Res. Popul. Ecol. (1984) 26, 221–234.

FACTORS AFFECTING LITTER SIZE IN THE RED-BACKED VOLE, *CLETHRIONOMYS RUFOCANUS BEDFORDIAE*, WITH SPECIAL EMPHASIS ON POPULATION PHASE

Keisuke NAKATA

Hokkaido Forest Experiment Station, Bibai, Hokkaido 079-01, Japan

INTRODUCTION

There are many interrelated variables that may affect litter size (e.g., season, food supply, body weight, age, parity, lactation, population density and social structure, physiological and genetic changes in constitution; cf. KREBS, 1964). But it is still unknown as to what extent each of these factors affects litter size in natural populations. Many studies have merely described reproductive differences within cyclic species, and in these there are some apparent contradictions on the causes of the changes in litter size.

In the research of population dynamics, litter size of voles has been discussed as a component of their driving factors. KREBS and MYERS (1974) reviewed the problems related to population cycle, and concluded that changes in litter size were not an important driving force in the population cycle. Afterward, some authors seem to agree with this conclusion (e.g., MYLLYMÄKI, 1977; STENSETH, 1978).

In this study, I analyze fundamental factors affecting litter size in the red-backed vole, *Clethrionomys rufocanus bedfordiae*. Emphasis is directed toward evaluating the influence of population phase on litter size.

MATERIALS AND METHODS

The study was conducted in a natural mixed forest at Mizuho, about 25 km east of Asahikawa in central Hokkaido, Japan. The forest, occupying an area of 140 ha, is a mixture of coniferous and broad-leaved deciduous trees and belong to the pan-mixed forest which is characterized by a mosaic pattern of the subarctic and the temperate tree species (TATEWAKI, 1958). The dominant tree species are *Abies sachalinensis*, *Picea yezoensis*, *Cercidyphyllum japonicum*, *Tilia japonica* and *Acer mono*. The undergrowth mainly consists of a dense *Sasa senanensis*, with scattered *Cacalia hastata* var. *orientalis*, *Pachysandra terminalis* and *Osmunda asiatica*. One grid, with an elevation of about 460 m, was established for conducting capture-mark-release studies of small rodents. The grid had 100 trap stations set 10 m apart in a 10×10 pattern. Within 1 m of each station, two shermann type live-traps were placed. As exceptions, a 5×6 pattern was arranged in June 1975; 7×6 pattern in August and October 1975; and 5×10 pattern in May and September 1976. The survey was carried out once a month in the snow-free season from

June 1975 to October 1979. The survey conducted in 1975 was preliminary. The live-traps were baited with oats, and cotton was supplied in early spring and late autumn. The traps were checked once a day. Small rodents were toe-clipped for indetification.

Rodents were sampled during three successive days of trapping. Assuming that the marked individuals were removed, estimated number of each species was calculated by the method of ZIPPIN (1956). The effective trapping area was estimated after DICE (1938). Mean observed range length (STICKEL, 1954) was calculated among voles captured three times during the three successive trapping days. Density per hectare was determined by dividing the estimated number by the effective trapping area. Three days trapping gives as reliable density estimates as five days trapping does (OTA and KOBAYASHI, 1975; NAKATA, unpublished). In May and June 1976, the number of voles captured on the second day of trapping was greater than that on the first day. In these cases, ZIPPIN's method was not applied: estimated number was calculated by means of multiplying the mean ratio (estimated number/actual number captured) by the actual number captured. Besides *C. rufocanus bedfordiae,* the following mammals were captured in the grid: *C. rutilus mikado, C. rex, Apodemus argenteus, A. speciosus ainu, Tamias sibiricus, Sorex unguiculatus, S. caecutiens saevus, S. gracillimus, Mustela nivalis* and *M. sibirica itatsi.*

Voles for autopsy were captured from trap lines located 250–500 m apart from the live-trapping grid. The vegetation in areas of the lines was almost the same as that in the grid. The lines consisted of live-traps, snap traps and pan-tyu traps; the last were made of plastic and were capable of catching and killing small rodents. Live-traps were baited with oats and the others with pumpkin seeds. The voles captured alive in the trap lines were killed immediately at every check in the early morning. The number of traps varied from 50 to 120 in each month. The lines were operated on the same schedule as the grid. In addition to the above schedule, only the lines were operated in several months of the snow season. The fluctuation of number of voles per 100 trap-nights was similar to that in the grid. The voles marked in the grid were not captured in the lines since the lines were placed over 250 m apart from the grid. A small number of voles killed by accidents in the grid was also used for autopsy. The following data were recorded: body weight, total length, tail length, embryos, placental scars and some measurements of the uterus. Skulls were removed for aging. The morphology, development and wear of the third upper molar (M^3) and formation of roots on the second upper molar (M^2) were used as indices of age (ABE, 1976). After age determination, the month of birth and of growth (within 30 days after bitrh; mainly corresponds to the juvenile period) were estimated for each female. The period of growth was defined as a pre-reproductive stage since matured females begin to appear as early as the 30th day of age (ABE, 1968).

Litter size was counted by embryos and the latest set of placental scars that formed dark, distinct nodules in the uterine wall. Almost sets of scars in materials measured above 3 mm in length, which corresponds to scars within one month after parturition (NAKATA, unpublished). Each set of scars was assigned to the division of population

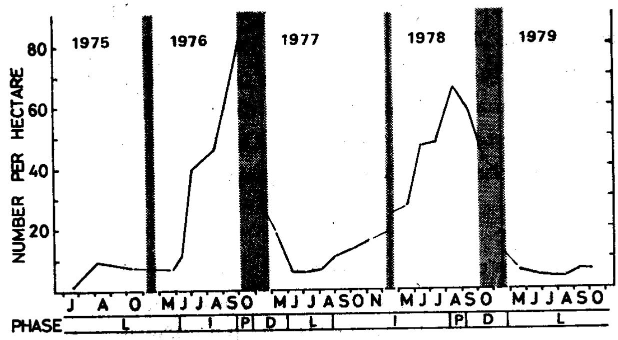

Fig. 1. Fluctuation in population density of *Clethrionomys rufocanus bedfordiae* and divisions of phase. L=low phase, I=increase phase, P=peak phase, D=decline phase. Shaded part=non-breeding period.

phase and density with little difficulty because the same process frequently lasted half a year. Resorbing embryos were excluded from the data.

The process of changes in population density was arbitarily divided into four phases (Fig. 1). Although it was difficult to make definite, the phase of low numbers was assigned to a period of below 10 individuals per ha in density; this phase lasted one year at the longest. The increase phase was defined as a period of rapid increase in numbers; this phase extended one year or less from spring to autumn or from summer to the next spring. The peak phase was assigned to one month because the vole number rapidly decreased just after the attainment of peak number. The decline phase was defined as a period of decrease in numbers. All the decline phases recorded in this study were of the type M (Chitty, 1955). The number dropped very rapidly from autumn to the next spring.

Reproductive females were separated into females of the current year and over-wintered females. Females were considered primiparous if there was evidence of only one pregnancy (either embryo alone or one set of scars), and multiparous if more than one set of scars, or scars plus embryos, were present.

Results

Population dynamics

Figure 1 shows the change of density in the red-backed vole. The population fluctuated at a two-year cycle in the sense of Krebs and Myers (1974). In 1975 the population remained low, but in 1976 it increased rapidly. A density of 86 individuals per ha was recorded in October 1976; this is one of the highest values obtained in forests of Hokkaido. If population reaches a high density in summer, it usually decreases during autumn (Fujimaki, 1969); however, the population in the present survey continued to increase from summer to autumn in 1976. The decline process from 1976 to 1977 fitted the type M of Chitty (1955). In 1977 the population remained low in summer and then increased during autumn. In 1978 it showed a typical pattern of seasonal change of density, reaching a peak in summer, a characteristic of the year of high population density. In 1979 the population remained low with no increase of number. The two-year cycle mentioned above was ascertained for the first time in Hokkaido. Population dynamics will be discussed in detail elsewhere (Nakata, in preparation).

Embryo and placental scar

Litter size obtained by counting embryos was 5.31 ± 0.21 (mean ± SE) and that by counting placental scars was 5.56 ± 0.17. There were no statistically significant differences between the two values ($t=1.02$, $df=116$, $P>0.2$) (Fig. 2). A similar result was obtained in every phase (e.g., $t=0$, $df=22$, $P>0.5$, in the increase phase when the overwintered females were pregnant; $t=0.06$, $df=22$, $P>0.5$, in the increase phase when the current year's females were pregnant). Therefore, the data from embryos and scars are combined in a later section of this paper. Zejda (1966) also observed that the mean number of scars was slightly higher than that of embryos.

Population phase and litter size

Table 1 shows the difference of litter size among females which had passed through different phases of the population cycle. To examine the period in which the mean litter size largely varies with phase, I performed one-way analysis of variance (Table 2). In all the females (Fig. 3; combine samples of the overwintered females with those of the current year's females), variation in litter size was found to be significant among the different phases at birth ($P<0.01$), during growth ($P<0.05$) and during pregnancy ($P<0.01$). It is remarkable that litter size in the period of pregnacy was enhanced in the increase phase and depressed in the decline phase in relation to the population cycle.

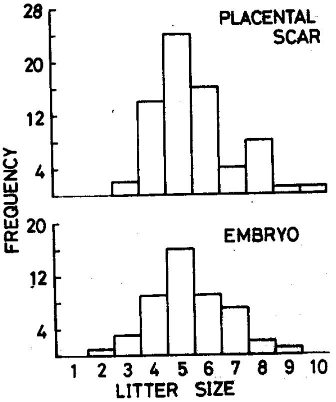

Fig. 2. Frequency distribution of litter size based on counts of embryos and of placental scars.

Table 1. Changes of litter size in females passing through different phases of population cycle.

Phase of the period			Mean litter size±SE	
Birth	Growth	Pregnancy	Overwintered female	Current year's female
low	low	low	8. 00 (1)	6. 00±0. 58 (3)
low	low	increase	6. 67±0. 88 (3)	6. 33±1. 45 (3)
low	low	decline	5. 50±0. 50 (2)	— (—)
low	increase	increase	6. 20±0. 58 (5)	5. 75±0. 85 (4)
increase	increase	increase	6. 82±0. 38 (11)	4. 50±0. 24 (16)
increase	increase	peak	5. 29±0. 36 (7)	4. 79±0. 42 (14)
increase	increase	decline	3. 50±1. 50 (2)	4. 67±0. 24 (18)
increase	peak	peak	— (—)	4. 50±0. 29 (4)
increase	peak	decline	6. 00 (1)	— (—)
peak	decline	low	6. 56±0. 60 (9)	— (—)
peak	decline	increase	6. 50±0. 50 (2)	— (—)
decline	decline	low	4. 60±0. 51 (5)	4. 00 (1)
decline	decline	increase	— (—)	6. 00±0. 50 (2)

( ) sample size

Table 2. *F*-values for differences of litter size among phases in birth, growth and pregnancy period.

	Birth		Growth		Pregnancy	
	F	*df*	*F*	*df*	*F*	*df*
Overwintered females	2. 18	3, 44	0. 26	3, 44	2. 67†	3, 47
Current year's females	5. 88**	2, 61	3. 53*	3, 60	0. 70	3, 59
All the females	6. 84**	3, 108	3. 40*	3, 110	4. 49**	3, 113

† $P<0.1$, * $P<0.05$, ** $P<0.01$.

There was an appreciable difference in litter size in the overwintered females which became pregnant during the different phases ($P<0.1$) (Fig. 3). The overwintered females had a higher mean litter size in the increase and the low phase than in the other phases. No significant difference in litter size was found in the overwintered females born and undergoing growth during the different phases respectively.

There was a significant difference in litter size in the current year's females born during the different phases ($P<0.01$). The litter size in the females was higher in the low and the decline phase than in the other phases. A similar result was also obtained in the current year's females undergoing growth during the different phases ($P<0.05$). Litter size slightly varied among the current year's females which became pregnant during the different phases, but the difference was not significant.

Population density and litter size

Multiple regression analysis was made on litter size versus density as they corresponded to the period of birth, growth and pregnancy. After dividing the population

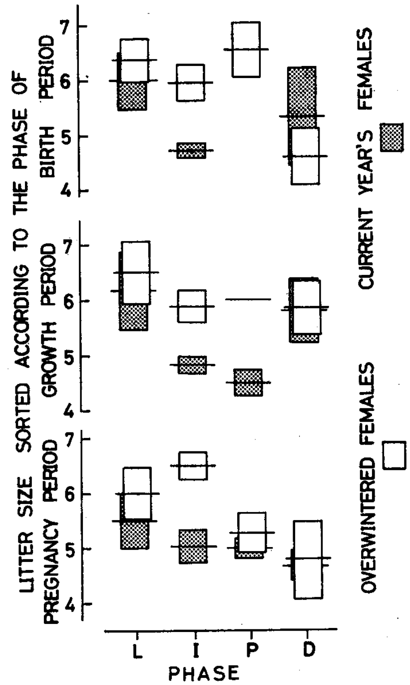

Fig. 3. Phase variation in litter size (mean ± SE). L=low phase, I=increase phase, P=peak phase, D=decline phase.

process at every 5 individuals per ha, I determined the density respectively. These relations were expressed as follows.

In the overwintered females:

$$Y=-0.064X_1+0.023X_2-0.061X_3+9.247$$
$$R^2=0.464\ (F=12.96,\ df=3,\ 45,\ P<0.01)$$

In the current year's females:

$$Y=-0.004X_1-0.023X_2+0.0001X_3+5.892$$
$$R^2=0.118\ (F=2.49,\ df=3,\ 56,\ P<0.1)$$

where Y=litter size; X_1, X_2 and X_3=density when the female was born, undergoing growth and pregnant respectively; R=multiple correlation coefficient.

Generally, the density showed a negative relationship to litter size. Since the regression coefficients are very small, the litter size is rather stable with the change of density to some extent and is heavily affected when the population is high. In the overwintered females, a significant relationship was detected; the density explained 46.4% of the change of the litter size. In the current year's females, the density hardly explained the change of the litter size.

Partial correlation coefficients (r) of each relatiosnhip were as follows:

In the overwintered females (df=45)

$$r_{YX_1 \cdot X_2X_3} = -0.308 \ (P<0.05)$$

$$r_{YX_2 \cdot X_3X_1} = 0.104$$

$$r_{YX_3 \cdot X_1X_2} = -0.675 \ (P<0.01)$$

In the current year's females ($df=56$)

$$r_{YX_1 \cdot X_2X_3} = -0.018$$

$$r_{YX_2 \cdot X_3X_1} = -0.097$$

$$r_{YX_3 \cdot X_1X_2} = 0.0001$$

The litter size had significant relationships with the density at the time when the overwintered females were born and pregnant. No significant relationships were found in the current year's females; the density hardly explained the change of the litter size. In simple correlations (Table 3), the density showed a negative relationship to litter size, and the highest absolute value was obtained between litter size and the density at the time when the overwintered females were pregnant ($r=-0.409$) and when the current year's females were undergoing growth ($r=-0.342$) respectively.

Age at pregnancy and litter size

Figure 4 shows the relationship between the age at pregnancy and litter size. The litter size rapidly increased with the age until 7–8 months of age and slowly diminished in older age classes ($F=3.24$, $df=5, 105$, $P<0.01$). I examined whether litter size showed a significant relationship with the age of pregnant females in each phase. The same significant trend in the change of the litter size was found in the increase phase ($F=3.72$, $df=5, 39$, $P<0.01$) and the decline phase ($F=2.63$, $df=4, 18$, $P<0.1$).

The overwintered females, which correspond to those aged 7–8 or more months, had a higher litter size than the current year's ones aged 5–6 or less months, as illustrated in Fig. 5 (mentioned later).

If litter size in females of the same age is constant from phase to phase in the cycle, difference in litter size related to phase is explained only by age composition of the females.

Table 3. Simple correlation coefficients between litter size (Y) and density at the time when female was born (X_1), undergoing growth (X_2) and pregnant (X_3).

		X_1	X_2	X_3
Y	OW	−0. 113	−0. 103	−0. 409**
	CY	−0. 324*	−0. 342**	−0. 240†
X_1	OW		0. 973**	−0. 685**
	CY		0. 926**	0. 576**
X_2	OW			−0. 655**
	CY			0. 713**

OW=overwintered female, CY=current year's female.
† $P<0.1$, * $P<0.05$, ** $P<0.01$.

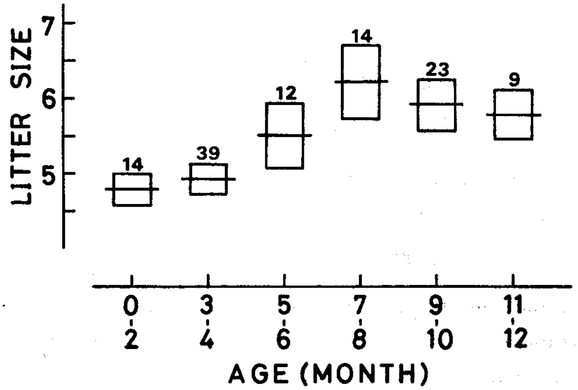

Fig. 4. Age variation in litter size (mean±SE). Number at the top of rectangle=sample size.

Table 4. *F*-values for differences of litter size among phases in each age class.

	Age class					
	0-2	3-4	5-6	7-8	9-10	11-12
F	3.90†	4.55*	1.11	2.32	3.35*	1.95
df	1, 12	2, 37	1, 7	2, 11	3, 17	3, 5

Samples of current year's female (5-6 or less months of age)=litter size sorted according to the phase of birth period, samples of overwintered female (7-8 or more months of age)=litter size sorted according to the phase of pregnancy period.
† $P<0.1$, * $P<0.05$.

This possibility was tested in Table 4. Litter size in females of the same age class varied with phase in a similar pattern shown in Fig. 3. Furthermore, the variations were significant in some age classes. Thus, the difference in litter size among phases was not due merely to the difference of age composition of the reproductive females.

Parity and litter size

Primiparous females had a higher litter size than multiparous females in the overwintered voles ($t=0.47$, $df=48$, $P>0.5$), and the reverse phenomenon was found in the current year's voles ($t=0.98$, $df=60$, $P>0.2$); however, there were no significant differences (Fig. 5). In natural populations of *C. rufocanus*, no apparent differences were also obtained between primiparous and multiparous females (KALELA, 1957; FUJIMAKI, 1981). To test the possibility that parity variation in litter size may be explained by the age of females, Fig. 6 shows the relationships among parity, age and litter size. Neither definite trends nor significant differences in litter size were found between primiparous and multiparous females. On the contrary, there was a significant difference in litter size

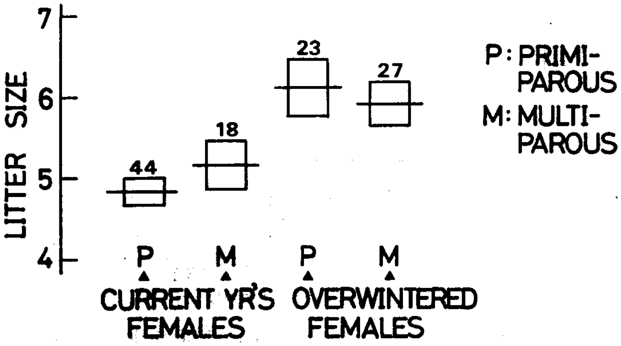

Fig. 5. Variation in litter size (mean±SE) with parity in current year's and overwintered females. Number at the top of rectangle=sample size.

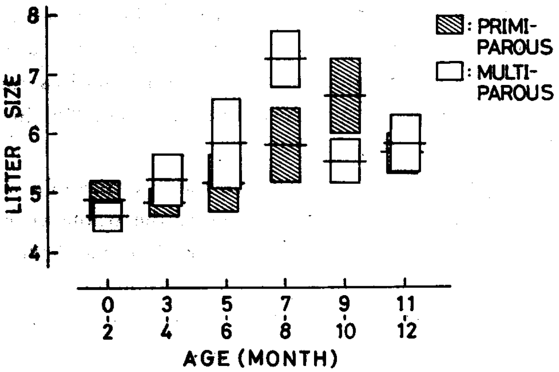

Fig. 6. Age variation in litter size (mean±SE) in primiparous and multiparous females.

among the age classes in primiparous and in multiparous females respectively ($F=2.59$, $df=5$, 60, $P<0.05$; $F=2.03$, $df=5$, 39, $P<0.1$). A similar age variation in litter size, although not significant, was also found in each phase in both groups of females. In conclusion, parity apparently does not affect litter size, and the difference in age of pregnant females accounts for the parity variation in litter size.

Body size and litter size

Employing regression analysis, I obtained a significant correlation between maternal body length (length of head and body) and litter size (Fig. 7). The body length explained a small portion, 14.9%, of the variation of the litter size ($r=0.386$, $df=33$, $P<0.05$). For the overwintered females, I have obtained $r=0.366$ ($df=13$) and for the current year's females, $r=-0.086$ ($df=18$). The correlation in all samples was mostly influenced by that in the overwintered voles. No apparent relationship was observed in any age class or any phase.

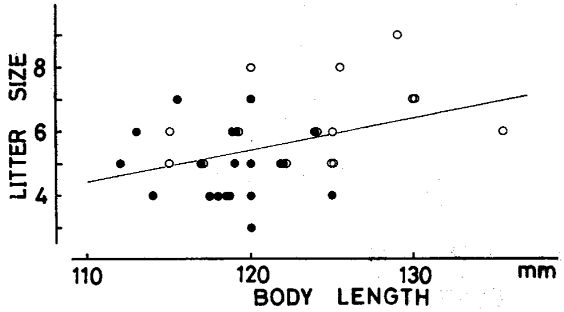

Fig. 7. Relationship between litter size and body length. Solid circle=current year's female, open circle=overwintered female.

Season, year and litter size

Figure 8 shows that litter size was higher in spring and lower in summer and autumn. Seasonal difference was thus shown to be significant (F=4.95, df=2, 65, P<0.01). Age composition of females in spring differed greatly from that in summer and autumn; the overwintered voles made up 100% of the sample in spring, 39% in summer and 26% in autumn (Fig. 8).

No definite relationships were found between the litter size of a whole year and the population process (cf. Fig. 1): Mean litter sizes of the whole year were 5.61±0.42 (mean ± SE) in 1976 (sample size, 18), 5.71±0.35 in 1977 (14), 5.23±0.15 in 1978 (71) and 6.00±0.42 in 1979 (14).

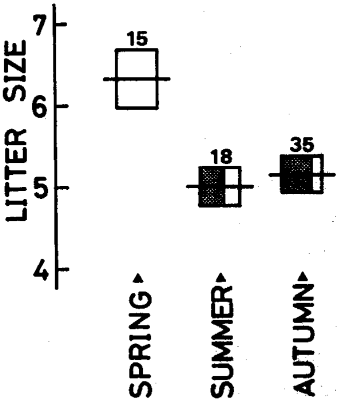

Fig. 8. Seasonal variation in litter size (mean±SE). Spring=May–June, Summer=July–August, Autumn=September–October. Number at the top of rectangle=sample size. Shaded part of rectangle=current year's females in sample. Samples were restricted to the litters gestated and born within each season.

DISCUSSION

Litter size was largely associated with the phase when the overwintered females were pregnant and the current year's females were born and undergoing growth. Litter size in the overwintered females was also explained by population density to some extent, especially at the period of pregnancy. In the population cycle, litter size was enhanced in the increase phase and depressed in the decline phase (Fig. 3); this fact shows that the changes in litter size are an important driving force in the population cycle.

Since prenatal mortality does not seem to vary systematically during the population cycle (KUWAHATA, 1966; KREBS and MYERS, 1974), litter size may be largely influenced by the number of ova. SCHADLER (1980) reported in an experimental study of the pine vole, *Microtus pinetorum*, that the number of preovulatory follicles was significantly smaller in crowded groups. Therefore, the diminished litter size observed in the population cycle might be explained by the effect of crowding. In the overwintered females which became pregnant during the different phases, the litter size in the increase phase was higher than that in the low phase, though the population density increased. This change in litter size may be expressed as a positive effect of crowding.

In the current year's females born and undergoing growth during the different phases, the litter size was diminished in the phase of increase and peak when the mutual stimulation was supposed to be heavy among individuals. The current year's females appeared to be influenced by the phase until they established their own home ranges after birth. This finding shows that the population phase affected litter size in the current year's females which became pregnant in the future.

Litter size in relation to phase of the cycle has been discussed in many papers. In their review of reproduction in voles and lemmings, KREBS and MYERS (1974) concluded that litter size, a component of reproduction, is not a critical link in the demographic machinery. But, in the literature, including the paper of KREBS and MYERS (1974), there are some errors which hinder correct understanding of the relationship between litter size and population phase. First, several authors have confused the terms "phase" and "density". Phase is not an absolute height of density but an aspect of population change; therefore, the term phase is essentially different from the term density. In this respect, I might have erroneously defined the low phase as the period below 10 individuals per ha in density, though this definition is very difficult. Second, several authors have combined the data of litter size from month to month or from year to year, and also the data of population process (i.e., KALELA, 1957; KREBS, 1964; KELLER and KREBS, 1970; etc.). This procedure mixes the data of various phases; for example, the year of high numbers frequently consists of increase, peak and decline phases. One good support of this error is that no relation was found between litter size and population process when the data of the whole year was summed up in the present survey. Third, several authors have defined the population cycle from only a few data (i.e., HOFFMANN, 1958; TANAKA, 1964; HANSSON et al., 1978; etc.). High density possibly represents the increase phase or the beginning of the decline phase, but not the peak phase. We must be suspicious of data obtained from only one or two trappings a year or from field samples collected only for a short summer period (KREBS and MYERS, 1974). Finally, several authors have combined the data from various survey areas (i.e., HOFFMANN, 1958; FULLER, 1969; KELLER and KREBS, 1970; etc.). This procedure overlooks the relationship between population cycle and change of litter size involved. These errors listed above account for the reasons why the relationships between litter size and population phase have not been detected up to now.

Change of litter size depends on age rather than parity of the female, and differences in litter size with parity seem to be explained by differences in the age of females. Age variation in litter size is well known in *Clethrionomys* (cf. ZEJDA, 1966; BUCHALCZYK, 1970; FUJIMAKI, 1981). Usually, the effect of age on litter size is shown by the fact that the overwintered females had a larger litter size than did the females of the current year (KALELA, 1957; KOSHKINA, 1957; ZEJDA, 1966; FUJIMAKI, 1981; etc.). In my samples, none of the females of the current year group bred at the age of 7–8 or more months. It is thus impossible to examine whether the difference of litter size between the overwintered females and the current year's females is explained merely by the difference of age.

Though KUWAHATA (1966) found no correlation between litter size and body length for *C. rufocanus,* a significant correlation was obtained in the present study. A similar result was also obtained for *C. glareolus* (ZEJDA, 1966). Moreover, the mean litter size tended to increase with the increase in the body weight (KALELA, 1957; ZEJDA, 1966; FUJIMAKI, 1981; etc.). As body length and weight distributions in cyclic populations seem to follow a distinct pattern of change (KELLER and KREBS, 1970), change of litter size related to body size may be explained by the population phase (or density) and the age of females.

Seasonal changes in litter size are usually considered to be due to changes in age composition of a population (OTA et al., 1964; INNES, 1978; FUJIMAKI, 1981; this study; etc.), but population phase (or density) is probably involved.

SUMMARY

Litter size in relation to population cycle was examined for the red-backed vole, *Clethrionomys rufocanus bedfordiae,* in a natural mixed forest of Hokkaido.

Litter size changed from phase to phase in the population cycle; it was enhanced in the increase phase and depressed in the decline phase. There was an appreciable difference in litter size in overwintered females which became pregnant during the different phases. Significant difference in litter size was found in current year's females born during the different phases. A similar result was also obtained in current year's females undergoing growth during the different phases.

Population density had a significant correlation with litter size in overwintered

females. Litter size was especially related to density at the time when overwintered females were pregnant. On the other hand, litter size of the current year's females was hardly explained by population density. Generally, density showed a negative relationship to litter size. Since the regression coefficients were very small, litter size was rather stable with the change of density to some extent.

There was a significant difference in litter size among age classes of pregnant females; the age variation was independent of the population phase. Difference in litter size with parity was considered to be explained by that of the age of the pregnant females. Litter size was related to body length, but the correlation coefficient was small.

ACKNOWLEDGMENTS: I wish to thank Drs. H. ABE, K. KAMIJO, K. KIKUZAWA and Y. SAITÔ for reading this manuscript and offering many helpful comments.

REFERENCES

ABE, H. (1968) Growth and development in two forms of *Clethrionomys*. I. External characters, body weight, sexual maturity and behavior. *Bull. Hokkaido For. Exp. Sta.* 6: 69–89 (in Japanese with English summary).

ABE, H. (1976) Age determination of *Clethrionomys rufocanus bedfordiae* (THOMAS). *Jap. J. Ecol.* 26: 221–227 (in Japanese with English summary).

BUCHALCZYK, A. (1970) Reproduction, mortality and longevity of the bank vole under laboratory conditions. *Acta Theriol.* 15: 153–176.

CHITTY, D. (1955) Adverse effects of population density upon the viability of later generation. 57–67. In *The Number of Man and Animals.* J. B. CRAGG and N. W. PIRIE (eds) Edinburgh. (cited from KREBS and MYERS, 1974).

DICE, L. R. (1938) Some census methods for mammals. *J. Wildl. Mgmt.* 2: 119–130.

FUJIMAKI, Y. (1969) The fluctuations in the numbers of small rodents. *Bull. Hokkaido For. Exp. Sta.* 7: 62–77 (in Japanese with English summary).

FUJIMAKI, Y. (1981) Reproductive activity in *Clethrionomys rufocanus bedfordiae.* 4. Number of embryos and prenatal mortality. *Jap. J. Ecol.* 31: 247–256.

FULLER, W. A. (1969) Changes in numbers of three species of small rodent near Great Slave Lake, N.W.T. Canada, 1964–1967, and their significance for general theory. *Ann. Zool. Fennici.* 6: 113–144.

HANSSON, L., J. LÖFQVIST and A. NILSSON (1978) Population fluctuations in insectivores and small rodents in northernmost Fennoscandia. *Z. Saugetierkunde* 43: 75–92.

HOFFMANN, R. S. (1958) The role of reproduction and mortality in population fluctuations of voles (microtus). *Ecol. Monogr.* 28: 79–109.

INNES, D. G. (1978) A reexamination of litter size in some North American microtines. *Can. J. Zool.* 56: 1488–1496.

KALELA, O. (1957) Regulation of reproduction rate in subarctic population of the vole *Clethrionomys rufocanus* (SUND.). *Ann. Acad. Sci. Fenn. Ser. A., IV.* 34: 1–60.

KELLER, B. L. and C. J. KREBS (1970) *Microtus* population biology. III. Reproductive changes in fluctuating population of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana, 1965–1967. *Ecol. Monogr.* 40: 263–294.

KOSHKINA, T. V. (1957) Comparative ecology of the red backed voles in the northern taiga. *Fauna and Ecol. of Rodents* **5**: 3–65 (English translation in Boreal Institute, Univ. of Alberta).

KREBS, C. J. (1964) The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. *Arctic Inst. N. Amer. Tech.* Paper 15.

KREBS, C. J. and J. H. MYERS (1974) Population cycles in small mammals. *Adv. Ecol. Res.* **8**: 267–399.

KUWAHATA, T. (1966) Studies on the population fluctuation of the red backed vole, *Clethrionomys rufocanus bedfordiae* (THOMAS). II. Reproductive activity. *Ann. Rep. Hokkaido Bra. For. Exp. Sta.* 1965, 210–236 (in Japanese with English summary).

MYLLYMÄKI, A. (1977) Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* **29**: 468–493.

OTA, K. and T. KOBAYASHI (1975) An examination of MacLulich's method for estimating population density of small mammals. *Honyurui Kagaku* (*Mammalian Science*) **31**: 19–32 (in Japanese with English summary).

OTA, K., H. ABE, S. TAKATSU and J. FUJIKURA (1964) Seasonal changes in the number of embryos of *Clethrionomys rufocanus bedfordiae* in Konsen District. *Zool. Mag.* **73**: 383–384 (in Japanese).

SCHADLER, M. H. (1980) The effect of crowding on the maturation of gonads in pine vole, *Microtus pinetorum*. *J. Mamm.* **61**: 769–774.

STENSETH, N. C. (1978) Demographic strategies in fluctuating populations of small rodents. *Oecologia* **33**: 149–172.

STICKEL, L. F. (1954) A comparison of certain methods of measuring ranges of small mammals. *J. Mamm.* **35**: 1–15.

TANAKA, R. (1964) Population dynamics of the Smith's red-backed vole in highlands of Shikoku. *Res. Popul. Ecol.* **6**: 54–66.

TATEWAKI, M. (1958) Forest ecology of the islands of the north Pacific Ocean. *J. Fac. Agri. Hokkaido Univ.* **50**: 371–486.

ZEJDA, J. (1966) Litter size in *Clethrionomys glareolus* SCHREBER 1780. *Zool. Listy* **15**: 193–206.

ZIPPIN, C. (1956) An evaluation of the removal method of estimating animal population. *Biometrics* **12**: 163–189.

エゾヤチネズミの一腹仔数に影響を及ぼす要因——特に個体群相を強調して——

中田圭亮

1975年から1979年にかけて旭川市東旭川町瑞穂の針広混交天然林において，エゾヤチネズミの個体群動態を調べ，一腹仔数と個体群要因，個体の属性との関係を評価した。一腹仔数は個体群相の間で有意に変化しており，増加相で増え，減少相で減少した。越冬繁殖雌の一腹仔数は妊娠期の個体群相と関連しており，増加相，低密度相，ピーク相，減少相の順に多かった。当年繁殖雌の一腹仔数は出生期と生長期（出生後30日までの期間，主に幼体期に該当）の個体群相に有意に関連しており，低密度相，減少相，増加相，ピーク相の順に多かった。個体群密度は越冬雌の一腹仔数と有意な相関関係がみられた。一方，当年雌の一腹仔数は個体群密度ではほとんど説明できなかった。個体群密度は一般に負の要因として一腹仔数に働いており，回帰係数がごく小さいことから多少，密度が変化しても一腹仔数は安定していること，またその影響は高密度時に強くみられることが示された。繁殖雌の妊娠時の齢と一腹仔数との間には有意な関係がみられた。この関係は個体群相に独立であった。出産経歴による一腹仔数の違いは繁殖雌の妊娠齢の違いによるものと考えられた。同齢かつ同個体群相の繁殖雌間で出産経歴による一腹仔数の相違に一定の傾向や有意差はみられなかった。体が大きい妊娠雌ほど一腹仔数の多い傾向がみられたが，その寄与率は14.9%と小さかった。