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DENSITY DEPENDENCE IN VOLES AND MICE: A COMPARATIVE STUDY

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Abstract. The presence of direct and delayed density dependence in populations of three sympatric rodent species (*Clethrionomys rufocanus*, *Apodemus speciosus*, and *A. argenteus*) in Hokkaido, Japan, was evaluated using triannual census data (spring, summer, and fall) spanning 30 years (1963–1992) on 79 populations for each species. The average abundance and population variability (the *s*-index) generally increased from spring to fall in *C. rufocanus* but were typically highest in summer for the *Apodemus* populations. Based on a comprehensive and comparative review of the population and community biology of the species we made four explicit predictions about the pattern of density dependence: (1) the three species were expected to exhibit socially induced direct density dependence, but (2) this was expected to be weaker in the *Apodemus* species than *C. rufocanus*; (3) delayed density dependence caused by predation was only expected in *C. rufocanus*; thus (4) time series of *C. rufocanus* were expected to reflect a second-order dynamic process, and those of the *Apodemus* species were expected to reflect a first-order process. Dennis and Taper's method based on the Gompertz model was used to test for direct and delayed density dependence and thereby to test the predictions. Direct density dependence was detected in most series (81.0–97.5%) for all three seasons and for all three species. A significant proportion of the time series of *C. rufocanus* (11.8–18.5%) exhibited negative delayed density dependence, whereas detection rates in the two *Apodemus* species did not differ from that expected by chance alone. Autoregressive analyses corroborated this: a second-order process was commonly found to be the appropriate model for the time series of *C. rufocanus*, whereas a first-order process was preferred for most time series of the *Apodemus* species. The high incidence of direct density dependence in all three species and the contrasting results on delayed density dependence between *C. rufocanus* and the *Apodemus* species are discussed with reference to social and trophic interactions. Territoriality, delayed maturation, and reduced pregnancy rates are probable causes for the high incidence of direct density dependence in all species. The more unpredictable variability in *Apodemus* food resource is argued to have a potential to disrupt social regulation and thus to lower the incidence of direct density dependence. A candidate mechanism for the incidence of delayed density dependence is differential vulnerability to predation: the demography of *C. rufocanus* is much more affected by predators than *Apodemus*.

Key words: Apodemus argenteus; Apodemus speciosus; Clethrionomys rufocanus; *density dependence, direct and delayed; Hokkaido (Japan); predation; social regulation.*

Introduction

The analysis of time series of small rodent populations is a commonly used approach for understanding cyclic fluctuations in abundance (Finerty 1980, Hansson and Henttonen 1985, Henttonen et al. 1985, Saitoh 1987, Turchin 1993, Hörnfeldt 1994, Saucy 1994, Bjørnstad et al. 1995, 1996, Stenseth et al. 1996*b*, Saitoh et al. 1997). These fluctuations appear to arise from an interplay between direct and delayed density dependence (see, e.g., Stenseth et al. 1996*a*). Direct density dependence may arise from self-regulation due to social effects on demographic rates (Stenseth et al. 1996*a*), typically resulting from territorial behavior (Bondrup-Nielsen and Karlsson 1985, Madison 1985, for reviews see Cockburn 1988, Ostfeld 1990), and delayed maturation during high densities (Kalela 1957, Bujalska 1970, Abe 1976, Saitoh 1981, Bondrup-Nielsen 1986, Gilbert et al. 1986, Nakata 1989). Generalist predators with switching or migratory response to prey abundance, may also induce direct density dependence (Hassell and May 1986, Bjørnstad et al. 1995). Delayed density dependence may arise as a consequence of tight interactions with specialist predators (Hassell and May 1986, Hanski et al. 1991,

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Bjørnstad et al. 1995, Hanski and Korpimäki 1995, Stenseth et al. 1996*a*, Turchin and Hanski 1997) or food resources (Agrell et al. 1995, Selås 1997).

Saitoh et al. (1997) demonstrate direct density dependence to be common in the grey-sided vole (*Clethrionomys rufocanus*) of northern Hokkaido, Japan; they also found delayed density dependence in several of the populations (see also Stenseth et al. 1996*b*). Here we address the effects of different life history traits and ecological interactions (represented by three different species) on rodent dynamics and patterns of density dependence. For this purpose, we investigate sympatric time series of the grey-sided vole, the large Japanese wood mouse (*Apodemus speciosus*), and the small Japanese wood mouse (*A. argenteus*). Through a review of the biology of these three species we make four predictions about similarities and differences in the incidence of density dependence. These predictions are tested against the data arising from rodent censuses over 30 years (1963–1992) at 79 different locations within an area of 8000 km^2 for which complete records are available triannually for all of the species.

THE SPECIES: NATURAL HISTORY AND PREDICTIONS

In order to understand differences and similarities in the dynamics of the grey-sided vole and the two wood mouse species, we provide a synoptic but rather comprehensive review of the ecology of the three rodent species, as background information.

Population ecology

The grey-sided vole, *C. rufocanus*, is a small-sized (30–40 g), short-tailed (~40% of head and body) rodent. It is widely distributed from Fennoscandia to eastern Asia (see e.g., Stenseth 1985, Stenseth et al. 1996*b*). The small Japanese wood mouse, *A. argenteus*, is endemic to Japan. It is small, weighing just 15–20 g, with a tail longer than its body. *Apodemus speciosus* is another Japanese endemic wood mouse; with a mass of 40–60 g, it is the largest of the three species analyzed here.

The spatio-social organization in *C. rufocanus* is so that breeding females establish an exclusive territory with a size ranging from 200 to 600 m^2 (depending on habitat and individual characteristics; see, e.g., Saitoh 1991). Males do not defend territories (Saitoh 1985). They have overlapping home ranges about twice the size of the female's range (400–1300 m^2; Ota 1984). The spatial organization of *A. speciosus* appears similar to that of the vole but with larger spatial requirements (home range of males: 800–2000 m^2; females: 600–1000 m^2; Kondo 1982, Oka 1992). The overall larger size of home ranges of *A. speciosus* compared to *C. rufocanus* is likely to reflect differences in diet, but also the generally higher mobility of *A. speciosus* (Nakatsu et al. 1991). *Apodemus argenteus* have similar home range size for the two sexes (Oka 1992). Reduction of home range size in a high-density population has been observed in *C. rufocanus* (Saitoh 1991); no similar information exists for *Apodemus.*

The main reproductive season for the three species is from April/May to September/October in Hokkaido (Fujimaki 1969*a*, *b*, 1972, 1973, 1975, Murakami 1974, Kondo and Abe 1978, Kuwahata 1984, Nakata 1987, 1998). The wood mice (the *Apodemus* species) tend to cease reproduction earlier than the vole (*C. rufocanus*, Fujimaki 1969*a*, *b*, Nakata 1998). The litter size is typically 4–7 individuals for all species (Fujimaki 1972, 1973, 1975, 1981, Kondo and Abe 1978, Takada 1983, Kuwahata 1984, Nakata 1984, 1986). Generally, the lifetime of free-ranging individuals is <1 yr (Yoneda 1982). Spring-born individuals attain sexual maturity in the year they are born. Fall-born voles remain reproductively inactive through the winter (Fujimaki 1975, Kuwahata 1984, Ota 1984, Flowerdew 1985).

Density-dependent reduction in reproduction is frequently demonstrated in the grey-sided vole in Hokkaido (Abe 1976, Saitoh 1981, 1990, Kawata 1987, Nakata 1989), and is believed to occur in both species of *Apodemus* (Kondo and Abe 1978, Nakata 1998). The main mechanism behind the reduction is a delay in maturation of juveniles (Saitoh 1981, 1990) and increased pregnancy failure in adult females (Kawata 1987, Nakata 1989). On this basis we obtain **Prediction 1**: *All species exhibit socially regulated reproduction and spacing. We predict these mechanisms to be sufficiently strong to induce significant density dependence in the growth of populations.*

Habitat and diet

The three species live sympatrically in indigenous forests as well as forest plantations in Hokkaido (Ota 1984, Abe 1986). Both species of *Apodemus* are typical forest species, while *C. rufocanus* is common in both forests and open habitats (Ota 1968, 1984). A dominant understory plant in these forests is the bamboo grass (*Sasa* spp.; Wada 1993). Vegetation cover and density of understory vegetation is high from mid-June to October (Yoneda 1983). The snow-rich period is associated with relatively high survival in *A. speciosus* (Kondo 1980) and *C. rufocanus* (Dewa 1975).

All three species have a wide diet in Hokkaido (Ota 1984). The main dietary items are seeds, green plants, and invertebrates (mainly insects). *Clethrionomys rufocanus* mainly feeds on green plants, which usually occupy >50% of its diet (Ota et al. 1959, Ota 1984). Leaves and shoots of bamboo grass dominate the food during winter, while various forbs and grasses are eaten during summer (Ota 1984). The diet is, thus, predominantly folivorous and subdominantly granivorous. The *Apodemus* species prefer seeds and invertebrates to forbs and grasses (Ota et al. 1959). There are no reports that green plants dominate over other food items in their diets in Hokkaido. *Apodemus argenteus* generally prefers smaller seeds and insects as compared with *A. speciosus* (Ota et al. 1959). The diets of the wood mice are thus predominantly granivorous and subdominantly animalistic. Caching behavior is well developed in *Apodemus* (Miyaki and Kikuzawa 1988, Soné and Kohno 1996). The three species, thus, appear to follow typical *Clethrionomys* and *Apodemus* dietary patterns (Hansson 1985*a*, *b*).

Seeds are known to be depleted by rodents (Hansson 1985*a*, *b*, Jensen 1985, Gurnell 1993), and the availability varies between years due to masting (Jensen 1982, King 1983, Wada 1993). The bamboo grass (*Sasa* spp.) as well as many of the tree species (such as *Quercus* and *Acer*) are masting species (Wada 1993). Insect abundance is also likely to be more variable than forbs and grasses. Superabundance of food has been documented to alter or disrupt the spatial organization of both voles and wood mice (Ims 1987, Montgomery et al. 1991). An unpredictable seed supply has been suggested to be of overriding importance in wood mouse dynamics (Flowerdew 1985). The interaction between social organization and resource supply has previously been speculated to introduce lower levels (shorter periods) of density dependence in wood mouse than in voles (Mallorie and Flowerdew 1994). On this basis we obtain **Prediction 2**: *The wood mice feed on more variable resources than the voles. This may disrupt the social regulation so that less of the potential regulatory mechanisms are manifested in populations of the wood mice. We predict direct density dependence to be weaker in the wood mice than the voles.*

Community interactions

Although sympatric, there is no evidence of competition between *Clethrionomys* and *Apodemus* (Abe 1986). Congeneric interactions are, however, thought to occur (Ota 1968, Abe 1986, Nakata 1995). A potential competitor of *C. rufocanus*, the northern red-backed vole (*C. rutilus*), is not common in northern Hokkaido (Ota 1968, Saitoh and Nakatsu 1997) and is thus likely to be relatively unimportant. *Apodemus speciosus* is dominant to *A. argenteus* (Sekijima and Soné 1994). Since other rodents are rare in the study areas, their influences on the three species of main concern in this paper are likely to be negligible.

Three mustelid species are important predators of small rodents in Hokkaido (in order of importance): *Mustela nivalis*, *M. itatsi*, and *M. vison*. *Martes zibellina* and *Mustela erminea* are also present but there is little information about them. The red fox (*Vulpes vulpes*), two owls (*Strix uralensis, Asio otus*), and four species of snakes (*Elaphe climacophora, E. conspicillata, E. quadrivirgata* and *Agkistrodon blomhoffii*) are also important predators of rodents. The proportion of *C. rufocanus* in the diet of the predators is invariably much higher than that of *Apodemus.* The reported percentages of occurrence in droppings or stomach contents of the two genera are: 30.7 vs. 0.3% in *M. vison* (Uraguchi et al. 1987), 30–60 vs. 1% in *V. vulpes* (Abe 1975, Misawa 1979, Kondo et al. 1986), 25–50 vs. 5–25% in *S. uralensis* (Matsuoka 1977, Yoneda et al. 1979), and 98–100 vs. 0.8–3.7% in *A. otus* (Matsuoka 1974). Actual mortality factors of the rodents themselves are scarcely known in Hokkaido. Yoneda (1979) calculated that mammalian predators accounted for 30–65% of deaths of the grey-sided vole. This agrees well with more detailed studies of *Clethrionomys* in northern Europe (Norrdahl and Korpimäki 1995). A conspicuously lower vulnerability of the wood mouse to predation has been attributed to its greater mobility (King 1985). Thus, the grey-sided vole appears to be tightly interacting with predators, whereas the Japanese wood mouse does not. Differential predation on the grey-sided vole by a generalist predator with switching, such as the fox, will induce direct density dependence (Hassell and May 1986, Bjørnstad et al. 1995) and thus accentuate Prediction 2. Specialist predators such as the mustelids, in contrast, are believed to participate in coupled dynamics with their prey. Such predator–prey interactions induce delayed density dependence (Hassell and May 1986, Bjørnstad et al. 1995, Stenseth et al. 1996*a*). On this basis we obtain **Prediction 3**: *The vole is more prone to predation by fox and mustelids. We predict the occurrence of delayed density dependence to be higher in the voles than in the wood mice.* **Prediction 4**: *The vole–predator interaction may induce second-order feedback in the dynamics of the voles. We predict time series of the voles to reflect a second-order process and time series of the wood mice to reflect a first-order process.*

METHODS

The study area and census

Hokkaido is the northernmost island (41°25′–45°31′ N, 139°46′–145°49′ E) of Japan and covers 78 073 km^2. The Forestry Agency of the Japanese Government has since 1954 carried out censuses of vole populations for management purposes at approximately 1000 sampling locations in forests all over Hokkaido. The forests managed by the Forestry Agency cover 28 300 km^2 (21 500 km^2 natural forests and 6800 km^2 planted forests; 1990 figures). These forests were in 1990 managed by 81 District Offices. Every District Office is divided into several Ranger Offices. The censuses were carried out by the individual Ranger Office, which also represents our basic unit of analysis. The data analyzed in this paper derive from the northern part of the island covering an area corresponding to ~10% of the island's total area.

Northern Hokkaido is a cold and snow-rich region. Snow usually covers the ground from December to April (SDMO 1991, 1992). Average monthly temperature is usually lowest in February (from −5°C to −8°C) and highest in August (from 18°C to 21°C). Generally the growing season for plants is from April to October, which corresponds to the breeding season of rodents. Total precipitation in a year is from 1000 to 1300 mm. Although precipitation in fall and winter is higher than in other seasons, there is no seasonal drought influencing the breeding of rodents.

Trapping was carried out three times a year (spring [May/June], summer [July/August], and fall [September/October]) on 0.5 ha (50 × 100 m) grids, where 50 snap traps with bait (a peanut or a pumpkin seed) were set at 10-m intervals for five or three nights and the traps were examined every morning. Each Ranger Office censused 2–6 separate grids. Census grids were located in fixed preselected habitats (planted forest and natural forests neighboring a planted forest), which together constitute a unit, for several years, though census grids were sometimes relocated within the area of a given Ranger Office. Samples from the natural forests were analyzed, since this represented the indigenous habitat of the species.

In addition to the three target species in this study, the northern red-backed vole (*C. rutilus*), the dark red-backed vole *(C. rex),* the Korean wood mouse (*Apodemus peninsulae*), and several shrews (*Sorex* spp.) are found within the region and are occasionally encountered in the censuses. Personnel of the Forestry Agency identified the specimens. *Clethrionomys* and *Apodemus* are easily distinguished from other rodents and from each other. Identifying species within a genus may, however, be difficult. Since the abundance of *C. rutilus* and *C. rex* is generally low in Hokkaido (Ota 1984), the impact of misclassification is likely to be small. Young individuals of *A. speciosus* may sometimes be misidentified as *A. argenteus.*

From 1963 to 1976 traps were set for five nights. From 1977 to 1992 a 3-d trapping scheme was adopted. Census data for the first 14 yr were transformed to three-night equivalents using the regression of the three-night (y) on the five-night (x) captures ($y = 0.681x + 0.077$, $r^2 = 0.941$ for *C. rufocanus*; $y = 0.645x$, $r^2 = 0.918$ for *A. argenteus*; $y = 0.645x$, $r^2 = 0.911$ for *A. speciosus*); when the five-night count was zero, the three-night equivalent was also set to zero. Thus the total number of captured voles per 150 trap nights was adopted as the numerical index of abundance at each site (Ranger Office). These transformations were determined from a subset of the data for which daily captures were recorded (see Saitoh et al. 1997). Although this introduced some unavoidable uncertainty in our analyses, this should not affect the results strongly. The fall records for the *Apodemus* species in the years 1971 and 1974 were unavailable. These records were therefore treated as missing values in the analyses.

More than 120 Ranger Offices carried out censuses every year in this region (the number of ranger offices varied slightly from year to year). Seventy-nine of the Ranger Offices provided complete triannual time series for the three species for 30 years (except for the fall records for the *Apodemus* species in the years 1971 and 1974). Averaged census values for three nights over all grids within natural forests in a Ranger Office were used as the index of abundance. In order to avoid numerical problems associated with zeros, a fixed number of unity was added to all observed abundance indices.

For comparison with previous studies, we calculated the *s*-indices (i.e., the standard deviation of the $\log_{10}$[abundance + 1]) as an index of variability in abundance for each population (Stenseth and Framstad 1980, Henttonen et al. 1985).

We also calculated the within-site correlation between the time series for different species and the between-site correlation within species to assess the regional and local interdependence between species (see also Bjørnstad et al. 1999). A bootstrap technique was used to generate confidence intervals for these correlations.

Testing for density dependence

The predictions that arise from the comparative ecology of the species pertain to the pattern of density dependence in the time series. Predictions 1 and 2 relate to the strength and occurrence of direct density dependence, Prediction 3 relates to delayed density dependence, and Prediction 4 relates to the order of the processes generating the series. Statistical methodology exists to test each of these predictions.

Denoting the abundance index at time t by N_t and writing the log-transformed abundance as X_t [$=\ln(N_t + 1)$], density-independent population growth is represented by $R_t = X_t - X_{t-1} = e_t$, where e_t is a sequence of independent, identically distributed random variables. In contrast to this null model, direct density-dependent population growth is represented by $R_t = F(N_{t-1}) + e_t$, where $F(N_{t-1})$ is some, typically monotonically, decreasing function. Two different models are commonly used to describe density dependence; the Gompertz population model (e.g., Royama 1992) where the density dependence is a log-linear function of abundance (i.e., $R_t = a - bX_{t-1}$), and the Ricker population model (Ricker 1954) where the dependence is a linear function of abundance (i.e., $R_t = a - bN_{t-1}$).

To distinguish between these functional relationships between the population growth rate and the abundance, we plot R_t against X_{t-1} and N_{t-1} (Fig. 1a, b). As can be seen, the data suggest log-linearity of the kind assumed in the Gompertz model in all three species. Thus, we employed the Gompertz model in the tests (see also Saitoh et al. 1997). To test for direct density dependence we employed the bootstrap method of Dennis and Taper (1994) using the Gompertz model as the alternative hypothesis (Saitoh et al. 1997). The regression of R_t on X_{t-1} is, thus, investigated (see also Kemp and Dennis 1993, Wolda and Dennis 1993). The test statistic is compared with its null distribution based on 10 000 bootstrap time series under the density-independent null hypothesis. Rejection of the null hypothesis was done at a nominal 5% level using a one-tailed test.

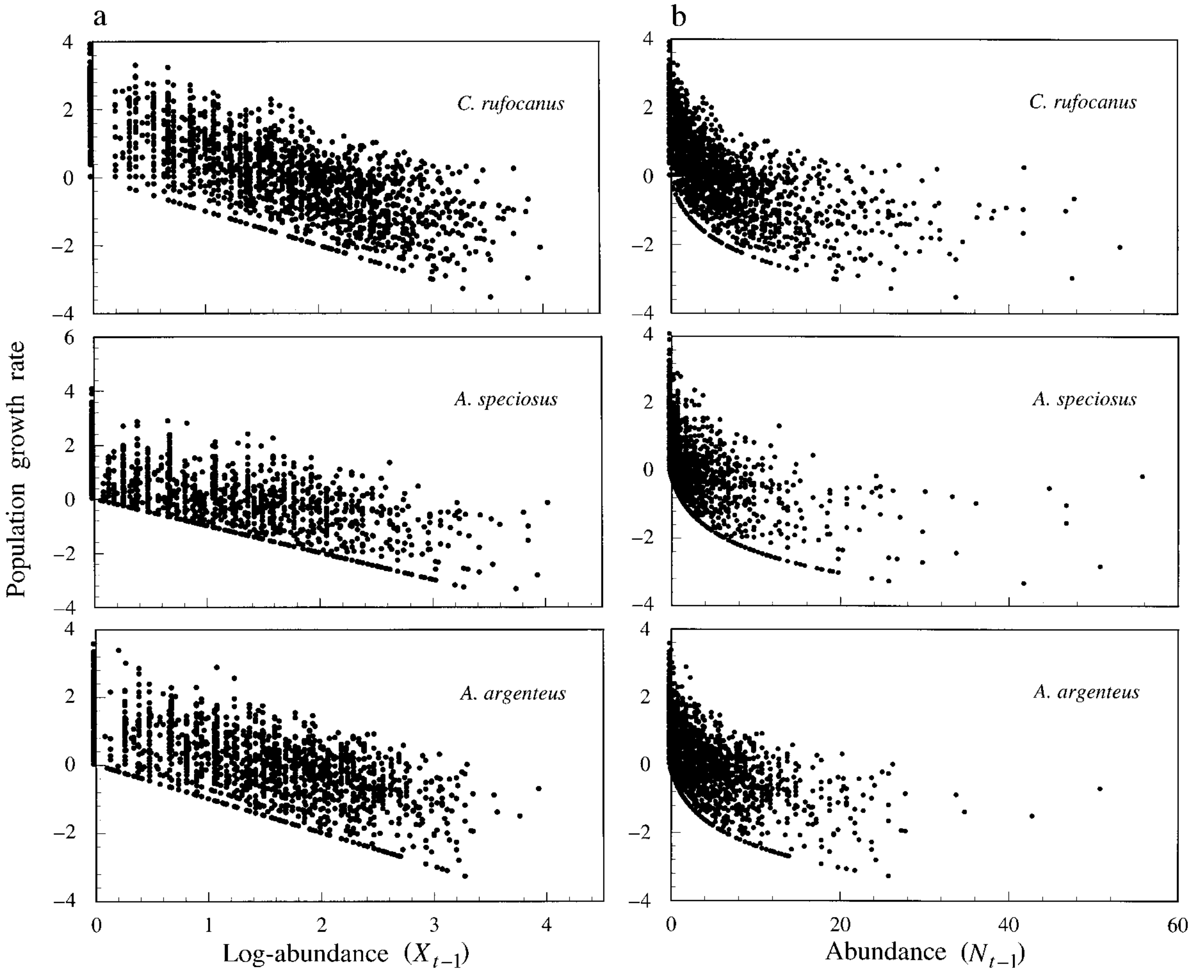

FIG. 1. Relationship between the population growth rate ($R_t = X_t - X_{t-1}$) and abundance index (a) using $X_t = \ln(N_t + 1)$ as the abscissa and (b) using N_t as the abscissa, for *C. rufocanus*, *A. speciosus*, and *A. argenteus* based on summer data.

When testing for delayed density dependence, effects of direct density dependence must be partialed out of the relationship between R_t and X_{t-2} both in the test statistic and in its null distribution. We therefore use the partial correlation coefficient as the test statistic (Holyoak 1994, Saitoh et al. 1997). We use 10 000 randomized time series to generate a null distribution for the test statistic. Rejection of the null hypothesis was done at a nominal 5% level using a two-tailed test (two-tailed because both negative and positive delayed density dependence can occur).

A population experiencing significant delayed density dependence will have a trajectory governed by a second-order process (Royama 1992, Bjørnstad et al. 1995, Stenseth et al. 1996*a*, *b*). Delayed density dependence may therefore also be assessed by testing whether the order of the process governing the time series is one or two. Under the Gompertz model this can be done by comparing the AIC$_c$-value of the first- and the second-order autoregressive model as applied to log-transformed data (Hurvich and Tsai 1989, Bjørnstad et al. 1995). A difference of unity in AIC$_c$ may be considered insignificant.

Nonstationary in the form of trends in the mean is nontrivial in most types of time series analyses because a trend in the mean is often associated with a trend in the variance. Detrending the mean by subtracting a trend will not alleviate the problem with the nonconstant variance. The tests for direct density dependence are generally believed to be robust towards trends in the mean (Wolda and Dennis 1993, Dennis and Taper 1994; but see Holyoak and Baillie 1996). In our experience, the test for delayed density dependence is very sensitive to nonstationarities (Saitoh et al. 1997). In the present data sets the majority of time series did not entertain any significant trends, but some did. We therefore tabulate the results separately for the series in which drift is suspected.

RESULTS

General features

Average abundance and its variability (*s*-index) generally increased from spring to fall in *C. rufocanus*,

TABLE 1. Averages (with 1 SE, in parentheses) over sites for both average abundance (over all years) and *s*-index for the three rodent species in the three seasons.

Variable	*C. rufocanus*	*A. speciosus*	*A. argenteus*
Average abundance			
Spring	2.56 (0.10)	0.97 (0.07)	2.23 (0.13)
Summer	5.67 (0.26)	2.62 (0.18)	3.89 (0.18)
Fall	8.20 (0.36)	3.06 (0.17)	4.08 (0.19)
s-index			
Spring	0.297 (0.005)	0.245 (0.008)	0.305 (0.007)
Summer	0.379 (0.006)	0.346 (0.010)	0.360 (0.007)
Fall	0.395 (0.007)	0.364 (0.008)	0.352 (0.006)

whereas they were sometimes highest in summer in the wood mice (Table 1). There were only three time series (3.8%) for *C. rufocanus* in which average abundance was higher in summer than in fall. For the *s*-indices the number of series in which the value was higher in summer than in fall was 27 (34.2%). The corresponding number for *A. speciosus* was 19 (24.1%) for average abundance and 29 (36.7%) for *s*-index. The tendency of summer maxima was greatest in *A. argenteus*: 28 (35.4%) for average abundance and 45 (57.0%) for *s*-index. The increase in average abundance from spring to summer was not different from that from summer to fall in *C. rufocanus* (Wilcoxon matched-pairs signed-ranks test, $Z = -1.04$, $P > 0.3$), whereas it was significantly smaller from summer to fall than from spring to summer in the two wood mouse species ($Z = -5.45$, $P < 0.01$ for *A. speciosus*; $Z = -6.70$, $P < 0.01$ for *A. argenteus*). The *s*-index in fall was significantly higher than in summer for *C. rufocanus* ($Z = -2.92$, $P < 0.01$) and for *A. speciosus* ($Z = -3.00$, $P < 0.003$), but not for *A. argenteus* ($Z = -1.16$, $P > 0.09$).

Clethrionomys rufocanus is the most abundant species in the study areas, particularly in fall. *Clethrionomys rufocanus* dominated numerically over the wood mice in 87.3% of time series in fall. The corresponding percentages for spring and for summer were 57.0% and 69.6%.

The *s*-indices for *C. rufocanus* were generally higher than those for the wood mice in summer and in fall (Wilcoxon matched-pairs signed-ranks test, summer: $Z = -2.86$, $P < 0.01$; fall: $Z = -2.84$, $P < 0.01$ between *C. rufocanus* and *A. speciosus*; summer: $Z = -2.45$, $P = 0.01$; fall: $Z = -4.64$, $P < 0.01$ between *C. rufocanus* and *A. argenteus*). There was no difference in *s*-indices for spring between *C. rufocanus* and *A. argenteus.* The *s*-indices for *A. speciosus* in spring were significantly lower than those for the other species ($Z = -5.01$, $P < 0.01$ between *C. rufocanus* and *A. speciosus*; $Z = -5.92$, $P < 0.01$ between *C. rufocanus* and *A. argenteus*). *Clethrionomys rufocanus* is, thus, the most variable of the three species.

Cyclic dynamics have been reported in *C. rufocanus* in Hokkaido (Bjørnstad et al. 1996, Stenseth et al. 1996*b*); no similar observation has been reported for the wood mice. A cyclic population of *C. rufocanus* is shown in Fig. 2a. This population oscillated with a 3- to 5-yr interval with high amplitude at a medium abundance (average abundance = 5.77, *s*-index = 0.45; based on summer data). The corresponding populations of the two *Apodemus* species are also shown in Fig. 2b, c. The population of *A. speciosus* was rather stable at low abundance (average abundance = 2.09, *s*-index = 0.36; based on summer data), while the one of *A. argenteus* varied at high abundance (average abundance = 5.72, *s*-index = 0.41; based on summer data). The Spearman rank correlations between these specific series are insignificant ($P = 0.09$–0.19) and range from 0.24 to 0.32.

The average correlation between the sympatric time series of the three rodent species, and the average correlation between the allopatric time series of each of the three species are given in Table 2. As can be seen the within-site synchrony between the species is positive, but generally of the same magnitudes as the region-wide intraspecific synchrony at around 0.2 (see Bjørnstad et al. 1999).

Density dependence

The bootstrap test of Dennis and Taper (1994) assuming log-linear density dependence (the Gompertz model) identified significant direct density dependence in the majority of time series for all three species and seasons (Table 3). The proportion of stations for which the null hypothesis was rejected (at the nominal 5%-level) is 0.94–0.97 in *C. rufocanus* (*Cr*; average across all seasons: 0.96), 0.85–0.87 in *A. speciosus* (*As*; average across all seasons: 0.86), and 0.76–0.91 in *A. argenteus* (*Aa*; average across all seasons: 0.85). Assuming independence between the stations (i.e., $n = 79$ in the test) and binomial variance, the rejection rate for the vole series was significantly higher than that for the wood mice (chi-square test, summer: *Cr* vs. *As*, $P = 0.02$; *Cr* vs. *As*, $P < 0.01$; *As* vs. *Aa*, $P = 0.66$).

The detection rates were generally lower in time series with trends in abundance. As pointed out above, the trends could influence the detectability of density dependence. However, even when comparing the detection rates in time series without trends, having similar levels of variability (*s*-indices from 0.3 to 0.45 in summer data), the results persisted (rejection frequency: 100% for *C. rufocanus* and 85.4% for each *Apodemus* species; chi-square test: *Cr* vs. *As*, $P < 0.01$; *Cr* vs. *As*, $P < 0.01$; *As* vs. *Aa*, $P = 0.68$).

The tests for delayed density dependence (1-yr lag) are summarized in Table 4. The extended bootstrap test using the Gompertz model detected negative delayed density dependence in a significant proportion of time series without trends for *C. rufocanus* in all three seasons. The rejection rate in both wood mice species did not differ from that expected from chance alone due to multiple testing. Assuming independence between the stations and binomial variance, the incidence of

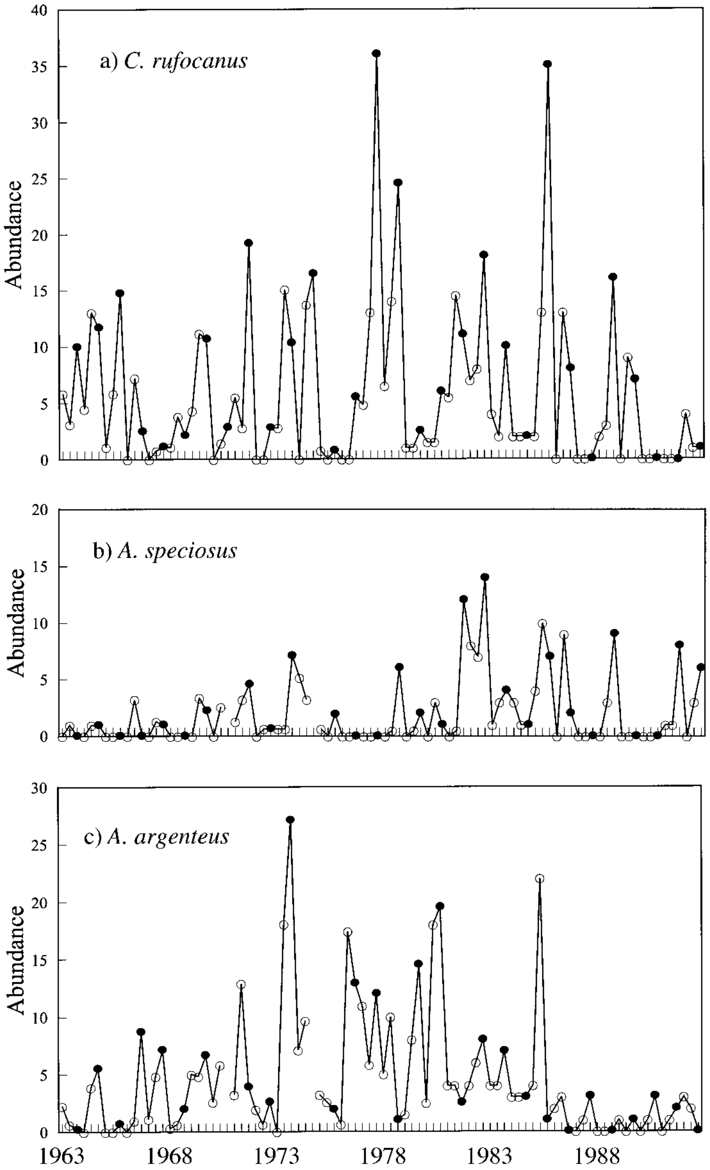

FIG. 2. Examples of density fluctuation pattern in a study site (Panke Ranger Office), in which the populations showed the typical density-dependence patterns: (a) the population of *C. rufocanus* exhibited strong direct density-dependence with negative delayed density dependence, and the populations of (b) *A. speciosus* and (c) *A. argenteus* exhibited strong direct density dependence without any significant delayed density dependence. Though this pattern was observed in five sites, the site in which the population of *C. rufocanus* exhibited the strongest delayed density-dependence was chosen. ○, spring or summer abundance; ●, fall abundance.

negative delayed density dependence was significantly higher in the vole series than in the wood mice series (chi-square test, summer: *Cr* vs. *As*, $P = 0.02$; *Cr* vs. *As*, $P < 0.01$; *As* vs. *Aa*, $P = 0.32$). Since the increase in detection rates for *C. rufocanus* from spring to fall may correlate with an increase in variability, we compared the detection rates for time series without trends, having similar *s*-indices between *C. rufocanus* and the wood mice. The detection rate of negative delayed density dependence was still significantly high for *C. rufocanus* (14.6%) and no greater than that expected by chance alone for the wood mice (2.4% for *A. speciosus* and 0.0% for *A. argenteus*).

The autoregressive analyses showed that a higher proportion of the series of the vole was consistent with a second-order process, and that a lower proportion of the wood mice series was *not* consistent with a first-order process. The percentage of time series that was consistent with a second-order process was 37–43% for *C. rufocanus*, 25–30% for *A. speciosus*, and 13–34% for *A. argenteus.* The percentage of time series that was *not* consistent with a first-order process was 16–25% for *C. rufocanus,* 5–16% for *A. speciosus,* and 5–6% for *A. argenteus.* The differences were, however, only statistically significant for the fall censuses and not for the summer and spring censuses.

Characterization of the density dependence

To characterize the species, we plotted the partial correlation coefficient between the population growth and the log density and the log density in the preceding year (Fig. 3). As can be seen, populations of *C. rufo-*

TABLE 2. Averages of Spearman rank correlation between the time series of the three rodent species.

Species	*C. rufocanus*	*A. speciosus*	*A. argenteus*
C. rufocanus			
Spring	0.22 (0.20–0.26)		
Summer	0.29 (0.27–0.34)		
Fall	0.37 (0.34–0.41)		
A. speciosus			
Spring	0.18 (0.14–0.23)	0.09 (0.07–0.13)	
Summer	0.22 (0.18–0.26)	0.16 (0.13–0.22)	
Fall	0.21 (0.17–0.25)	0.19 (0.16–0.25)	
A. argenteus			
Spring	0.22 (0.18–0.26)	0.09 (0.05–0.14)	0.18 (0.15–0.23)
Summer	0.22 (0.18–0.26)	0.18 (0.12–0.23)	0.23 (0.19–0.28)
Fall	0.14 (0.10–0.19)	0.14 (0.09–0.19)	0.16 (0.14–0.20)

Notes: The diagonal represents the average (and the 95% confidence interval, in parentheses) of the correlation matrix of the 79 allopatric time series of the three species (the region-wide synchrony). The average correlation (and the 95% confidence interval) between the species is the mean across the 79 sympatric species (the within-site interspecific synchrony). The confidence intervals for the correlations are calculated using the bootstrap by sampling with replacement among the stations (1000 bootstrap iterations; Efron and Tibshirani 1986; see also Bjørnstad et al. 1999).

canus exhibited on average stronger (negative) delayed density dependence than those of the *Apodemus* species, even though there was some overlap.

The averages of the partial correlation coefficient (1 SE) for direct and for delayed effects were −0.70 (0.01) and −0.16 (0.02) for *C. rufocanus.* The averages (1 SE) for wood mice species were very similar to each other; −0.62 (0.01) and 0.07 (0.02) for *A. speciosus,* and −0.64 (0.01) and 0.10 (0.02) for *A. argenteus.* Both wood mice species exhibited significantly less negative partial correlation coefficients than the vole (assuming independence between stations, Wilcoxon matched-pairs signed-ranks test, $Z = -2.90$, $P < 0.01$ for *A. speciosus*, $Z = -3.7$, $P < 0.01$ for *A. argenteus* for direct effects; $Z = -5.43$, $P < 0.01$ for *A. speciosus,* $Z = -5.64$, $P < 0.01$ for *A. argenteus* for delayed effects).

In the wood mice species, populations with strong direct density dependence are more likely to exhibit positive delayed density dependence. Under strong direct density effects, the positive delayed density dependence could spuriously appear, if direct effect was not completely partialed out (see Saitoh et al. 1997). In contrast, the significant proportion of *C. rufocanus* populations exhibited negative delayed density dependence even in the presence of strong direct density dependence.

DISCUSSION

Direct density dependence was found in most time series for all three species in the three seasons; the detection rate was particularly high in *C. rufocanus.* Delayed density dependence was found only in *C. rufocanus,* except for one time series for *A. speciosus* in summer.

The breeding season of *C. rufocanus* ranges from April to October, while the *Apodemus* species tend to cease their breeding earlier than *C. rufocanus* in Hokkaido (Fujimaki 1969*a*, *b*, Nakata 1998). This is reflected in the higher population variability in fall for *C. rufocanus* than that for the *Apodemus* species. The variability of abundance influences the test power for density dependence (Dennis and Taper 1994). The highest detection rate for delayed density dependence in times series of *C. rufocanus* in fall may partly reflect the higher variability of these populations in fall. Since

TABLE 3. Results from the testing for direct density dependence between yearly data using Dennis and Taper (1994) test based on the Gompertz model.

	C. rufocanus			*A. speciosus*			*A. argenteus*		
Tests	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall
Without trends									
Total	68	62	65	58	61	54	61	57	63
Significant	68 (100%)	62 (100%)	65 (100%)	53 (91.4%)	53 (86.9%)	49 (90.7%)	49 (80.3%)	47 (82.5%)	59 (93.7%)
With trends									
Total	11	17	14	21	18	25	18	22	16
Significant	6 (54.5%)	15 (88.2%)	12 (85.7%)	14 (66.7%)	15 (83.3%)	20 (80.0%)	15 (83.3%)	18 (81.8%)	13 (81.3%)

Notes: The number of time series that exhibited significant density dependence are shown for populations without trends and with trends. The length of time series was 30 yr for spring and summer, whereas it was 28 yr for fall (due to two missing years).

TABLE 4. Results from the testing for delayed density dependence between yearly data using the extended Dennis and Taper (1994) test based on the Gompertz model for the three species for three seasons.

	C. rufocanus			*A. speciosus*			*A. argenteus*		
Tests	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall
Without trends									
Total	68	62	65	58	61	54	61	57	63
Negative	8	9	12	0	1	0	0	0	0
	(11.8%)	(14.5%)	(18.5%)	(0%)	(1.6%)	(0%)	(0%)	(0%)	(0%)
Positive	1	0	1	2	2	3	0	1	2
	(1.5%)	(0%)	(1.5%)	(3.4%)	(3.3%)	(5.6%)	(0%)	(1.8%)	(3.2%)
With trends									
Total	11	17	14	21	18	25	18	22	16
Negative	0	0	0	0	0	0	0	0	0
	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)
Positive	0	1	1	1	5	5	1	3	2
	(0%)	(5.9%)	(7.1%)	(4.8%)	(33.3%)	(20.0%)	(5.6%)	(13.6%)	(12.5%)

Note: The number of time series that exhibited density dependence are shown separately for populations without trends and with trends. The length of time series was 30 yr for spring and summer, whereas it was 28 yr for fall (due to two missing years).

these effects should be taken into consideration for comparing the results between *C. rufocanus* and the *Apodemus* species, we chose to be conservative and relied on the results obtained from the time series in summer.

On the basis of our survey of the biology of the three species, we arrived at four exploratory predictions about the differential pattern of density dependence in the three species. Our results strongly support Predictions 1 and 3 pertaining to the high incidence of direct density dependence in these small rodents and the relatively higher incidence of delayed density dependence in the vole and give good support to Prediction 2 about the relative higher incidence of direct density dependence in voles and Prediction 4 about the order of the dynamics of the wood mice and the vole.

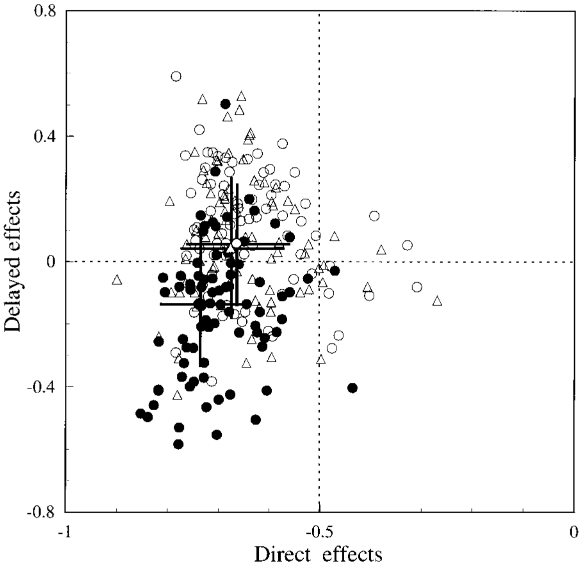

FIG. 3. Relationship between partial correlation coefficient for direct density effects against partial correlation coefficient for delayed density effects. ●, *C. rufocanus*; ○, *A. speciosus*; △, *A. argenteus.* Symbols with bars represent the average with 2 SD.

Previously, we have studied the population dynamics of *C. rufocanus* from northern Hokkaido in detail (based on a subset of the present data; Bjørnstad et al. 1996, Stenseth et al. 1996*b*, Saitoh et al. 1997). We have demonstrated that the abundance of the vole is governed by both direct and delayed density dependence (Stenseth et al. 1996*b*, Saitoh et al. 1997). A regionally changing pattern of delayed density dependence gives rise to multiannual cyclic dynamics in western and inland populations (Bjørnstad et al. 1996, Stenseth et al. 1996*b*). Regional transitions in the pattern of cyclicity and density dependence are a feature of the population dynamics of microtine rodents elsewhere (Hansson and Henttonen 1985, 1988, Hanski et al. 1991, Stenseth and Ims 1993, Bjørnstad et al. 1995). Varying influences of direct and delayed density dependence thus appear to be quite general in microtines (Turchin 1993, Hörnfeldt 1994, Saucy 1994, Bjørnstad et al. 1995, Stenseth et al. 1996*a*, *b*). No similar pattern has earlier been reported for wood mice. Rather, the European species appear to have dynamics dominated by irregular outbreaks related to years of abundant seed production (Flowerdew 1985, see also Montgomery 1989*a*, *b*).

The comparison of density dependency between *Clethrionomys* and *Apodemus* provides a basis for speculating on the underlying mechanisms creating the observed patterns. Microtine rodents, and in particular the genus *Clethrionomys*, show strong spatial and social organization (see Bondrup-Nielsen and Karlsson 1985, Bujalska 1985, Gipps 1985 for review). Female grey-sided voles are often seen to establish territories as well as to exhibit delayed maturation at high densities, both of which may cause direct density dependence in the population growth rate. In Hokkaido territoriality in the grey-sided vole is commonly observed and maturation rates and pregnancy rates are reduced at high densities (see *The species*). Although available information is insufficient for the two species of wood mice, spatial exclusiveness of breeding females and density-dependent reduction in reproduction have been suggested in both. Whatever the mechanisms underlying the density dependence in the vole and the wood mice, they are clearly sufficiently strong to exert a regulatory influence on the dynamics (see also Stenseth et al. 1996*a*, *b*, Saitoh et al. 1997).

For European woodland rodents, weaker (direct) density dependence in *Apodemus* compared to *Clethrionomys* is thought to be due to differences in diet and dynamics of food renewal (Flowerdew 1985, Mallorie and Flowerdew 1994). *Apodemus* greatly depends on seeds. Masting of seeds improves reproduction and survival of *Apodemus* (Montgomery et al. 1991, see Wilson et al. 1993 for review) and often causes a high density of *Apodemus* populations with less territoriality (Jensen 1982, Miguchi 1988, Mallorie and Flowerdew 1994; see also Ims 1987).When populations of *Apodemus* are influenced by environmental factors, in addition to the density dependence, social regulation may be disrupted so that less of the potential regulatory mechanisms are manifested in the dynamics. We believe that we see the traces of this in the present data.

In addition to the diet, the other ecologically important difference between *C. rufocanus* and the *Apodemus* species in Hokkaido is predation; *C. rufocanus* is selectively taken. Predation by generalists is generally assumed to increase in response to rodent density without lag, while specialist predators are thought to track rodent densities with a time delay (Hassell and May 1986, Bjørnstad et al. 1995, Hanski and Korpimäki 1995, Stenseth et al. 1996*a*). Such predator–prey interaction is the dominant explanation to explain the cyclicity and the biogeographic transitions in dynamics in Fennoscandia (Hansson and Henttonen 1985, 1988, Henttonen et al. 1985, Hanski et al. 1991). The predator–prey community in northern Fennoscandia is dominated by specialist predators with few alternative prey species, whereas a multitude of alternative prey for a variety of generalist predators exists in Hokkaido (Henttonen et al. 1992). Thus, the present result that most time series showed direct density dependence may also be consistent with a generalist predator–prey model. However, the strong direct density dependence was also detected in the *Apodemus* populations, which are only slightly affected by predators but have a similar spatiosocial system to *C. rufocanus.* We emphasize, therefore, that self-regulation through spacing behavior and social interactions between individuals is the most likely explanation of direct density dependence.

For delayed density dependence specialist predators may be a most plausible candidate (Hassell and May 1986, Bjørnstad et al. 1995, Stenseth et al. 1996*a*). Many predators specialize on *C. rufocanus* in Hokkaido; even the red fox, which is a typical generalist predator, selectively takes *C. rufocanus* (Yoneda 1979). This fact corresponds well to the present contrastive results that the significant proportion of *C. rufocanus* populations exhibited delayed density dependence but almost none in the *Apodemus* species. An alternative source of delays in regulation is in rodent–vegetation interactions (Agrell et al. 1995, Selås 1997). Selås' (1997) mast depression hypothesis provides a direct method for delays and deserves future scrutiny. The role of snow cover in interaction with predation is a future issue that needs clarification (Hansson 1987). Seasonality appears to be a subtle modifier of dynamics in both Fennoscandia (Hansson and Henttonen 1985, Hansson 1987) and Hokkaido (Bjørnstad et al. 1996, Stenseth et al. 1996*b*).

We believe that the comparative approach taken in this study is rewarding in the sense of being able to facilitate ecologically relevant inference from time series analysis. Besides contributing to the field of comparative population dynamics, we hope that this study has developed a platform for future experimental studies.

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