribution of individuals over the island was defined by the distribution of the geometrical centres of their home ranges. For this purpose the geometrical centres of home ranges of individuals recorded.

Table 7

Distribution of squares in trapping grid depending on number of centres of home ranges.

Year	Period	Distribution of the number of individuals						Avg.
		0	1	2	3	4	5	
1966	April	111	33	4	1	1	—	0.3
	June	62	58	29	9	1	—	0.9
	July	28	40	38	31	15	7	1.9
	Sept.	25	55	44	22	10	2	1.8
	Oct.	57	63	25	14	—	—	1.0
1967	April	107	44	5	3	—	—	0.4
	June	85	47	25	1	1	—	0.6
	July	79	46	26	7	1	—	0.8
	Sept.	55	72	26	5	1	—	0.9
	Oct.	81	54	20	4	—	—	0.7

in a given trapping series were plotted on a map of the island. The surface of the island was divided according to the distribution of catch points. The distribution of the geometrical centres of home ranges of individuals in the various squares was compared with Poisson's theoretical distribution. Analysis was made jointly for all individuals in a given trapping series, and also separately for various cohorts.

It was found that the distribution of geometrical centres of home ranges over the island agrees with Poisson's distribution in all the trapping series when the whole population is taken into consideration (Table 7). When the varius cohorts were taken separately, it was only in

one case that a clumped distribution was obtained, namely in July 1966 for cohort K_2, the youngest in the given trapping series. Cohort K_2 was very numerous this year (Fig. 2), and in July is formed 70% of the individuals of the whole population. It is possible that the individuals belonging to this young cohort shared nests and had not yet dispersed.

7.2. Degree to Which Geometrical Centre of Home Ranges Shifts during the Course of the Year

In order to determine how great is the shift in geometrical centre of home ranges in time, the geometrical centres of home ranges of each individual were plotted on a map of the island for each of two successive censuses. Having marked two geometrical centres of home ranges which
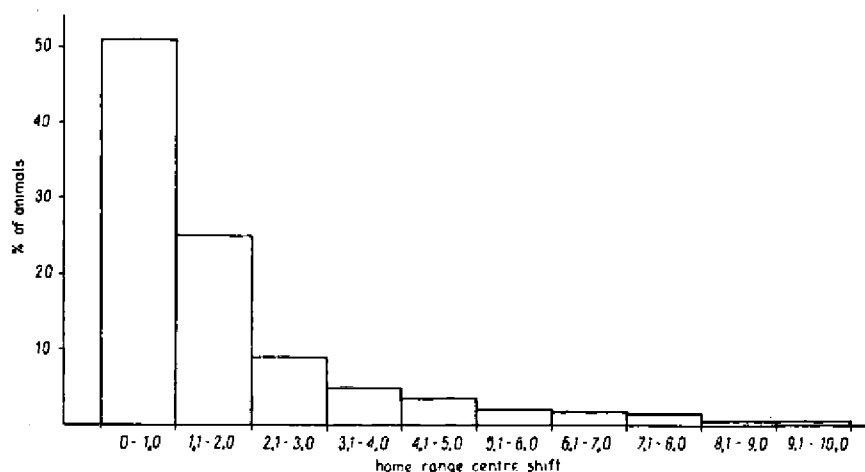

Fig. 7. Extent of shift in home range centre between two successive censuses (unit = 15 m, interval between traps).

correspond to two successive censuses, the distance was measured between them. In this way the extent of shift taking place during the interval between censuses was obtained. Calculation was made of the distribution of extent of shift in the geometrical centre of the home range jointly for all the individuals examined (a total number of 805 shifts was measured) (Fig. 7). Calculation was made of the mean shift in centres between consecutive censuses for females and males within cohorts K_0, K_1, K_2 in both study years (Fig. 8).

Analysis showed that 51% of all the individuals shifted the centre of their home ranges only slightly over the course of 1.5 months (on an average 7.5 m), 25% of individuals shifted it, an average of 15 m and only

24% of individuals shifted these centres to a greater extent (from 30 to 150 m) (Fig. 7).

Comparison of the average shift in geometrical centre of home ranges of males and females in the different cohorts showed that in the majority of cases the shift was greater in the case of males then females belonging to the same cohort (Fig. 8). Comparison of consecutive shifts in these centres for the cohorts K_0, K_1, K_2 in both years showed that there is
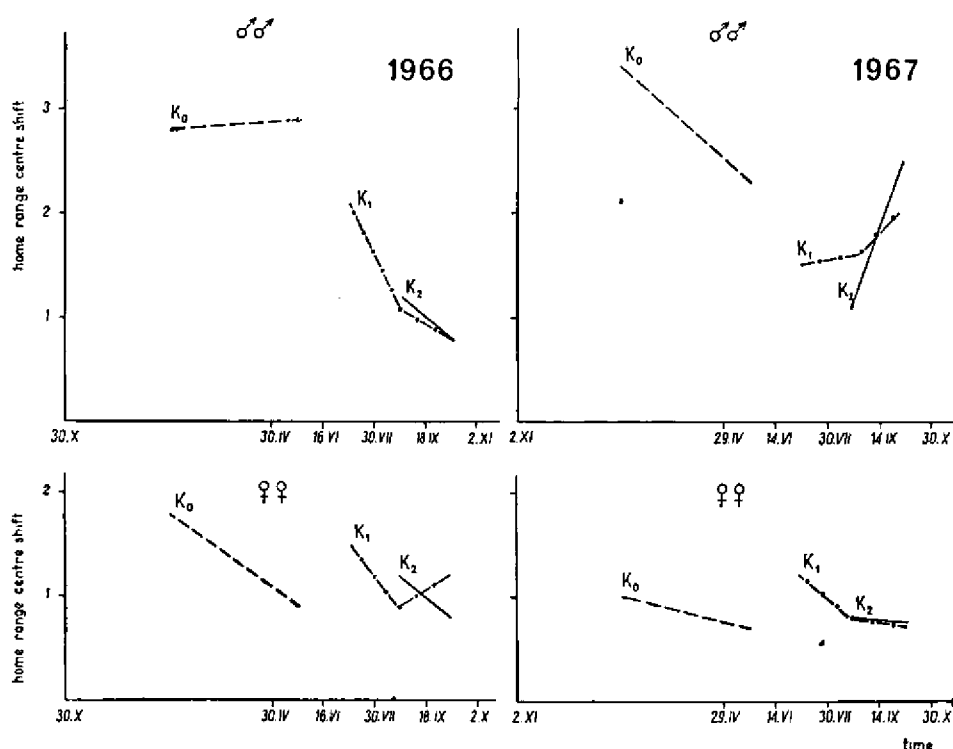

Fig. 8. Mean shift in home range centre (1 = 15 m) of different cohorts in 1966 and 1967.

a tendency to decrease of the value of shift in time (Fig. 8). An exception is formed by males in cohorts K_1 and K_2 in 1967. Cohort K_0, in particular the males, exhibits a considerable shift between November and April in both years, but this shift takes place over a period four times longer (5.5 months) than shift in the case of cohort K_1 and K_2 (1.5 months).

Analysis of differences in extent of shift of these centres for females and males within the different cohorts (described by the ratio of error of mean to the mean) (Table 8) showed that cohorts are not homogeneous

groups, and the degree of differentiation of individuals depends on the numbers of the cohort and density of the whole population. Particularly striking differences occur in the degree of differentiation of individuals in cohort K_2 in 1966 and 1967. In 1966 owing to the high population numbers there are only slight differences between individuals in this cohort in respect of shift in centres of home ranges. In 1967 the entry of new individuals into the population took place gradually (there is no distinct peak in numbers) and the differentiation of individuals in cohort K_2 is far greater, particularly among males.

Cohort K_1, the numbers of which were similar in both years, exhibits a similar degree of differentiation in respect of amount of shift of the centre of home ranges. This degree has a tendency to increase in the case of males, and to remain on a similar level for females.

Table 8

Coefficient of variation in shift of home range centres of individuals belonging to different cohorts taking place between successive censuses.

Cohort	Sex	1966					1967				
		XI-IV	IV-VI	VI-VII	VII-IX	IX-XI	XI-IV	IV-VI	VI-VII	VII-IX	IX-XI
K_0	♂♂	13.5	10.5	—	—	—	9.5	14.5	—	—	—
	♀♀	19.8	18.1	—	—	—	10.8	14.9	—	—	—
K_1	♂♂	—	—	8.5	17.4	15.2	—	—	13.0	16.6	15.3
	♀♀	—	—	15.2	16.2	12.5	—	—	17.1	13.3	14.1
K_2	♂♂	—	—	—	8.9	11.5	—	—	—	21.1	25.6
	♀♀	—	—	—	8.0	8.8	—	—	—	17.8	14.9

To sum up it was found that: distribution of the geometrical centres of the home ranges for individuals in the whole population and in different cohorts (except for cohort K_2 in July 1966) was random in all censuses. The shift in the geometrical centres of home ranges in time was slight in the majority of cases, but greater for males than females. Differences between individuals in the various cohorts in respect of extent of shift in centres of home ranges would appear to depend on numbers of the cohort and population density.

8. ARRANGEMENT OF HOME RANGES IN THE AREA

8.1. Methodical Remarks

Analysis of the distribution of geometrical centres of home ranges in the study area showed that their distribution is random. The elliptical shape of the home range, however, suggests that external factors have
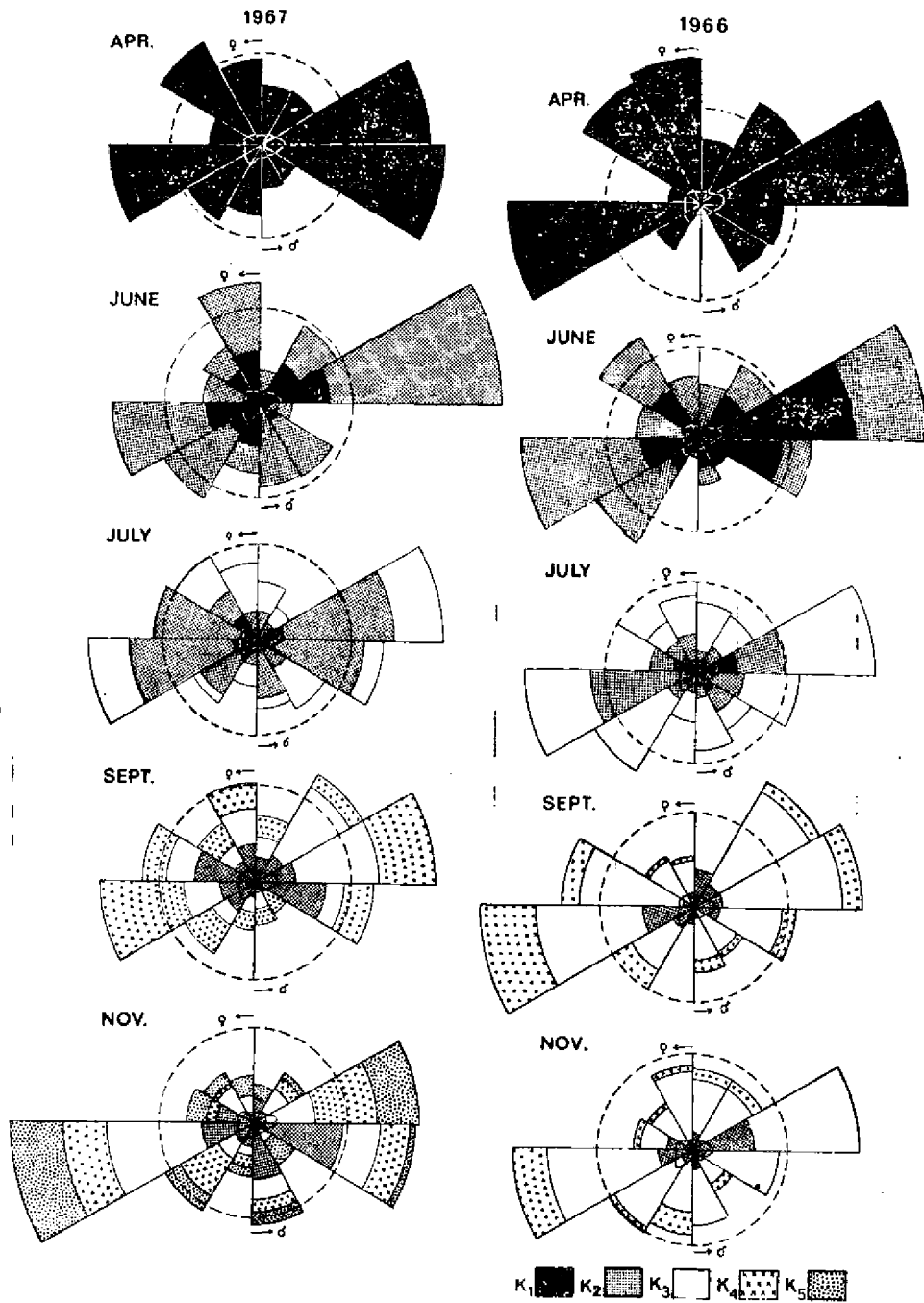
Fig. 9. Location of home range of females and males in 6 directions distinguished
in successive censuses.
———— standarized average for all censuses.

a varying influence on the way in which the individual moves over the area. It may be assumed that the long axis of the elliptic home range is the direction in which the individual prefers to move, rather than a direction corresponding to the short axis of the home range.

Analysis was made of the directions in which the home ranges were arranged in the study area. The analysis was based on calculations of the following data for each individual: (1) angle φ formed by long axis of the ellipse with the axis of the catch point grid in the area, describing the direction of location of the home range in the study area, and (2) the eccentric of the ellipse, which is a measure of the ratio of the main axes of the ellipse and simultaneously a measure of its flattening in the range of 0—1 (in the case of a circle it is zero, and in the case of a straight line — unity) (a detailed description of the method is to be found in the study by M a z u r k i e w i c z, 1970).

Table 9

Distribution of individuals depending on direction in which their home ranges are located in the study area.

Year	Month	0—29°		30—59°		60—89°		90—119°		120—149°		150—180°	
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1966	April	0	5	4	5	5	1	11	6	6	2	3	0
	June	3	6	2	10	7	1	15	16	5	10	3	2
	July	16	12	9	8	13	14	21	25	8	17	9	8
	Sept.	14	7	11	10	19	22	32	36	28	16	7	4
	Oct.	11	12	7	8	11	8	23	24	10	14	10	13
1967	April	2	6	2	7	9	3	8	11	3	5	3	4
	June	8	12	8	6	3	5	21	13	8	10	3	7
	July	8	8	10	11	14	11	20	17	4	8	7	5
	Sept.	7	14	4	8	15	14	23	18	16	10	8	6
	Oct.	5	9	5	4	7	14	24	13	11	5	6	3

Histograms were made of the main directions of arrangement of home ranges described by total sum of eccentrics for each trapping series (Fig. 9). The range of angles 0—180° was considered in relation to the axis x of the catch point grid in the area (short axis of the island). This range was divided into 6 classes with 30° intervals between them. The difference between the total sum of eccentrics and the standarized mean for all trapping series was taken as a measure of preferences for a given direction. Simultaneously for the sake of comparison the absolute numbers of females and males were given, the home ranges of which were arranged in the 6 different classes of angles, for all the trapping series (Table 9).

8.2. Main Direction of Location of Home Ranges

It was found that the degree of use made of the distinquished directions varied in successive trapping series. The degree to which different directions were used coincided for females and males (correlation coefficient — 0.582, significant on a level of 0.05).

The chief direction in which home ranges were located in the study area was the direction contained in the angle class 90—119°. In all the trapping series the total sum of eccentrics revealed a value considerably above the accepted mean (Table 10). In relation to the study area the angle class 90—119° corresponds to the longest axis of the island. This would mean that individuals extend their home ranges in the direction offering the greatest possibilities of penetration.

Table 10

Intensiveness of use made of directions in which home ranges are located in the study area.

Year	Month	0—29° ♂♂	0—29° ♀♀	30—69° ♂♂	30—69° ♀♀	60—89° ♂♂	60—89° ♀♀	90—119° ♂♂	90—119° ♀♀	120—149° ♂♂	120—149° ♀♀	150—180° ♂♂	150—180° ♀♀
1966	April	0	7.86	4.06	7.34	4.50	1.73	11.79	10.45	6.33	2.63	3.33	0
	June	2.50	3.30	1.81	6.31	6.14	3.52	12.15	9.61	4.49	6.37	2.91	0.79
	July	4.06	4.12	3.39	3.17	5.54	5.02	9.54	8.96	3.39	6.25	3.48	2.60
	Sept.	3.59	2.56	2.99	3.04	5.37	7.07	9.04	11.45	7.60	5.00	1.88	1.08
	Oct.	4.01	4.38	2.61	2.59	4.56	2.23	8.99	9.52	4.22	5.13	4.16	4.50
1967	April	2.32	4.60	2.23	6.20	10.00	2.60	8.99	8.30	3.34	4.54	3.17	3.65
	June	4.44	6.36	4.64	3.42	1.73	2.93	13.01	7.78	4.83	5.78	1.73	3.71
	July	3.62	4.11	4.41	5.05	6.85	5.66	9.97	9.07	1.89	3.93	3.07	2.38
	Sept.	2.11	5.14	1.77	3.20	6.29	6.07	9.72	8.25	6.67	4.29	3.34	2.45
	Oct.	2.47	5.04	3.03	2.54	3.45	8.65	13.09	8.84	5.43	3.13	2.77	1.98

A n d r z e j e w s k i *et al.* (1967) found that individuals considered as dominating in the population on the basis of maximum trappability occupy the coastal strip of the island. Consequently a check was made to determine the location of the geometrical centres of home ranges in the case of individuals for which the long axes of elliptic home ranges are located along the long axis of the island (90—119°). This analysis was made as follows. A coastal strip was marked out which contained the two external rows of catch points and half the distance to the next row. Individuals were next chosen for which the centres of home ranges were situated in this belt, and individuals for which the centres of home ranges were situated in the remaining central part of the island. The same analysis was made for individuals for which the location of home

ranges corresponded to angle classes 0—59° and 150—180°, that is, the width of the island and ranges least used by the individuals.

It was found that the percentage of individuals, for which the centres of home ranges were situated in the demarcated coastal belt, was similar (difference not statistically significant) in both the preferred angle class and in the class of avoided angles. Thus individuals with home ranges elongated in the direction of the long axis of the island do not prefer its coastal belt.

Comparison was made of the trappability of individuals with home ranges located along the long axis of the island with the mean trappability of individuals in successive trapping series (G l i w i c z, 1970). It was found that they coincide, and thus the trappability of these individuals is not higher than the average trappability of all individuals. Individuals possessing home ranges in a direction coinciding with the long axis of the island were not found to possess the features mentioned by A n d r z e j e w s k i et al. (1967) as characteristic of individual dominating in a population.

8.3. Changes in Arrangement of Home Ranges in the Area During the Year

The location of home ranges in the directions defined in successive trapping series from April to November alter in respect of number of directions more intensively used and in the intensiveness of their use. It would appear that the location of the home ranges depends on the dynamics of population numbers, and partly on phenological factors.

In 1966 there was a rapid increase in population numbers from April to July (Fig. 2) accompanied by gradually increasing uniformity of use of all directions. In April (1966) in addition to the main direction along the long axis of the island (90—119°) males also prefer the neighbouring direction (120—149°), and females the direction along the short axis of the island (0—29°) and its neighbour (30—59°) (Fig. 9). In June males and females use preferred directions with the same intensiveness as in April (Fig. 9). In July, at the peak of population numbers, only the direction along the long axis of the island remains the preferred direction in which home ranges are located (Fig. 9). As numbers decrease from July to September preferences for other directions increase, in the case of males in class 120—149°, and females in class 60—89°. With continuing decrease from September to November there is a more uniform distribution of home ranges in all the observed directions, in addition to the main preferred direction.

The year 1967 was distinguished by gradual increase in population numbers from April to November (Fig. 2). As a result more uniform use

was made of the various directions in consecutive censuses than in 1966 (Fig. 9). Females preferred the same directions as in 1966, but with lower intenseness from April to September, while in November there is an increase in the use made of the direction in class 60—89°. Males use directions with similar intenseness in consecutive censuses from April to September. In November there is increased preference for the main direction, contrary to 1966, when it continued to be used to the same extent as in September.

Comparison of dynamics of numbers (Fig. 2) with location of home ranges in the study area of individuals belonging to the different cohorts (Fig. 9) revealed that the greater the population numbers at the time of entry of the cohort, and the later the entry of the cohort into the population, the more random the directions in which the home ranges of the given cohort are located.

To conclude it may be said that: there is one main preferred direction in which home ranges are located; high population numbers cause more random location of home ranges in the study area; the later the cohort enters the population, the more random the location of the home ranges of members of this cohort in the population area.

9. DISCUSSION

A large number of data indicate that the shape of the home range is longitudinal in the majority of cases (G o d f r e y, 1954; T a n a k a, 1953), and that the animals move along defined paths, preferring certain directions (H o w a r d, 1949; D a v i s, 1953; K a y, 1961). In particular M o h r (1965) found that the home range is elliptic in shape, but used a rectangle to describe the size of the home range.

D i c e & C l a r k (1953) taking a circular home range as a model, make the reservation that the assumption that all parts of a given circular area are uniformly used by an individual constitutes a great simplification of the animal's real movements. The model of the home ranges presented in the present study, which is a modification of the circular model (D i c e & C l a r k, 1953; C a l h o u n & C a s b y, 1958), is an attempt at creating greater possibilities of analysing the shape of the home range. It does not, however, completely solve this problem, as it provides no opportunity of indicating the cases in which the individual prefers more (e.g. two) directions within its home range. From the point of statistical premises it is not necessary to accept the assumption of a circular shaped home range, that is, that the average deviation in distance of capture sites of an individual from the geometrical centre of the home range is uniform for all direction. These deviations be calcu-

lated independently for the two axes of co-ordinate (Appendix). In this way we obtain a generalization of the model based on the assumption that the home range is circular (D i c e & C l a r k, 1953; C a l h o u n & C a s b y, 1958).

The presented results of investigations of the shape of the home range in over 1000 individuals show that an ellipse is more similar to the real distribution of captures of an individual in the area than a circle (Fig. 4).

It must be emphasised that the elliptic shape found for the home range of individuals is not the result of the limited area of the island or its shape. In an open forest area individuals also had elliptic home ranges, and the average elongation of home ranges was 3.6 for both females and males (M a z u r k i e w i c z, 1969).

The influence of external habitat, biocenotic or intrapopulation factors may have a limiting effect on some of the directions in which the individuals move, and a stimulating effect on others. The assumption that the home range is circular limits such action, since it is assumed then that either external factors exert no influence on the movements of the individual, or do so with uniform strength from all sides.

When the size of the circular and elliptic home ranges is compared it can be proved mathematically that the elliptic home range containing the same percentage of captures of an individuals will always be smaller, and thus more filled with information in the form of captures than the circular home range. The circular home range includes too much »empty« space, i.e. space offering no proof that the individual has entered it. The more elongated the real home range the greater the error in estimated size of the home range when using the model based on a circular home range.

The acceptance in this study of an ellipse containing 95% of captures of an individual for the purpose of describing the size of the home range was dictated by the ease of conversions (Appendix) and corresponds to 2.8 δ after C a l h o u n & C a s b y (1958).

Use of an elliptic model introduces a new parameter in description of the home range, the parameter of direction, making it possible to examine the distribution of individuals' home ranges in the area, which is not the case with the circular model of the home range.

A minimum number of 5 captures of an individual was accepted in the present study in order to estimate home range size, since it was found that subsequent captures do not exert any significant effect on the value of standard deviations (Section 4). Similar results were obtained by L i d i c k e r (1966) and Q u a d a n g u o (1968) for *M. musculus*. Numerous authors, however (B l a i r, 1942; H a y n e, 1950; S t i c k e l,

1954) state that the real size of the home range of small rodents can be calculated after obtaining 10 captures of an individual. R a j s k a (in litt) who used the method of assessing home range given by A d a m c z y k et al. (1966), and analysed the same material as that discussed in this paper, found that the size of the home range increases indefinitely together with the number of captures for old individuals, particularly males. In the case of young individuals, however, especially females, the size of the home range is established after only a few captures. The error in assessing the size of the home range by means of determining the geometrical centre and standard deviations may be due to the fact that standard deviations from the centre determined after several captures are not sufficiently sensitive to single new capture sites of an individual.

The material analysed in respect of shape and size of the home range and distribution of individuals in the area was elaborated in detail in respect of dynamics of population numbers, age structure and reproduction (B u j a l s k a et al., 1968; G l i w i c z et al., 1968; P e t r u s e w i c z et al., in litt.). Numerous authors, whose investigations were primarily concerned with the the size of the home range, found that it varies depending on a large number of factors, such as population density (Y e r g e r, 1953; S t i c k e l, 1960; G e t z, 1961), age and sex structure (N a u m o v, 1951; Y e r g e r, 1953), cover of the area (B l a i r, 1951; Y e r g e r, 1953), food, season of the year (Y e r g e r, 1953). The simultaneous action of these factors on the spatial distribution of the population frequently makes it impossible to trace the most important factor acting at the given moment.

The shape of the home range did not exhibit any direct dependence on population density, neither did the age of individuals directly affect the degree of elongation of the home range. M o h r (1965), who gives several examples of elongated home range of small mammals, states that the degree of elongation of the home range is constant, and it is only its size which varies.

The differentiation in size of home range depending on sex, most distinctly expressed in cohort K_0, agrees with the data obtained for C. glareolus by M a n v i l l e (1949), N a u m o v (1951), B r o w n (1956), R a d d a (1968), R a j s k a (in litt.). Slight differences between the size of the home range of females in the various cohorts and slight variations in home range size in time show that the female is less active than the male. R a d d a (1968) found that the females of C. glareolus visit the same or neighbouring catch points. Males on the other hand change their activity and the size of home range during a year, probably depending on the part which they play in reproduction. Great activity increases both the possibility and frequency of contact with females, and the

decrease in activity in autumn is probably due to the termination of the reproduction season. The second basic relation found is the effect exerted by the time of entry of individuals into the population on the size of the home range. Thus it is not only the age of individuals, but also the current composition of individuals in the population, which influences spatial relations between individuals. Similar results were obtained by R a j s k a (in litt.). G l i w i c z (1970) found that the later a cohort entered the population, the lower its trappability. On the basis of studies by C r o w c r o f t & J e f f e r s (1961) and A n d r z e j e w-s k i et al. (1967) this author interprets these differences as being caused by social relations between individuals. It would appear that the observed differences in home range size of the same cohorts can also be explained by these phenomena. The different course taken by variations in home area size of different cohorts during the season in both years may result from the different dynamics of numbers and different duration of the reproduction period (B u j a l s k a in litt.), and also climatic and habitat differences.

The size of the home range probably depends not only on population density, as shown by decrease in size of the range from spring to autumn independently of population dynamics. The degree of overlapping of home ranges, however, is the function of variations in population numbers and size of home range. Similar results were obtained by K a r a-s e v a (1956) and R a j s k a (in litt.). The considerable overlapping of home ranges in spring in relation to numbers may be explained by the size of the home range. It is mainly males which are responsible for this, as during this time their home ranges are very extensive. Decrease in overlapping of home ranges in autumn (not coinciding with population dynamics in 1967) is due to individuals reducing the size of their home ranges at this time.

The random distribution of geometrical centres of home ranges found in the study would appear to confirm the assumption that individuals of the population organize themselves spatially by reducing or increasing their home ranges.

Analysis of location of home ranges in the 6 directions distinguished showed that they vary depending on the level of population numbers. The direction of location of home ranges corresponding to the longest axis of he island is most intensively used in consecutive censuses in both years. Location of home ranges in the other directions distinguished is more random when population numbers are high (July 1966).

Analysis of shift in geometrical centres of home ranges showed that there is a tendency to a slight but constant shift of home ranges over the area (Section 4 and 7.3). This agrees with the data given by M i l l e r

(1958), Soldatova (1962), Row (1963), Kikkawa (1964). The greater shift in the centres of the home ranges of males than females shows that females are characterized by not only a fairly constant size of the home range but also by its location in the study area. Males extend or reduce their home ranges, simultaneously shifting them. When there are only slight variations in the size of the home range there is a tendency to reduction in shift in time (females of cohort K_1 and K_2 in 1966, 1967, males of cohorts K_1 and K_2 in 1966), while sudden changes in the size of the home range (males of cohorts K_1 and K_2 in 1967) are connected with considerable shift in the centre of the home range, which,
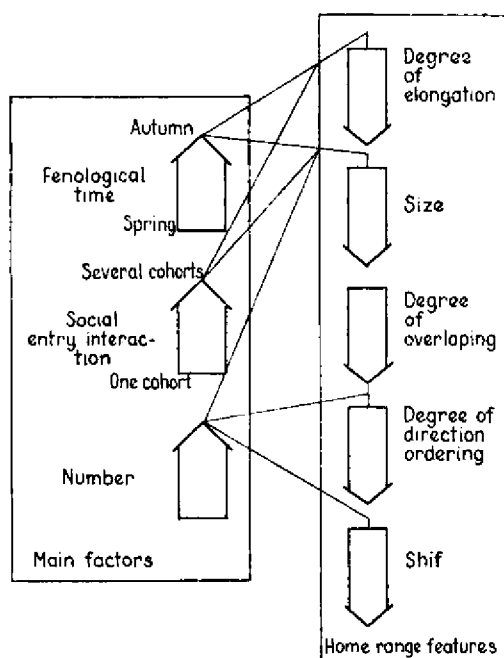
Fig. 10. Main factors influencing the home range characters investigated.

with reduction in the home range between September and November leads to the location of the central part of the home range in the part which was previously peripheral.

Spatial organization of the population on the island can thus be described as follows: in spring the population consists of individuals which have lived through the winter. Males have large and elongated home ranges, located in several of the most convenient direction corresponding to the location of the home ranges of females. This creates favourable conditions for reproduction which begins at that time, since it permits of frequent contacts between males and females.

The place in the spatial organization of cohorts entering the population from June to October depends on many factors. It would seem that the basic factors are the current composition of individuals and population numbers at the time of the cohort's entry, and the numbers and role in reproduction of the latter. This is shown by the relation between the order in which the cohorts enter the population and the size, shape and location of home ranges in the study area.

After the reproduction season has ended features such as age, sexual maturity and participation in reproduction do not significantly influence the spatial organization. Consequently in autumn differentiation between cohorts (age) and between males and females (sex) decreases, and the overlapping of home ranges lessens, as does the size of home ranges, particularly of males.

The character of the influence exerted by factors considered as basic ones on the observed features of the home range are shown in Fig. 10.

Studies were made on an isolated population (island) where there were no possibilities of individuals immigrating or emigrating. It is not known what effect isolation has on the spatial organization of the population, and therefore further studies are required on the spatial organization of populations inhabiting open wooded land.

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APPENDIX

DEMARCATION OF THE ELLIPTIC HOME RANGE ON THE BASIS OF CAPTURE SITES OF AN INDIVIDUAL

Let us assume that the following are determined for a given individual from empirical data:

m_x — abscissa of geometrical centre

m_y — ordinate of geometrical centre

(1) δ_{xx} — variance of abscissae of capture sites

δ_{xy} — covariance of abscissae and ordinates of capture sites

δ_{yy} — variance of ordinates of capture sites

It is easy to interpret this information in a suitably chosen system of rectangular co-ordinates. We choose this system (for the given individual) so that its beginning coincides with the centre of the home range and the covariance of abscissae and ordinates in this system is equal to zero.

If we indicate the co-ordinates of the new system by u, v, then the following equation will take place between old and new co-ordinates (old co-ordinates — co-ordinates connected with the trap grid in the study area)

(2) $u = x' \cos \varphi + y' \sin \varphi$

$v = -x' \sin \varphi + y' \cos \varphi$

where $x' = x - m_x$, $y' = y - m_y$ and φ is the angle formed by the axis of abscissae of the new system with the axis of abscissae of the old system. Thus, if the co-ordinates of the trapping site of an individual in the old system were (x_i, y_i), then in the new system they will be (u_i, v_i).

Equations (2) enable us to express the variances, co-variances and centres in the new system of co-ordinates through parameters (1) calculated empirically in the old system:

$m_u = 0$

$m_v = 0$

(3) $\delta_{uu} = \delta_{xx} \cos^2 \varphi + 2\delta_{xy} \sin \varphi \cos \varphi + \delta_{yy} \sin^2$

$\delta_{uv} = \delta_{xy} \cos^2 \varphi - \dfrac{1}{2} (\delta_{xx} - \delta_{yy}) \sin 2\varphi$

$\delta_{vv} = \delta_{xx} \sin^2 \varphi - 2 \delta_{xy} \sin \varphi \cos \varphi + \delta_{yy} \cos^2$

If in accordance with the premises we now accept an angle φ so that $\delta_{uv} = 0$, then from (3) we obtain the equation:
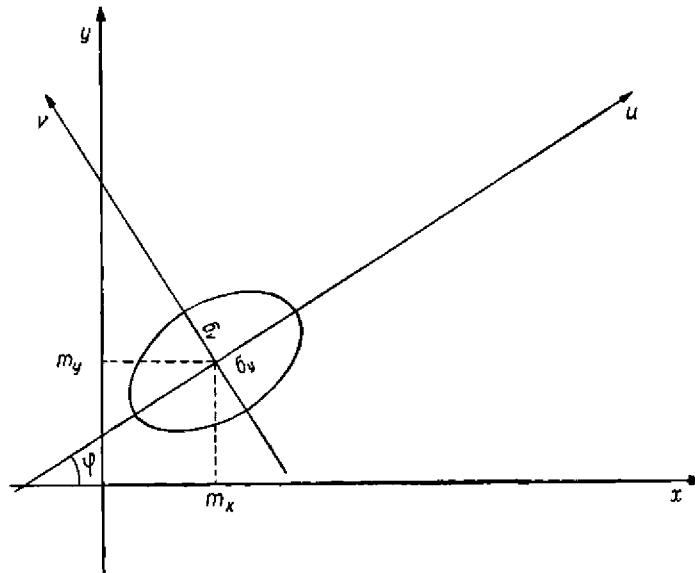

Fig. 11. Connection between old and new system of co-ordinates.

$$\delta_{uv} = \delta_{xy}\cos 2\varphi - \frac{1}{2}\left(\delta_{xx} - \delta_{yy}\right)\sin 2\varphi = 0$$

which permits to find the angle φ:

(4) $\operatorname{tg} 2\varphi = 2\delta_{xy}/(\delta_{xx} - \delta_{yy})$

With this choice of angle φ from (3) we obtain by means of easy trigonometrical conversions the following equations:

(5)
$$\begin{aligned}
m_u &= 0 \\
m_v &= 0 \\
\delta_{uu} &= \delta_{xx} + \delta_{xy}\operatorname{tg}\varphi \\
\delta_{uv} &= 0 \\
\delta_{vv} &= \delta_{yy} - \delta_{xy}\operatorname{tg}\varphi
\end{aligned}$$

Knowledge of angle φ, which can easily be calculated from (4) and of co-ordinates of the some range centre enables us to define completely a new system of co-ordinates (Fig. 11). This system is convenient because the two-dimensional function of density of probability is expressed in it by the following simple equation:

(6) $f(u, v) = \dfrac{1}{2\pi\, \delta_u\, \delta_v}\, \exp\left[-\dfrac{1}{2}\left(u^2 / \delta_{uu} + v^2 / \delta_{vv}\right)\right]$

where $\delta_u = \sqrt{\delta_{uu}}$, $\delta_v = \sqrt{\delta_{vv}}$ are standard deviations of the co-ordinates of capture sites in the new system of co-ordinates. Curves of uniform density of probability in this system are the curves

$f(u, v) = \text{const}$

that is, ellipses with equations

(7) $u^2 / \delta_{uu} + v^2 / \delta_{vv} = \text{const}$

These ellipses have their centre at the beginning of the system of co-ordinates (u, v) (that is, in the centre of the individual's home range) and their main axes lie on the axes of the co-ordinates of the new system (and are thus inclined to the axis of the old system at an angle φ).

If we assume

(8)
$$\begin{aligned}
u &= \varrho \cdot \delta_u \cos\alpha \\
v &= \varrho \cdot \delta_v \sin\alpha
\end{aligned}$$

then the function of distribution of density of probability (6) takes on the particularly simple form:

(9) $f\left(\varrho, \alpha\right) = \dfrac{1}{2\varPi}\, \exp\left(-\varrho^2 / 2\right)$

and curves of uniform density of probability are expressed by the equation:

(10) $\varrho = \text{const}$

Equation (10) defines the same ellipse as equation (7). Probability of occurrence of a capture site within the ellipse with equation

(11) $\varrho = r$

(assuming that the distribution of capture sites is in fact a normal distribution)

can be calculated by integrating the function of density (6) over the area demarcated by ellipse (11):

(12)

$$P(r) = \int_0^{2\Pi} \int_0^r \frac{1}{2\Pi}\left[\exp\left(-\varrho^2/2\right)\right]\varrho d\varrho \, d\alpha = \int_0^r \exp\left(-\varrho^2/2\right)\varrho d\varrho = 1 - \exp\left(-r^2/2\right)$$

In particular, assuming $r = \sqrt{2}$ from (12) we obtain

$$P(\sqrt{2}) = 0.6321$$

Ellipse with equation $\varrho = \sqrt{2}$ has in the system of co-ordinates u, v the equation

$$u^2/\delta_{uu} + v^2/\delta_{vv} = 2$$

that is the length of its half-axes respectively equal

(13) $\sqrt{2}\,\delta_u, \quad \sqrt{2}\,\delta_v$

If we assume $r = \sqrt{6}$ we obtain

$$P(\sqrt{6}) = 1 - \exp(-3) = 0.9502$$

The ellipse with equation $\varrho = \sqrt{6}$ has axes $\sqrt{3}$ times longer than axis (13).

Maria MAZURKIEWICZ

KSZTAŁT I WIELKOŚĆ ORAZ ROZMIESZCZENIE AREAŁÓW OSOBNICZYCH
CLETHRIONOMYS GLAREOLUS (SCHREBER, 1780)

Streszczenie

Prześledzono zmiany kształtu i wielkości areałów oraz rozmieszczenie osobników w zależności od struktury wiekowej, płciowej i dynamiki liczebności populacji. Analizę przeprowadzono przy zastosowaniu zaproponowanego eliptycznego modelu areału będącego uogólniającą modyfikacją przyjętego dotąd modelu kolistego (C a l h o u n & C a s b y, 1958). Modyfikacja ta, jak wykazały niniejsze i późniejsze badania, lepiej oddaje sposób poruszania się osobnika po powierzchni i pozwala na analizę kształtu areału i kierunków chętniej przez osobnika wykorzystywanych, jest też zgodna z obserwacjami wielu autorów wydłużonego areału drobnych ssaków.

Materiał analizowany został uzyskany w latach 1966, 1967 z badań populacji C. *glareolus* zamieszkującej wyspę o powierzchni 4 ha na jeziorze Beldany (północna Polska) (Fig. 1), która pokryta była 159 punktami połowu gryzoni. Metodykę zbierania danych oparto na zasadzie łowienia i znakowania zwierząt, wypuszczania i ponownego łowienia (CMR). Co roku od wiosny do jesieni przeprowadzono 5 serii połowów.

Gliwicz et al. (1968) i Petrusewicz et al. (in litt.) określili metodę spisu powszechnego liczebność osobników na wyspie w kolejnych seriach połowu oraz podzielili wszystkie osobnika populacji na kilka grup różniących się czasem urodzenia a obejmujących osobniki o podobnym wieku (Fig. 2). Wyróżnione pokolenia: wiosenne, wczesnoletnie, późnoletnie i jesienne były podstawą analizy zależności między strukturą wiekową populacji a parametrami jej struktury przestrzennej.

Analiza szczegółowa objęła osobniki, które uzyskały co najmniej 5 złowień w jednej serii połowów (Tab. 1). W poszczególnych seriach osobniki zrealizowały średnio od 7,7 do 14,9 złowień. Ogółem przeanalizowano 1157 osobników o łącznej liczbie 13 882 złowień (Tab. 2).

Analiza uzyskanych wyników wykazała, że:

1. Kształt areału osobniczego (mierzonego stosunkiem osi areałów eliptycznych) był wydłużony, średnio o jednej osi 2,5 raza dłuższej od drugiej. Na 1157 analiz areał bliski kolistego (stosunek osi 1—1.57) posiadało 30% osobników. Areał o stosunku osi 1,57—2,51 posiadało 40% osobników, a bardziej wydłużony areał o stosunku osi 2,51—10 posiadało 30% osobników (Fig. 4).

Stopień wydłużenia areału spada od wiosny do jesieni. Najbardziej wydłużone areały miały samce w okresie wiosennym. Im później się rodziły osobniki, tym ich areały były bardziej koliste (Fig. 5, Fig. 6).

2. Średnia wielkość areału (wielkość areału określono powierzchnią elipsy zawierającej 95% złowień osobnika) wyliczona dla całej populacji spada od wiosny do jesieni niezależnie od dynamiki liczebności różnej w obu latach. Stopień nakrywania się areałów zależy od wielkości areałów i poziomu liczebności populacji (Tab. 6). We wszystkich seriach połowów stwierdzono zróżnicowanie w wielkości areałów między samcami i samicami. Samce miały większe areały niż samice, największa różnica wystąpiła w kwietniu i czerwcu wśród przezimków. Zarówno samce jak i samice miały w momencie wejścia do populacji mniejsze areały niż osobniki, które wcześniej się urodziły (Fig. 7, Fig. 8).

3. Rozmieszczenie osobników na powierzchni scharakteryzowane rozmieszczeniem geometrycznych centrów ich areałów było losowe (Tab. 7). Przesunięcie geometrycznych centrów areałów osobniczych między kolejnymi seriami połowów (1,5 miesiąca) było niewielkie. 51% ogółu osobników przesunęło centra swoich areałów średnio 7,5 m, 25% osobników średnio 15 m, a tylko 24% osobników przesunęło centra swoich areałów na większe odległości (od 30 do 150 m) (Fig. 9). Porównanie średniego przesunięcia geometrycznego centrum areałów samic i samców w różnym wieku wykazało większe przesuwanie centrum areału przez samce niż przez samice w tym samym wieku, szczególnie przy gwałtownych zmianach wielkości areału. (Fig. 10, Fig. 11).

4. Analiza ułożenia areałów na powierzchni określonego przy pomocy kąta nachylenia długich ich osi do osi rzędów sieci punktów połowu wykazała, że głównym kierunkiem ułożenia areałów był kierunek odpowiadający najdłuższej osi wyspy (Fig. 12, Fig. 13). Wysoki poziom liczebności powodował bardziej przypadkowe ułożenie areałów na powierzchni. Również poszczególne grupy wiekowe im później wchodziły do populacji, tym bardziej przypadkowo były ułożone areały osobników do nich należących. Mogłoby to sugerować, że kształt areału i kierunek jego ułożenia jest wynikiem ograniczonej powierzchni wyspy i jej kształtu. Jednak wstępna analiza (Mazurkiewicz, 1969) wykazała, że eliptyczny kształt miały również areały osobników C. *glareolus* na terenie leśnym, otwartym (Kampinowski Park Narodowy).

Przedstawione wyniki wskazują, że eliptyczny model areału osobniczego jest bliższy rzeczywistemu rozłożeniu złowień osobnika niż stosowany ogólnie model kolisty. Pozwala on jednocześnie na pełniejszą charakterystykę struktury przestrzennej populacji poprzez wprowadzenie nowych parametrów dla jej badania: kształtu areału i kierunków ułożenia areałów na powierzchni.