A C T A   T H E R I O L O G I C A

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Dispersion of Young Bank Voles from Their Place of Birth

[With 6 Tables & 4 Figs.]

The effect of population density and the quality of the habitat in the animals' place of birth on the distance and direction in which the young disperse was studied. The material used for analysis was obtained during the period 1968—1971 from individual marking of bank voles *Clethrionomys glareolus* (Schreber, 1780) on an island 4 ha in extent, during the period of life in the nest. It was found that the distance covered by the animals in dispersing is in inverse proportion to the density of the whole population. In years with high density 46% of the young individuals remained at their place of birth, whereas in years with low density the corresponding figure was only 18%. Individuals born in a suboptimal habitat show a greater tendency to remain in their place of birth, whereas individuals born in an optimum habitat occupied mainly by adult individuals move away to the suboptimal habitat. The distance traversed by those individuals remaining in an optimal habitat is smaller than that covered by individuals remaining in a suboptimal habitat.

1. INTRODUCTION

The dispersion of the young of small mammals from the place in which they were born enables them to find suitable unoccupied places in which to establish their own home range before reaching sexual maturity, counteracts inbreeding, makes possible the extension of the geographical range of the species, the reinvasion of destroyed areas *etc.*

The degree of dispersion may be modified by intrapopulation factors such as social structure (Christian, 1970; Metzgar, 1971), population density (Hamilton, 1942; Calhoun & Webb, 1953), the current age structure of the population (Metzgar, 1971) and habitat factors (Nikitina, 1970; Bock, 1972).

The purpose of the present study was to investigate the effect of population density and the quality of the habitat in the place in which an individual was born on the degree, distance and direction of dispersion of the young of the bank vole *Clethrionomys glareolus* (Schreber, 1780).

2. AREA, METHOD, MATERIAL

The study is based on material obtained during the period from 1968—1971 from individual marking of voles during the period of nest life on an island 4 ha in extent, situated in a lake in northern Poland (53°40'N, 21°35'E).

The island is covered by a tree stand belonging to 3 phytosociological associations (Fig. 1), 23% of the area being occupied by the *Circaeo-Alnetum* Oberdorfer, 1953 and *Salici-Franguletum* Malc., 1929 associations. The habitat is

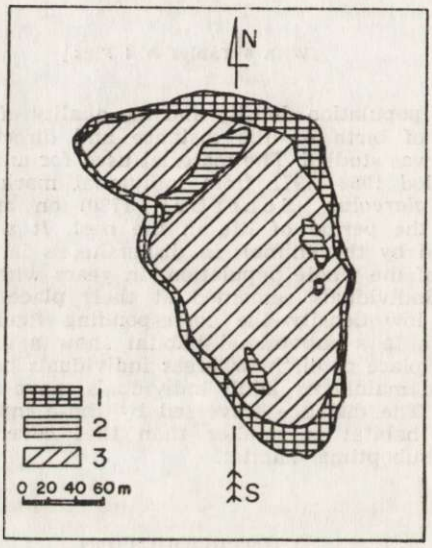

Fig. 1. Distribution of forest associations on »Crabapple« island.
1 — *Salici Franguletum*, 2 — *Circaeo-Alnetum*, 3 — *Tilio-Carpinetum* (after Traczyk, 1965).

wet, with a large supply of the vegetation preferred by the bank vole (Wrangel, 1930; Turček, 1960; Chełkowska, 1969). 77% of the area consists of the dry habitat of *Tilio-Carpinetum* Traczyk, 1962 (Traczyk, 1965).

The island was covered throughout the whole study period by a grid of 69 wooden nesting boxes of the Howard type, spaced at 30×30 m intervals (Ryszkowski & Truszkowski, 1970).

Each year during the reproductive season (from April to September) the nest boxes were inspected frequently, once every two weeks during the first study year (1968) and once every six weeks in sebsequent years.

During the inspections of the nesting boxes the age of all individuals caught was determined on the basis of the criteria given by Sviridenko (1959). Individuals from 7—14 days old were marked individually by toe-clipping

(N a u m o v, 1951). This operation was not found to cause the female to move the young to another place and consequently did not affect the observed phenomenon of dispersion.

During the same period 10-day series of captures were regularly carried out on the island at six-week intervals, and during these periods the whole island was covered by a network of live traps arranged in a grid 15×15 m. The method of collecting data was based on the *CMR* principle.

The population numbers during successive trapping series (five times each year) were defined by the general census method.

The fact that the trapping series on the island took place at the same time as the marking of young voles in the nest made it possible to examine dispersion in relation to the different dynamics of population numbers.

The material analysed consists of a total of 208 individuals, recorded after leaving the nest in one trapping series (Table 1). Assuming after K o w a l s k i (1964) that voles are capable of independent life at the age of 21 days, and knowing the age of individuals at the time of marking them and the date of their first capture, it was possible to calculate at what period after the time the individual leaves the nest its dispersion occured. It was found that 79% of the individuals were observed to disperse 7—21 days from the time they left the nest, and the remainder after 22—26 days.

Table 1

Number of individuals examined in study years.

Year	Females	Males
1968	51	61
1969	24	14
1970	26	14
1971	11	7

3. RESULTS

3.1. Density of Young Individuals before Dispersion

On account of the differences in the island habitat a check was made to determine the relative density of individuals during the period of nest life in the two types of habitat distinguished: that optimal for the bank vole — *Circaeo-Alnetum* and *Salici-Franguletum* and suboptimal — *Tilio-Carpinetum*. Only those individuals which were observed to disperse were taken into consideration. It was, however, accepted that the index obtained is in proportion to the density of all animals born in a given habitat. Calculation was made of the average number of individuals per nest box in each of the two habitats. The material was analysed for years with high (1868, 1970) and low (1969, 1971) numbers of the whole population (Table 2).

It was found that the average number of individuals per nest box is higher in the optimal habitat, whether the density of the whole population is high or low (Table 3). In the optimal habitat there is also a smaller variation in the average number of young born per unit area, depending on the density of the whole population. The ratio of the average number of young born at high density to the average number born at low density was 2.3 in this habitat, whereas in the suboptimal habitat the figure was 3.1.

3.2. Distance over which Individuals Disperse from Their Place of Birth

In order to ascertain how far young individuals settle away from their place of birth the following analysis was made: the geometrical centre of the home range was calculated for each individual from the first trapping series for the given rodent (H a y n e, 1949). Both the geometrical centre of the home range and the site of the nest box in

Table 2

Dynamics of numbers and average population density per hectare from 1968—1971

Month	1968	1969	1970	1971
April	70	69	29	—
June	332	147	85	30
July	368	142	280	196
September	364	170	316	194
October	225	141	221	145
Avg.	161.4	72.8	116.2	82.0

Table 3

Average number of young individuals per nesting box in the two habitats distinguished with low and high density of of the whole population.

Habitat	Density Low	Density High
Optimal	1.29	2.94
Suboptimal	0.56	1.72

which the given individual was marked were next entered on a map of the island and the distance between these two points measured (Fig. 2). The average distance traversed by males and females was calculated for years with high and low population numbers and the distribution of individuals analysed depending on the distance traversed.

It was found that in years with low population numbers young individuals settled further from their place of birth than in years in which population numbers were high (Table 4). The average distance traversed both by males and females was significantly greater when the population density was low ($p>0.001$). The distribution of individuals depending on distance traversed also exhibits differences depending on population density. In years with high population numbers 46% of the individuals moved to distances less than 15 m, whereas in years of low numbers this figure was significantly smaller, namely 18% ($p>0.001$).

As the nearest trapping sites were situated at a distance of 7.5 and 15 m from the nest boxes, individuals which dispersed such distances should be considered as remaining in the place of their birth. The percentage of individuals which moved distances greater than 60 m was significantly higher, with $p > 0.001$, in years of low population numbers (33%) than in years of high population density (11%) (Fig. 3). The distance traversed

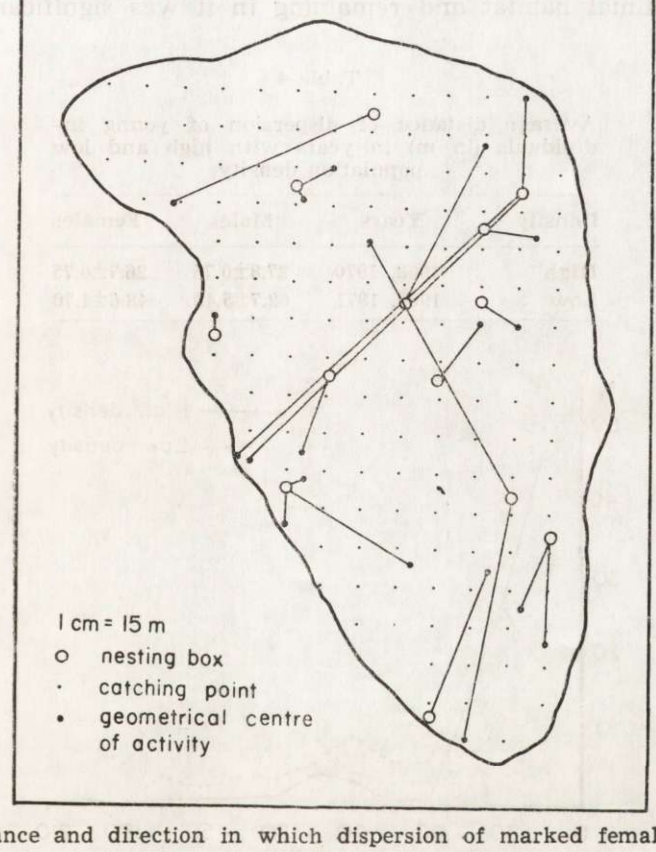

Fig. 2. Distance and direction in which dispersion of marked females took place from May to July 1969 from nesting boxes.

by males and females at a given population density does not exibit any significant difference, although males have a tendency to cover greater distances in years of low population numbers (Table 4).

3.3. Effect on Dispersion of the Quality of the Habitat in the Animals' Place of Birth

In order to discover what effect is exerted on the dispersion of young individuals by differences in the quality of the habitat in the place of their birth the intensity, direction and distance of dispersion in the two types of habitat distinguished were analysed. As the material available was not plentiful the tendency to remain in the birth habitat or to change was analysed for all the individuals treated jointly, but the distance over which individuals from the two habitat types dispersed was calculated separately for years with either high or low population numbers (Table 5).

It was found that the percentage (82.2%) of young individuals born in a suboptimal habitat and remaining in it was significantly greater

Table 4

Average distance of dispersion of young individuals (in m) in years with high and low population density.

Density	Years	Males	Females
High	1968, 1970	27.8±0.75	26.7±0.75
Low	1969, 1971	62.7±5.40	48.6±4.70

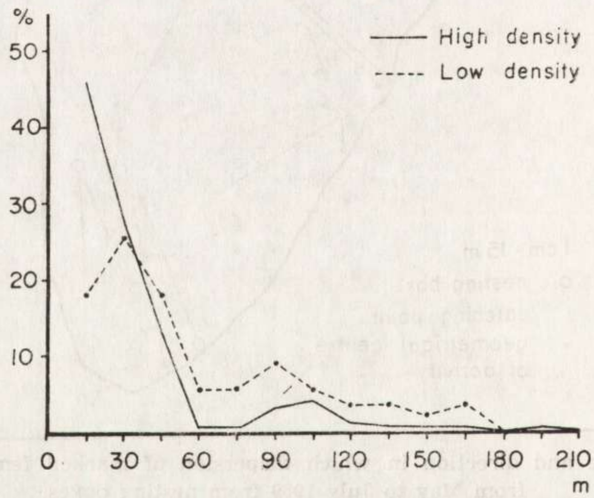

Fig. 3. Distribution of individuals depending on distance of dispersion.

($p > 0.001$) than the percentage (41.7%) of young animals born and remaining in the optimal habitat. Among the latter the percentage of females (51%) is significantly greater ($0.001 > p > 0.01$) than that of males (20.5%).

The distance traversed by individuals emigrating from the optimal to the suboptimal habitat is greater than that covered by individuals remaining in the habitat, this applying to both males and females.

Individuals born in a suboptimal habitat, whether remaining in it or emigrating, exhibit similar distances of dispersion. The distance traversed by individuals emigrating from optimum to suboptimum and vice versa is very similar, and is in inverse proportion to density (Table 6). A similar dependence on density is shown by the distance traversed by individuals remaining in the habitat in which they were born (Fig. 4).

4. DISCUSSION

For many authors the concept of dispersion constitutes a synonym for intrapopulation migrations (Calhoun & Webb, 1953; Christian, 1970; Myers & Krebs, 1971; Lidicker, in press). Dispersion

Table 5

Number of young individuals remaining in and migrating from their birth habitat.

Density	Sex	Optimal		Suboptimal	
		Residents	Emigrants	Residents	Emigrants
Low	M	2	5	10	4
	F	7	8	16	3
High	M	6	16	44	9
	F	15	13	41	8
Total	M+F	30	42	111	24

Table 6

Average distance of dispersion of young individuals remaining in and changing their birth habitat (in meters).

Density	Sex	Optimal		Suboptimal	
		Residents	Emigrants	Residents	Emigrants
Low	M	28.5±0.1	77.0±4.5	48.0± 3.2	41.0±3.9
	F	30.0±1.5	46.5±8.5	46.5±10.8	46.5±3.0
High	M	13.5±1.1	27.0±1.8	27.0± 6.1	27.0±1.1
	F	13.5±1.2	37.5±8.2	28.5± 9.1	33.0±0.9

in this sense includes all migratory movements of individuals in the population, together with their causes and consequences. On the other hand it is not known to what degree the dispersion of young animal from their place of birth (nest) is a qualitatively different process from the very common migration taking place within the population.

The time of leaving the nest, which is equivalent to the beginning of independent life, is undoubtedly an important moment in an individual's life. It then enters a fully formed spatial and social organization which may significantly influence its further fate, the possibility of its establishing its own home range, beginning reproduction etc. On the other hand the appearance in the population of young individuals may also cause important changes in social relations and spatial structure of the population and consequently plays a part in the processes regulating population numbers. From this point of view analysis of the dispersion of young animals under conditions of habitat differentiation (optimum and suboptimum) and high and low population density would appear interesting.

It was found that dispersion of individuals from their place of birth was in inverse proportion to density (Table 4). The percentage of individuals not moving away from their place of birth was also significantly higher when density was high (Fig. 3).

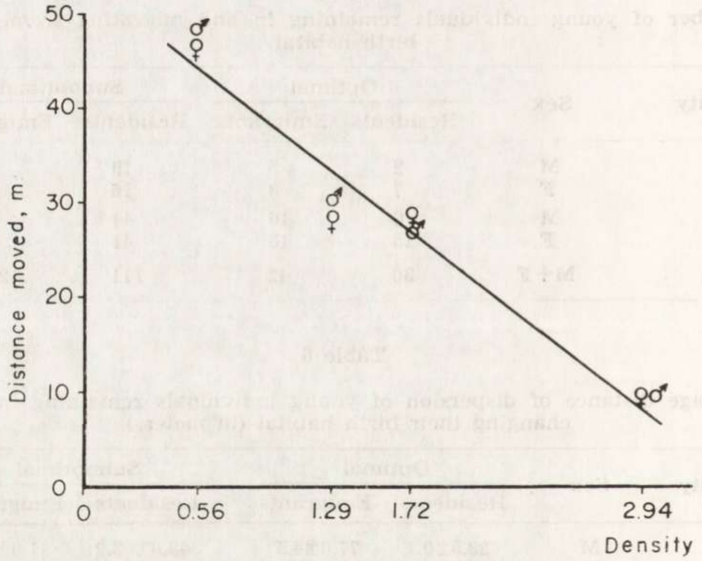

Fig. 4. Distance traversed by individuals remaining in their birth habitat and density of young individuals in this habitat (after Table 3).

The study population, living in an enclosed area, reaches a greater density than a population living in an open forest (Mazurkiewicz, 1972). This in turn leads to more sharply defined relationships between individuals (Kołodziej, Pomianowska & Rajska, 1973; Rajska, in litt.). Adult individuals, particularly old adults, play a dominant role in the population. Adult males have the largest home ranges (Mazurkiewicz, 1971; Andrzejewski, Petrusewicz & Waszkiewicz-Gliwicz, 1967), and adult or growing females exhibit territorial tendencies (Bujalska, 1970). These individuals occupy more a favourable habitat — the optimum — than do the young individuals (Andrzejewski, Petrusewicz & Waszkiewicz-Gliwicz, 1967; Bock, 1972), which avoid contact with them (Kołodziej, Pomianowska & Rajska, 1973; Rajska in litt.). It has been shown in the present paper that a significantly higher percentage of individuals born in suboptimal habitats remain in them than is the case with young animals born in an optimal habitat. Bock (1972), in analysing the distribution of different categories of individuals in the population forming the object of these studies in the two habitats distinguished, found that the degree of preference for the optimum is in proportion to age, but that increase in population numbers causes an increase in the intensity of the utilization of the suboptimum, without affecting the degree to which the optimum is utilized. Thus it is not only population density, but also the spatial distribution of adult individuals, which influences the settling process of young individuals. The pressure of adult animal on young individuals, consisting in driving them from better habitats into poorer habitats, which the adult animals use to a lesser degree, leads to equalization of density between the two types of habitats (Bock, 1972).

The smaller distance covered in dispersion by individuals remaining in the optimal habitat, irrespective of whether population density is high or low, in relation to the distance traversed by individuals remaining in a suboptimal habitat, may be due to the always greater occupation of the suboptimal habitat, which therefore affects the distance of dispersion through population density (Fig. 4).

The results obtained provide an explanation of many of the facts established in relation to this population. *C. glareolus* is a species characterized by a pre-overcrowding type of dispersion (Lidicker, in press). When living in a confined area the degree of ineffectual dispersion rises, which intensifies the space-social relations between individuals (Bock, 1972; Rajska, in litt.). This in turn leads to a retardation of the individuals growth (Mazurkiewicz, 1972), limitation of the number of reproductiong females (Bujalska, 1972) and high mortality in the late summer and autumn generation than in the spring generation (Petrusewicz *et al.*, 1971).

The differentiation in the habitat of the study island permits density regulation by emigration from the optimal to suboptimal habitats to a certain extent only (Bock, 1972). Therefore, owing to the spatial isolation, the other mechanisms referred to above for the regulation of population numbers are put into effect to a greater degree than are dispersion and migration.

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DYSPERSJA MŁODYCH NORNIC Z MIEJSCA URODZENIA

Streszczenie

Zbadano wpływ zagęszczenia populacji i jakości środowiska w miejscu urodzenia na wielkość, odległość i kierunek dyspersji młodzieży *Clethrionomys glareolus* (Schreber, 1780). Podstawą analizy były materiały obejmujące 208 osobników uzyskane w latach 1968—1971 (Tabela 1). Terenem badań była 4 ha wyspa na jeziorze Bełdany (Ryc. 1), na której rozmieszczono domki gniazdowe w odstępie 30×30 m. Domki te regularnie przeglądano i znakowano indywidualnie nowonarodzone osobniki. W tym samym czasie przeprowadzono na wyspie regularnie serie połowów w celu oceny liczebności populacji (Tabela 2).

Stwierdzono, że w latach niskiej liczebności populacji osobniki młode osiedlają się dalej od miejsca urodzenia niż w latach wysokiej liczebności (Tabela 4). Również rozkład osobników w zależności od długości przemieszczenia wykazuje różnice w zależności od zagęszczenia populacji (Ryc. 3). Procent osobników nie przemieszczających się z miejsca urodzenia jest istotnie większy w latach wysokiej liczebności.

Analiza wpływu jakości środowiska w miejscu urodzenia na intensywność dyspersji wykazała, że osobniki urodzone w środowisku suboptymalnym dla nornicy pozostają w nim istotnie większym procencie niż młode urodzone w środowisku optymalnym. Przy czym wśród osobników pozostających, przewagę stanowią samice. Dystans przemieszczania się osobników pozostających w środowisku optymalnym jest mniejszy niż osobników pozostających w środowisku suboptymalnym (Tabela 6, Ryc. 4).

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