Regulation of reproduction in a natural population of the small Japanese field mouse, *Apodemus argenteus*

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Abstract. Changes in reproductive parameters were analyzed quantitatively in a natural population of the small Japanese field mouse, *Apodemus argenteus*. Among individuals born in the current year, the lightest female weighed 8 g at sexual maturity and the lightest male weighed 10 g. Irrespective of season, the lightest mice were found only during the phase of population increase. Among mice that had over-wintered, the lightest individuals of each sex to reproduce during the spring population decline weighed 10 g. In years of high population density, the reproductive rates of females, even at their peak during August, was below 10%. In contrast, in low-density years, much higher rates, over 69%, lasted until October during the increase phase. The patterns for males were almost the same as those of females during survey years. According to multivariate analysis, the reproductive rate of males was largely explained by population density (partial correlation, 0.732), whereas the reproductive rate of females was largely explained by the fluctuation phase (0.848). The number of each sex to reproduce increased in proportion to the density of potentially reproductive mice at lower densities, but then decreased at higher densities. The observed maximum number of reproductively active mice was 15 males and 21 females in a one-hectare grid. Temperature appeared not to cause any variation in the breeding season in this population.

Key words: age at sexual maturity, breeding season, limitation of reproduction, population density, temperature.

In contrast to the considerable amount of information available on arvicoline rodents (*e.g.*, Alibhai and Gipps 1985, Taitt and Krebs 1985), little is known about the multi-annual fluctuations of murine rodent population densities, particularly of *Apodemus* species. In almost all cases reported so far, *Apodemus* populations usually repeat similar seasonal patterns of density change from year to year (*e.g.*, Fujimaki 1969, Watts 1969, Bobek 1973, Nishikata 1979, Flowerdew 1985, Moreno and Kufner 1988, Lin and Shiraishi 1992). These repeating patterns have led to analyses of density variation in relation to extrinsic factors such as seed crops and temperature, which show marked seasonal variation. With the exception of aggression among adult males (see Watts 1969), however, the effects of intra-population or intrinsic factors affect-

ing *Apodemus* species have been little studied.

Reproductive inhibition has been stressed as one of the most critical aspects of population regulation in small rodents. For example, limitation of the number of reproductively active individuals is corroborated in natural populations of arvicoline rodents, and the limitation is interpreted as a key attribute in explaining delayed maturation in individuals of the year (*e.g.*, Saitoh 1981, Ostfeld 1985, Nakata 1989).

Montgomery (1989) described spatial density-dependence in the reproductive activity of female *Apodemus sylvaticus*, a dependence which he suggests is a likely regulatory mechanism leading to reproductive inhibition. Temporal density-dependence in reproduction, however, has hardly been studied in *Apodemus* species.

The present study was designed, therefore, to make quantitative analyses of: 1) multi-annual density fluctuations, and 2) the parameters of reproductive inhibition in the small Japanese field mouse *Apodemus argenteus*.

MATERIALS AND METHODS

The study was conducted in a natural mixed forest at Mizuho (43°42'N, 142°39'E), about 25 km east of Asahikawa, in central Hokkaido, Japan. This semi-boreal forest consists of both coniferous and broad-leaved trees (Tatewaki 1958, Hamet-Ahti *et al.* 1974). The dominant tree species are *Abies sachalinensis*, *Picea yezoensis*, *Cercidiphyllum japonicum*, *Tilia japonica* and *Acer mono*, and the undergrowth consists mainly of a dense layer of *Sasa senanensis*. The output of seed from these species appeared to be rather constant from year to year during the years of the study according to local foresters. Climatic data for the study area can be found in Nakata (1989).

Capture-mark-release studies were undertaken from June 1975 to October 1979 in a trapping grid set at an elevation of about 460 m. One hundred trap stations were set 10 m apart in a 10 × 10 pattern in this grid. During 1975, and for two months of 1976, however, the trapping pattern of the grid was changed. A 5 × 6 pattern was used in June 1975, a 7 × 6 pattern in August and October 1975, and a 5 × 10 pattern in May and September 1976. Two Sherman-type live traps, baited with oats, were set less than one metre apart at each trapping point, and one trapping session was conducted on three consecutive days each month during the snow-free seasons.

Captured mice were sexed, weighed, their point of capture was noted, and their reproductive condition recorded. Assuming that marked individuals were removed, the size of the population was estimated using Zippin's (1956) methods. In order to estimate the effective trapping area (Dice 1938), the mean observed range lengths were calculated from mice which were captured three times at two or three different trap points during each trapping session. The population density per hectare was obtained by dividing the estimated number of mice by the effective trapping area. The study area and the trapping procedure are described in more detail in Nakata (1986, 1989).

Males with descended testes were regarded as sexually active, while sexually active females were those either visibly pregnant, or with medium or large nipples indicating that they were lactating, or those with perforated vaginae.

In order to obtain further reproductive data, mice for autopsy were captured from trap lines located 250-500 m away from the live-trapping grid. These trap lines were situated in the same vegetation as the main trapping grid, however some additional trapping sessions were undertaken during months with snow-cover. The following data were recorded from these mice: weight, total length, tail length, length of testes, condition of the epididymal tubules (visible to naked eyes or not: see Jameson 1950), number of embryos, number of placental scars and uterus width. In addition, the development and wear of the third upper molar (M^3) were used as indices of age (Fujimaki 1966).

In order to be able to make comparisons with other rodent studies, a "cyclicality" index was calculated for the population: $s = \sqrt{(\log N_i - \log \bar{N})^2 / (n - 1)}$, where $\log N_i$ is the log density at the same time each year, $\log \bar{N}$ is its mean and n the sample size (Stenseth and Framstad 1980, Henttonen *et al.* 1985). This index is the standard deviation of the log density.

Four phases of the fluctuating population were arbitrarily defined (Fig. 1), these were: 1) the low phase when there were fewer than eight individuals/ha, 2) the increase phase when increase was rapid, 3) the peak, and 4) the decline phase when decrease was rapid. These four phases occurred in rapid succession during a period of less than one year (Krebs and Myers 1974).

In order to assess the effect of temperature on the population (see Fig. 5) temperature records were obtained from the Higashikawa Meteorological Station (alt. 216m) 10 km south-west of the grid. Records of monthly precipitation and snow depth can also be found in Nakata (1989).

RESULTS

1. Density changes

During the course of our five year study, the *Apodemus argenteus* population varied in size, such that some years were high-density, and others were low-density (Fig. 1). In 1976 and 1978, high-density years, the population density increased rapidly from May to July, reached its peak in August, then declined from September onwards. In contrast, in 1977 and 1979, low-density years, the population decreased from May to June or even August, then increased until October. The autumnal increases were not gradual, and they were at similar rates of growth as found during high-density years. The changes in density recorded in 1975 may be somewhat over-estimated as a result of bias caused by the small-scale of trapping at that time, however, despite that, the changing pattern was similar to that observed in both 1977 and 1979.

The highest density recorded during the study was 78.5 individuals/ha in August 1978, whereas the lowest density was 2.8 individuals/ha in August 1977. The amplitude of the change was 28-fold. As described above, a sharp con-

Fig. 1. Fluctuation in population density of live-trapped *Apodemus argenteus*. L=low phase, I=increase phase, P=peak phase, D=decline phase.

trast was found between different summers and consequently the s-values varied during the five years being 0.453 in June, 0.567 in August and 0.173 in October.

The duration of the increase phase was highly variable, ranging from three months (from September to July in 1976) to eleven months (from September 1977 to July 1978). The over-winter decline phases were rather longer, namely from September 1976 to May 1977 and from September 1978 to June 1979. The low phase lasted for three months in 1977, and in 1979 there was no low phase between the decline and increase phases. The population declined just after attaining its peak density, and accordingly the peak phase was regarded as a brief time covering just one month.

2. Age and body weight at reproduction

Among mice of the year, the lightest sexually mature males weighed 10 g (one male in June 1976), and the lightest sexually mature females 8 g (two females in July 1976 and October 1977; see Fig. 2). Irrespective of season, these lightest mice were found only during the increase phase. Among the autopsied mice, the youngest male was 2-4 months old, and the youngest female was 1-2 months old (Appendix 1).

Among those mice that had over-wintered, the lightest individuals to reproduce weighed 10 g (one male and one female in May 1977, and one female in May 1979), when the population was in the decline phases (Fig. 2). These light mice were presumably more than eight months old, given that reproductive activity stopped early in the preceding year (no reproductive females were live-trapped either in October 1976, or during September and October 1978). The existence of shortened reproductive seasons was corroborated by the findings from the autopsied samples (Appendix 1).

3. Reproductive rate and the number of reproductively active individuals

Temporal changes in the reproductive rate of *Apodemus argenteus* were examined. In order to quantify the reproductive rate (the percentage of individuals reproductively active), males were considered capable of reproducing

Fig. 2. Body weights of live-trapped male and female *A. argenteus*. Each small rectangle represents one mouse. ■ = reproductively active mouse, □ = immature mouse including post-reproductive males, ▣ = post-reproductive female. Numbers are sample sizes. Other symbols are as in Fig. 1. All mice trapped in May had over-wintered except for one female of the year in 1978 (see text).

when they weighed 10 g or more, and females were considered capable of reproducing when they weighed 8 g or more.

Rates of reproduction were closely associated with fluctuation phase and population density (Fig. 3). The proportion of reproductively active females during the peak phase in August in high-density years was just 1% in 1976 and only 5% in 1978, whereas in low-density years (1977 and 1979) much higher rates, over 69%, lasted until October during the increase phase. Very similar patterns were found for males, except that in July 1979 the proportion suddenly dropped to 52% and then remained lower than that of females.

The effects of the three important variables, population density, fluctuation phase, and season, were estimated using the quantification-I method (a multiple regression analysis using dummy variables: Hayashi 1952, Tanaka *et al.* 1984). Population density and fluctuation phase were each divided into four categories, while the seasons were divided into three (Table 1, for internal correlations see Appendix 2). For males, the rate of reproduction was largely explained by population density (partial correlation, 0.732), whereas for females the rate of reproduction was largely explained by the fluctuation phase (0.848). Furthermore, season contributed considerably to the variance of the rate for each sex (0.514 or 0.456), however its partial correlation coefficients were the smallest among the three variables. Thus the intra-population variables affected the reproductive rates of the two sexes in different ways, and made a greater contribution in explaining the reproductive rates than did the climate variable.

Fig. 3 Changes in the reproductive rate of *A. argenteus*. ● = males, ○ = females. Numbers are sample sizes of less than six. Samples from the live-trapping grid and trap-lines were pooled to increase sample size. Other symbols are as in Fig. 1.

Table 1. Variables and their category scores correlated with reproductive rates of the two sexes in *Apodemus argenteus*.

Variables	Categories	Freq.	Males		Females	
			Scores	Partial cor.*	Scores	Partial cor.*
Population density(/ha)	0-19	10	21.715	0.732	10.631	0.466
	20-39	9	-4.124		-0.965	
	40-59	5	-5.994		-4.390	
	60-79	4	-37.518		-18.920	
Fluctuation Phase	Increase	11	11.508	0.679	6.999	0.848
	Peak	3	-8.171		-28.727	
	Decline	6	-26.822		-39.146	
	Low	8	7.357		30.509	
Season	May-Jun	9	15.246	0.514	12.688	0.456
	Jul-Aug	9	-3.435		-4.827	
	Sep-Nov	10	-10.630		-7.075	
Multiple correlation coefficient (R^2)				0.811		0.838

*Partial correlation coefficient.

Reproductively active mice were trapped until August or September during the decline phase in the high-density years of 1976 and 1978, whereas they were found until October or even November during the increase phase of the low-density years 1977 and 1979 (Fig. 2). In the latter two years, the extended reproductive activity included elements of the following two cohorts. During 1979, for example, the mice that had over-wintered continued to breed until as late as October, and a large number of mice of the year bred between July and October (see also Appendix 1). Similarly, both continuance and participation were found in 1977. In contrast, in the high-density years of 1976 and 1978, over-wintering mice played a large part in reproductive activity by June or July compared with just a few mice of the current year which reproduced by July.

Regarding the relationship between the number of reproductively active mice and the number of potentially reproductive mice (the potential density), the number of reproductively active females increased in proportion to the potential female density at lower density levels, but then decreased at higher potential female densities (Fig. 4). A similar relationship was found for males. The maximum number of reproductively active males in a one-hectare grid was lower than that of reproductively active females: 15 males and 21 females.

Reproductively active mice were found in November 1977, when the mean temperature was 4.0 °C, but not in either October 1976 when the temperature was 10.4 °C, or September 1978, when it was 14.3 °C (ten day means were obtained from meteorological data). Furthermore, reproductively active mice occurred naturally in October 1977 and October 1979, when the mean temperatures were both 11.0 °C. Thus the relationship between autumn temperature and the occurrence of reproductively active mice was contradictory.

Fig. 4 The relationship between the number of reproductively active individuals and of potentially reproductive individual live-trapped *A. argenteus*. ●=males, ○=females.

DISCUSSION

Henttonen *et al.* (1985) used an *s*-value greater than 0.5 and a summer decline to classify populations as cyclic. Furthermore, among *Microtus* populations, Taitt and Krebs (1985) revealed that the amplitude of a cyclic population is usually more than ten-fold. The present study population was found to have an *s*-value of 0.567 in August samples; decline during summer; and have an amplitude of more than 28-fold. According to Henttonen *et al.*'s (1985) and Taitt and Krebs' (1985) criteria, the fluctuation observed during this study may be regarded as cyclic.

The population fluctuations of *A. argenteus* have been commonly found to be rather stable, repeating similar seasonal patterns from year to year (*e.g.*, Fujimaki 1969, Nishikata 1979). The density variation described in this study substantiates the wider variability of population fluctuation, and essentially provides the first example of cyclicity in a population of this species.

Age and body weight at sexual maturity were closely associated with the fluctuation phase. Mice matured sexually as early as 30–60 days of age during the increase and low phases (see Appendix 1). The rapid maturity achieved among the autopsied samples was exactly the same as that under laboratory conditions (Fujimaki and Kuwahata 1985). In contrast, delayed maturity occurred with greater frequency during the peak and decline phases in the

high-density years. Such changes in maturation closely resemble those of arvicoline rodents (Krebs and Myers 1974, Nakata 1989).

Reproductive intensity was found to be both density- and phase-related (Table 1, Figs. 2, 3 and 4). Considering that decreasing rates of reproduction, and delayed maturation, both occurred earlier in high-density years, these changes are thought to suppress reproductive output and thus accelerate population decline. It suggests, therefore, that the principal regulating factors act on the density- and phase-related reproductive activity. Density-related population regulation has also been described by Montgomery (1989) for *Apodemus sylvaticus*, although Murakami (1974) disregarded the significance of density in population regulation of *A. speciosus*.

The limitation of the number of reproductively active mice may be a key attribute causing reproductive inhibition in a given year. Although a temporal reduction in the proportion of reproductively active adult females has been reported at high densities in some *Apodemus* populations (e.g., Watts 1969, Nishikata 1979, Montgomery 1989), the factors limiting the number of reproductively active mice has hardly been demonstrated so far. Ostfeld (1985, 1990) hypothesized that female numbers are self-regulating through female territoriality, and that female numbers partly or wholly determine male numbers in relation to mating success. Although the mechanism was not elucidated in our study population, Ostfeld's (1985, 1990) arvicoline-based hypothesis is as plausible for *A. argenteus* as for *A. sylvaticus* (see Wilson et al. 1993). In comparison with the sympatric *Clethrionomys rufocanus*, reproduction of *A. argenteus* was suppressed at lower density levels with smaller observed maximum number of reproductively active individuals for each sex, though the density amplitudes for both species were almost the same (Nakata 1989). Such interspecific differences in reproductive suppression were also observed among mature females of the sympatric *A. agrarius* and *Microtus arvalis* (Bujalska 1981). These findings suggest that reproduction inhibition is more intense in *Apodemus* than in arvicoline species. In other words, reproduction inhibition probably depends on differences in home range size and in socio-spatial organization between mice and voles.

Geographical variation in the timing of the breeding seasons of *A. speciosus* and *A. argenteus* seems to be related more intimately with temperature than with day length (Murakami 1974, Kimura 1977). According to Nishikata (1979), *A. argenteus*' breeding seasons occur in spring when mean temperatures range from 2.5 to 13 °C, and in autumn when they range from 22.5 to 11.5 °C. In our study population, however, reproduction occurred in autumn 1979 at temperatures well below 11.5 °C and contrarily reproduction did not occur above 11.5 °C in autumn 1978 (Fig. 5). Thus temperature does not always cause the variations in the breeding season of wild *A. argenteus*.

When a population fluctuates in a uniform pattern from year to year, the effect of climate on the breeding season is likely to be well documented. In contrast, when a population exhibits significant multi-annual fluctuations, the effects of ecological factors such as density, seed yield and/or predation are

thought likely to be of importance relative to the proximate factors. Adamczewska (1961) found that an *A. flavicollis* population reproduced either in autumn or in spring-summer, and assumed that the crop of tree seeds exerted an important influence on the duration of the breeding season. Jensen (1982) then found that *A. flavicollis* extended its breeding season into winter in years when trees produced large crops of seeds. Furthermore, *A. semotus*' summer decline in breeding, described by Lin and Shiraishi (1992), is a consequence of large numbers of yearlings entering the population. These findings also discredit the effect of temperature on breeding by *Apodemus* spp.

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Fig. 5 Monthly mean temperature records at Higashikawa Meteorological Station. △ = 1975, ○ = 1976, □ = 1977, ● = 1978, ▼ = 1979.

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Appendix 1. Age distribution of trapped *A. argentus*. Each small rectangle represents one autopsied mouse. ■ = reproductive, ▨ = post-reproductive, □ = immature mouse. Age classes were: I = 25 days old, II = 1-2 months old, III = 2-4 months old, IV = 4-10 months old, and V = 10-18 months old.

Appendix 2. Simple correlation coefficients between reproductive rate (Y), population density (X_1), fluctuation phase (X_2), and season (X_3)

	Males			Females		
	X_1	X_2	X_3	X_1	X_2	X_3
Y	0.746	0.562	0.618	0.637	0.822	0.410
X_1		0.184	0.467		0.386	0.458
X_2			0.178			0.083