ACTA THERIOLOGICA
Vol. 28, 19: 301—315, 1983

Survival Rate and Mobility in an Enclosed Population of Red-backed Vole, Clethrionomys rufocanus bedfordiae

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Saitoh T., 1983: Survival rate and mobility in an enclosed population of red-backed vole, *Clethrionomys rufocanus bedfordiae*. Acta theriol., 28, 19: 301—315 [With 1 Table & 6 Figs.]

Survival rate and behavior (mobility) of red-backed voles were investigated from 1978 to 1979 using a one-hectare out-door enclosure in a northern forest in Japan. Sex ratio of new-born young was even, but that in the breeding population deviated toward females. The prevailing female ratio in the breeding population was produced by the two factors: the females matured earlier than the males, and the survival rate of the females was higher than that of the males during maturation. The home range changed position markedly in both sexes during maturation. Home range length increased considerably in the males when they began to mature, but in the females this tendency was not evident. Consequently, the range length of the males became 1.5—2.0 times as long as that of the females after maturation. Sallies outside the home range were recorded more frequently in the males than in the females and most frequently during maturation. Life expectancy of the males which made sallies was much shorter than that of the more sedentary males. Survival rate decreased in the following order: mature females, mature males, maturing females, and maturing males. The order of mobility, however, was completely the reverse.

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1. INTRODUCTION

Fluctuations of vole and lemming population have been studied by many researchers in the northern hemisphere. Reviewing these works, Krebs & Myers (1974) concluded that behaviour and genetics might be important factors behind population fluctuations. Regarding these findings, Tanaka (1953), Bujalska (1970, 1973), Myers and Krebs (1971a) and Metzgar (1979), etc., observed territoriality and dispersal of rodents under natural conditions, while Hilborn & Krebs (1976), Tamarin (1978), Boonstra (1978) and Chełkowska (1978), etc., worked on them experimentally. Though many of these authors emphasized the importance of behavior in the mechanism of population fluctuations, they could not fully test their hypotheses, *e.g.*, their data lacked, among other things, information on the changes in behavior during the process of maturation.

In this study, the author investigated the changes in spacing behavior and the survival rate in the developing process of red-backed voles, *Clethrionomys rufocanus bedfordiae* (Thomas).

2. MATERIAL AND METHODS

This experiment was carried out from 7 September 1978 to 1 September 1979 in Tomakomai Experiment Forest of Hokkaido University, which is located in the south-central part of Hokkaido in Japan. A one-hectare enclosure (100 m× ×100 m) fenced with galvanized iron sheets extending 0.9 m underground and 0.9 m above ground was used for this experiment. The enclosure is located in a secondary broad-leaved forest with undergrowth dominated by *Daphne kamtschatica* (Maxim.), *Pachysandra terminalis* (Sieb. *et* Zucc.), and *Lilium cordatum* (Koidz.). Although this vegetation is not commonly a desired habitat for voles, the area surrounding the enclosure was inhabited by abundant voles which had followed the wood mouse, *Apodemus argenteus* (Temminck).

The catch-mark-release method was applied with live traps at 100 trap stations distributed at 10 m intervals. One trap was set at each station, and all of the traps were covered by a wooden box with two holes to protect animals captured and to facilitate trapping work in deep snow.

Fifty-four voles (32 ♀♀ & 22 ♂♂) were taken from a population in a wind shelter-belt of Ishikari Plain (about 80 km north of the study area) and introduced into the enclosure on 7 September 1978. Their body weight were 19.5—37.5 g in the case of the females and 20.5—40.5 g in the case of the males; the animals were thus regarded as spring or summer born individuals.

Five consistent days of trapping were carried out twice a month (once in September 1978), and the traps were examined twice daily. Each vole was marked by toe clipping at first capture, and following data were recorded at each capture: individual number, sex, location on grid, body weight and reproductive condition.

Reproductive activity was judged referring to Saitoh's criteria (1981). Voles that showed the following characteristics were considered as mature: in females, perforated vagina and estrous phase of vaginal smear, pregnancy, large nipples or open pubic symphysis; in males, large (about 10 mm) and scrotal testes.

In order to investigate the influence of different environments on the mobility of voles, the author removed the undergrowth in the south-west half of the enclosure, which was divided by a diagonal line. The richer cover area was designated as grid A and the poorer one as grid B. A handful of oats (about 50 g) was placed as supplementary food at every trap station on the last day of each trapping session.

3. RESULTS

3.1. Demographic Changes

Changes in numbers. The number of voles trapped is shown in Fig. 1. The total number decreased in autumn just after the introduction of voles into the enclosure, was rather stationary under snow cover in winter, abruptly increased in spring and decreased in summer. The decrease in summer was mainly attributed to the probable death of some spring born individuals and the absence of birth in summer. Such a summer pause in reproduction has often been reported in this species (Ota *et al.*, 1959; Kinoshita & Maeda, 1961; Kuwahata, 1966; etc.).

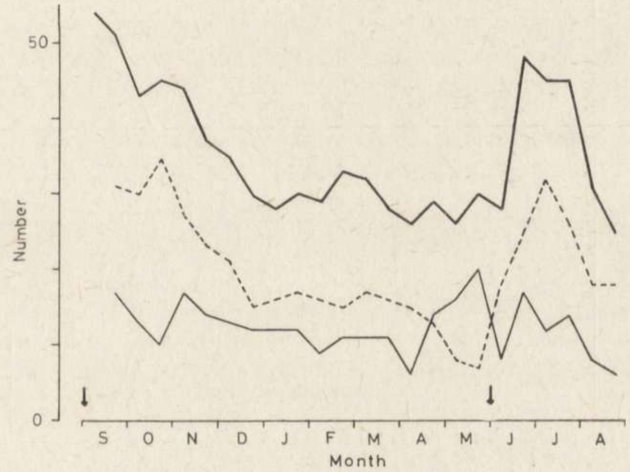

Fig. 1. Changes of vole numbers in a one-hectare enclosure during 1978—1979. Upper solid line: total number; broken line: population number on grid A (area with richer plant cover); lower solid line: population number on grid B (area with poorer plant cover). Arrows indicate time when undergrowth was removed at grid B.

About two-thirds of the initial voles that were released into the enclosure, became residents of grid A, while the remainder colonized in grid B. The difference in numbers between the grids was reduced with the withering of undergrowth in grid A in autumn. The tendency toward identity was strengthened in the succeeding snow season. After the manipulation of undergrowth in spring, the distribution reverted to a similar state as in the previous September.

Sex ratio and recruitment. Number of recruits was considered as a parameter indicating the intensity of reproduction. In January and February, newly appearing voles (10 animals) were trapped indicating winter reproduction. Reproduction in spring was most active before June, and the appearance of newborn young diminished from July to August (Fig. 2).

The total population showed a sex ratio biased toward females from April to June, and it was more or less balanced in the other periods (Fig. 2). The former period was the early breeding season when almost all of the voles participated in reproduction. Extracting the breeding population from the total, sex ratio was greatly deviated toward females as compared with that of the total population during the main breeding period.

Fig. 2. Sex ratios and recruitments (born in the enclosure) during 1978—1979. Upper solid line: male ratio in total population; broken line: male ratio in breeding population; lower solid line: number of newly appeared voles in the enclosure.

Survivorship curve and maturity age. The change in survival rate with advancing age and maturation age are indicated in Fig. 3. The total number of voles used for this calculation was fifty-two (26 ♀♀ & 26 ♂♂); those voles were born in the enclosure and first captured in April, May or June 1979. The changes in survival rate are represented by survivorship curves, though the study period was not long enough to complete the curve.

The total number of voles that were born during the three months must be used to make the survivorship curve. In field studies, however, it is impossible to enumerate all of the new-born voles because they become trappable only after 15—25 days of age. Therefore, the author first estimated the number of parturitions during the three months examined by the sudden decrease in body weight of the pregnant females and the condition of the nipples, and multiplied the estimated number of parturitions by the mean litter size (5.4) of this species (Kuwahata, 1966). The birth date of each newly trapped vole was estimated on the basis of body weight, condition of pelt and other external characters at the first capture.

Survival rate from birth to 21—25 days, *i.e.*, the preweaning period, was estimated to be 62.8%. Ryszkowski and Truszkowski (1970) and Chełkowska (1978) estimated it to be 47—61% and 47—77% respectively. Thereafter, the survival rate became slightly higher, and this was maintained for about seventy days. After this age, the survival rate rose in both sexes; all of the survivors remained for the following ten days. The author was unable to represent the survivorship curve after that age but could predict it from the data obtained on the population released in the autumn of 1978. In this case, the survival rate per ten days was about 10% higher than that of the younger voles.

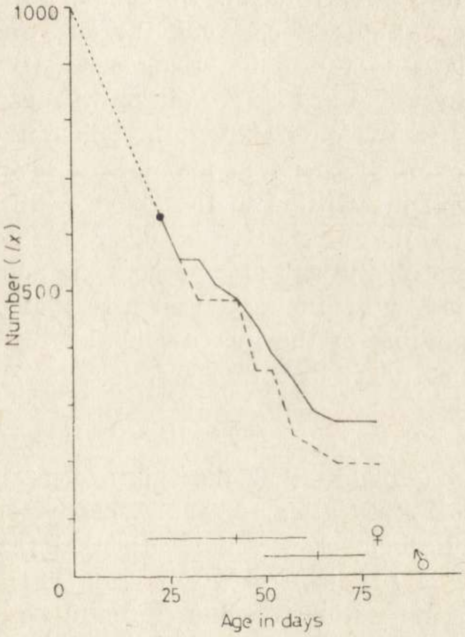

Fig. 3. Survivorship curve (below 75 day age) and maturity age in spring born individuals (born in April, May and June 1979). Solid curve: female; broken curve: male; lower horizontal line: range of maturing age in each sex; vertical line: the mean. Solid circle indicates the age when voles become trappable.

A difference in survival rate between both sexes began to appear from about fifty days. Survival rate in the males tended to be lower than that in the females until about seventy days, though there was statistically on significant difference, so that the number of males decreased to about three-quarters of that of the females by this age Thereafter, survival rate was high and similar in both sexes. The survival rate of the released population was nearly equal in both sexes during almost all of the periods, expect for that of the males which was lower than that of the females in March and April 1979.

The females matured at 20—60 days (eman 42.7 days) and the males at 50—75 days (mean 63.7 days). In comparison with other studies (Kinoshita & Maeda, 1961; Abe, 1968), the age was slightly earlier in the females and later in the males, Ueda *et al.* (1966) pointed out that maturing was affected by food conditions. These differences might reflect differences in the environment in which the experiments were done. The tendency of precocity in females, however, was also reported by Kuwahata (1966) in addition to the above mentioned workers.

The following relationships between survival rate and maturing age were observed. Firstly, the age at divergence of survival rates between the sexes coincided with the age that the males began to mature. Secondly, the beginning of the increase in survival rate coincided with the attainment of maturity in both sexes.

3.2. Spacing Behaviour

The above results suggest that there is a close relationship between survival rate and maturation. Spacing behavior, moreover, is also associated with survival rate or maturation (Getz, 1961; Smyth, 1968; Myers & Krebs, 1971a; Lidicker, 1975; Saitoh, 1981). In order to analyze spacing behavior, the author examined the distance of movement of the home range position, its size, its exclusiveness, and the sallies out side it. The voles used in this analysis were the same as those used in the survivorship curve and maturing age studies.

Changes in the position of home range. Distance of home range shift was measured by the following procedure. The geometric center of home range was determined for each vole for every trapping session and the distance between the previous or the next centers was measured.

Distance of shift increased with developing, decreased from about 50 days, and then was stabilized at a low level after 70 days. The peak of shift was at 35 days in the females and 45 days in the males (Fig. 4a). These were the ages reached just before attaing maturity in both sexes. Thus the distance was shown according to the developmental

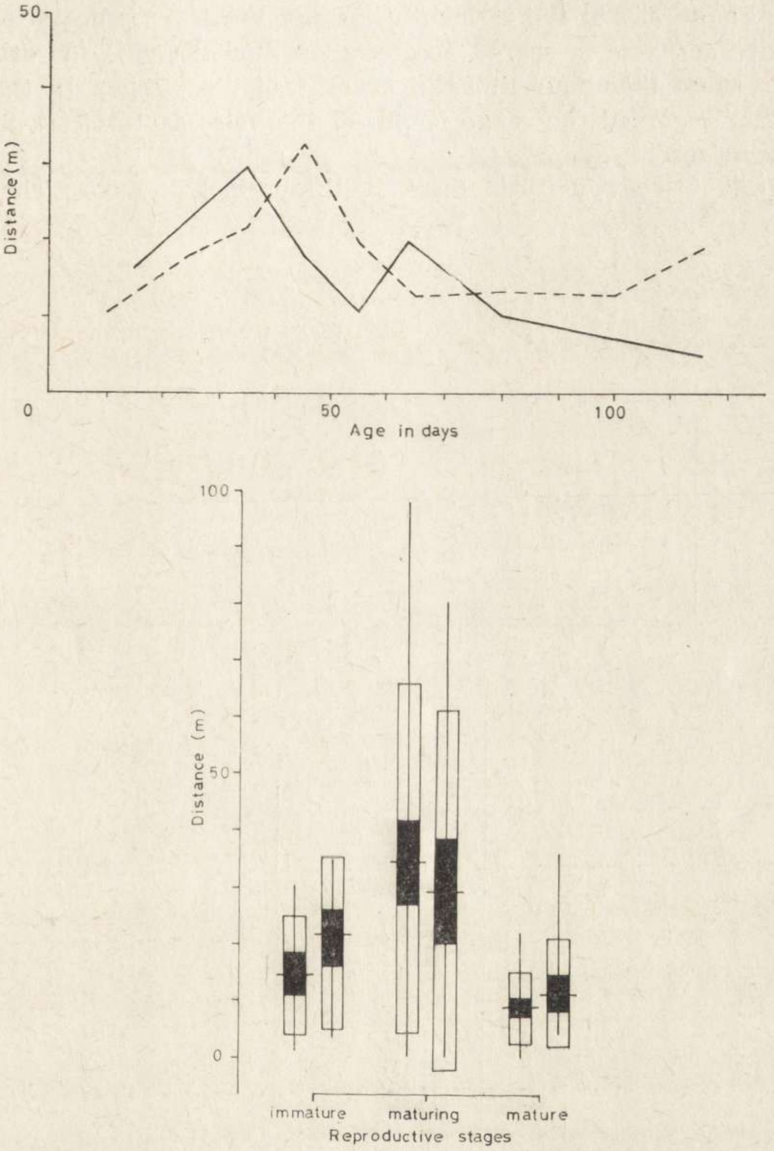

Fig. 4. a. Changes in distance of home range shift with day age. Solid line: female; broken line: male. b. Distance of home range shift in each developmental stage. Left: female; right: male.

stages, immature, maturing and mature, on Fig. 4b. The distance was longer in the maturing stage than the other two stages in both sexes, and a significant difference was present between the maturing and the mature stages in the females (t-test, $P<0.025$).

Home range size. Range length was adopted as an indicator of home range size and was measured according to Stickel (1954) for each vole captured more than four times in every trapping session. In this case, the author regarded the range length of the voles captured at only one trap site as zero.

Range length gradually increased with age in both sexes. The length

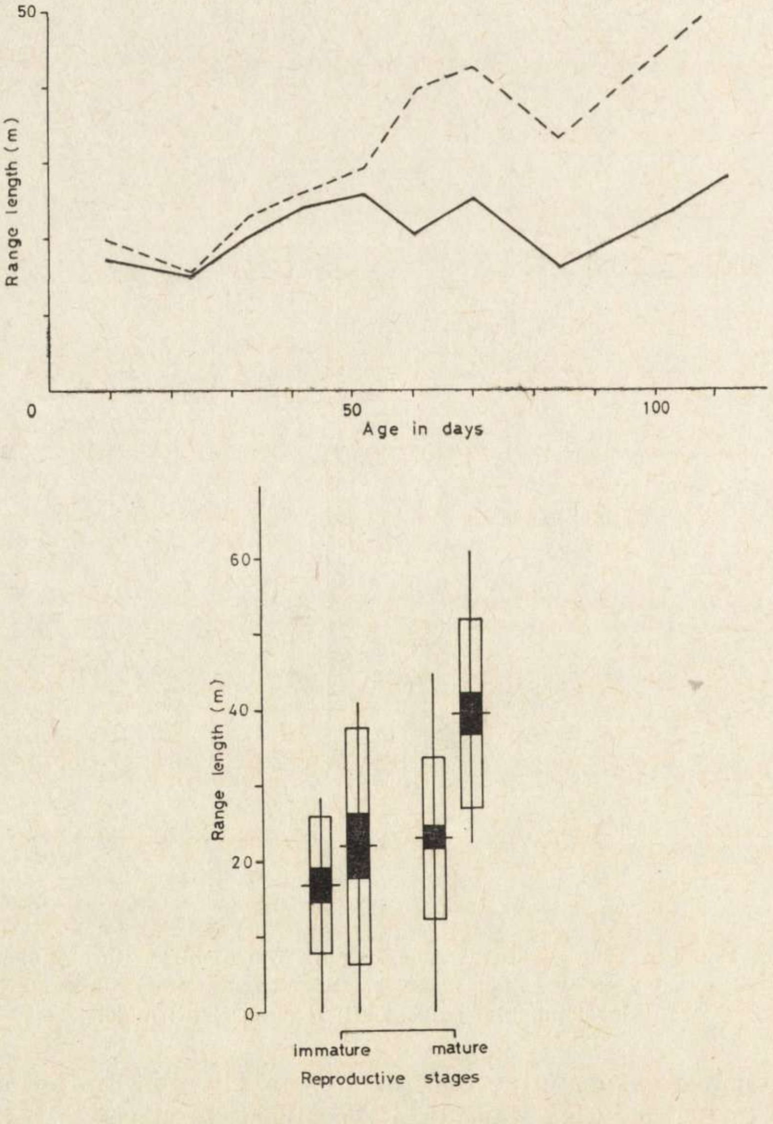

Fig. 5. a. Changes in range length with day age.
Solid line: female; broken line: male. b. Range length in each developmental stage. Left: female; right: male.

however rapidly increased after age 50 days in the males, while no great change was observed in the females. The length in the males, therefore, became 1.5—2.0 times as long as that in the females at a later stage of age (Fig. 5a). In the case of the immature and mature developmental stages, the length was larger in the mature than in the immature stages in both sexes (Fig. 5b; *t*-test, $P<0.05$ in females and $P<0.005$ in males). A difference between the sexes was found in the mature voles (*t*-test, $P<0.001$), and the mean value in the males was about 1.7 time as long as that of the females.

Sallies out of the home range. Depicted ranges which are used daily by animals usually fall within a limited area called home range. The author, however, sometimes observed voles trapped at the sites unusually far from the area. These records have been considered to be a result of unhabitual behavior and are usually omitted from data determining home ranges (Burt, 1943; Stickel, 1954). This type of behavior is called a sally.

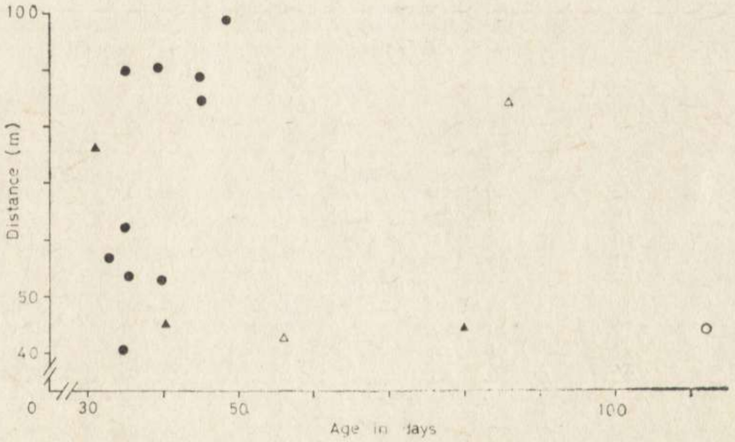

Fig. 6. Distance of sally and the day age at sallying.
Solid triangle: immature female; open triangle: mature female; solid circle: immature male; open circle: mature male.

Salling behavior was observed sixteen times, five by five females and eleven by ten males (Fig. 6). It occurred more frequently in the males than in the females because the number of investigated voles had an even sex ratio (26 animals each). In the males, sallies were recorded most frequently during 30—50 days of age, and almost all of the voles which sallied were immature.

A large fraction of the males that sallied (seven out of ten) were not trapped thereafter. The life expectancy of these individuals was much shorter than that of the same aged males which did not sally; this tendency was not found in the females probably because of the scarce data.

Exclusiveness of home range. Up to now, the author has considered mainly the rather quantitative changes in spacing behavior. In this section, the quality change in spacing behavior, which represents the exclusiveness of home range due to interaction with other voles, will be shown.

Exclusiveness of home range is expressed as the capture frequency at trap sites where a certain number of voles was recorded (Table 1). Ages were classified into four stages. Sixty-one days' old females and seventy-six days' old males were the oldest in the largest age class.

Table 1

Capture frequencies at trap sites where a certain number of other same sexed voles were recorded in each age class.

Age class	Number	Frequency of capture at trap sites with other visitor(s)							
		0		1		2⩽		Total	
		%	No.	%	No.	%	No	%	No.
				Females					
⩽20	17	30	20	44	29	26	17	100	66
21—30	16	60	52	21	18	19	16	100	86
31—40	20	55	71	42	54	3	4	100	129
41⩽	21	66	88	29	39	5	7	100	134
				Males					
⩽20	19	27	18	26	17	47	31	100	66
21—30	17	40	37	30	28	30	28	100	93
31—40	21	51	68	32	43	17	22	100	133
41⩽	22	55	95	34	59	11	19	100	173

Older adults than these were omitted from this analysis, because two totally opposite aspects, mutual interference with others to obtain resources and the parent-young relationship, could not be separated clearly.

Younger voles were more frequently captured at trap sites where two or much same sexed voles were trapped, while older ones were seldom trapped at these trap sites and often visited at trap sites where no other same-sexed voles of both sexes were recorded ($\chi_2^2=49.96$, $U<0.001$ in females and $\chi_2^2=43.95, P\ 0.001$ in males). So the voles has more exclusive home range with advancing age.

Differences between the sexes were observed also in the younger three age classes ($\chi_2^2=7.32$, $P<0.005$ in ⩽20 days, $\chi_2^2=7.64$, $P<0.05$ in 21—30 days and $\chi_2^2=13.70$, $P<0.01$ in 31—40 days); the females were more intolerant than the males.

The voles preferred a more richy covered area, so the density of voles was higher in grid A than in grid B. Though we may expect more frequent movements from a high density area to a low density one, this tendency was not found.

4. DISCUSSION

Two types of seasonal changes have been recorded in populations of *Clethrionomys rufocanus bedfordiae*, *i.e.*, the first having two major periods of reproduction in spring and autumn, and the second lacking a later reproductive period. The former is common to populations of normal moderate density while the latter is usually observed in high density populations (Ota *et al.*, 1959; Kinoshita & Maeda, 1961; Kuwahata, 1962, 1966; Ueda, *et al.*, 1966; Fujimaki, 1972, 1973, 1975; Abe, 1976). It was not reported whether this experiment population had a second reproduction in the autumn of 1979 or not. However this population was considered to be similar to the first type for the following reasons; there was a little but obvious reproduction in the autumn of 1978; in addition, though the voles bred in winter, the main breeding season was in spring and was not carried on until summer; moreover, the peak density of voles in 1979 was not very high (48/ha) for this species, which often reaches over 100 individuals per hectare (Ueda *et al.*, 1966; Abe, 1976).

The sex ratio in this population deviated toward the females in the main breeding season (Fig. 2). This fact was reported in this species also by Fujimaki (1973) and Abe (1976), and in other microtines by Kalela (1971), Myers & Krebs (1971b), and Redfield *et al.*, (1978). In the present study, the prevailing female ratio in the total population was attributed to the great deviation of sex ration in the breeding population, because, the sex ratio at birth was normally balanced in voles (Kalela, 1971; Myers & Krebs, 1971b); the sex ratio of voles born in the enclosure and first captured in April, May or June 1979, was even.

How does the sex ratio change from even at birth to favor females at the reproductive age?

Myers & Krebs (1971b) noticed the following factors affecting sex ratio. (1) Sex ratio of new-born voles. (2) Differential survival. (3) Differential movement; if males have a larger home range than females, the effective trapping area will be larger for males, thus biasing sex ratio in favor of the males in the trapping population. (4) Differential trappability between the sexes. (5) Differential growth; the recruitment of males and females as jvueniles, subadults or adults will be affected by growth rate of two sexes. The present results can be explained by the second and the fifth factors.

If we assume that the survival rate after seventy-five days is 90% per ten days (average survival rate of adult voles) in both sexes, and when the survivorship curves shown in Fig. 3 are extended at this rate to terminate on the time axis, the accumulated number of voles, which are present for each ten days after the mean maturity age in both sexes, is 5223.2 in females and 2501.2 in males. The hypothetical breeding population shows a sex ratio of approximately 2 : 1 in favor of females. This value is almost consistent with the results of Abe (1976) in a natural breeding population of this species and of the present study.

Survival rate was actually higher in the females than in the males during the process of maturation but it was almost equal between the sexes after maturation, though there might be a seasonal variation. This might have produced the characteristic sex ratio in the adult voles mentioned above. Spacing behavior might be an important factor for the divergence in sex ratio (Getz, 1961; Myers & Krebs, 1971a).

We are able to observe behavior of preweaning young voles only in the laboratory. According to Abe (1968), young voles rapidly attain ability to walk after the stage of eye-opening. They usually become trappable at around 20 days, and at this stage, they move about with their mother in her home range. This is seen in the fact that they are sometiems trapped with an adult female or sibs. In the present study, with the advance of maturation (30—50 days), young voles showed high mobility and left their mother's home range (Fig. 4a, 4b & Table 1). At around the time when almost all of the young attained maturity (about 70 days), the mature ones maintained their own exclusive range and their mobility was reduced (Fig. 3 & Table 1). Thus spacing behavior was deduced to be closely related to maturation. In addition, the three factors; survival rate, maturation and spacing behavior, changed reciprocally with each other.

The above basic fact was common to both sexes. The following differences, however, were observed betwen the sexes. (1) Change in spacing behavior occurred earlier in the females. (2) Home range size considerably increased in the males at around the age that they began to mature, though in the females no this tendency was revealed. (3) Sallies were recorded more frequently in the males.

Survival rate was higher in the following order: mature females, mature males, maturing females and maturing males, while the order of mobility was completely the reverse, *i.e.*, an inverse relationship between survival rate and mobility.

Many factors may play a part in determining survival rate. Lidicker (1975) qualitatively distinguished dispersal into two types, saturation and presaturation, and stated that saturation emigration was the outward movement of surplus animals from the population living at or near its carrying capacity. Moreover, such individuals were found to have only a very small chance of survival to reproduce successfully. In this study, the survival rate was lower in the voles that showed high mobility, *i.e.*, instability of home range, which might reflect a change of social status or some physiological conditions. This result is consistent with Lidicker's statement of saturation dispersal. However, the author was unable to determine the death rate of the dispersers and the proportion of their deaths among the total number of deaths. Further investigations on the change in spacing behavior throughout the whole life of voles, with relation to the fate of voles, are required to clarify this point.

Acknowledgements: I witsh to thank Drs K. Ota and H. Mori for their kind encouragement, and Drs. H. Abe and K. Ishigaki for their help in conducting the field experiment and for carefully reading the manuscript. I am indebted also to the staff of Tomakomi Experiment Forest of Hokkaido University for their kind assistance, and Miss M. Koyama for her kind advice on English expression.

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Accepted, March 18, 1983.

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PRZEŻYWALNOŚĆ I RUCHLIWOŚĆ W ZAMKNIĘTEJ POPULACJI *CLETHRIONOMYS RUFOCANUS BEDFORDIAE*

Streszczenie

Badania przeprowadzono w latach 1978 i 1979 w lasach północnej Japonii, przy użyciu 1 ha zagród (Ryc. 1). Stosunek płci u nowonarodzonych młodych był równy, lecz w rozradzającej się populacji występowała przewaga samic (Tabela 1; Ryc. 2). Tę przewagę samic powodowały dwa czynniki: samice dojrzewały wcześniej niż samce i przeżywalność samic była wyższa niż dojrzewających samców (Ryc. 3). Areał osobniczy różni się znacznie u osobników obu płci w czasie dojrzewania. Wielkość areału osobniczego wzrasta istotnie u samców w momencie dochodzenia do dojrzałości płciowej, a u samic ta tendencja nie zaznacza się (Ryc. 4). Areał osobniczy samców jest 1.5—2.0 razy większy niż dojrzałych samic (Ryc. 5). Migracje notowano częściej u samców niż u samic (Ryc. 6). Przeciętna długość życia samców migrujących była krótsza niż samców osiadłych. Tempo przeżywania obniża się w następującym porządku: dojrzałe samice, dojrzałe samce, dojrzewające samice i dojrzewające samce, natomiast ruchliwość układa się w dokładnie odwrotnym porządku.