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Citation	Population Ecology, 49(3), 249-256 https://doi.org/10.1007/s10144-007-0041-9
Issue Date	2007-07
Doc URL	http://hdl.handle.net/2115/33872
Rights	The original publication is available at www.springerlink.com
Type	article (author version)
File Information	Saitoh_et_al_2007.pdf



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Effects of acorn masting on population dynamics of three forest-dwelling rodent species in Hokkaido, Japan

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Abstract

The effects of acorn (*Quercus crispula*) abundance on the population dynamics of three rodent species (*Apodemus speciosus*, *A. argenteus*, and *Clethrionomys rufocanus*) were analyzed using time series data (1992–2006). The data were obtained in a forest in northern Hokkaido, Japan, by live trapping rodents and directly counting acorns on the ground. *Apodemus speciosus* generally increased in abundance following acorn masting. However, the clear effect of acorn abundance was not detected for the other two rodent species. Acorns of *Q. crispula* contain tannins, which potentially have detrimental effects on herbivores. *Apodemus speciosus* may reduce the damage caused by acorn tannins with tannin-binding salivary proteins and tannase-producing bacteria, whereas such physiological tolerance to tannins is not known in the other two rodent species. The differences in the effects of acorns between the three species may be due to differences in their physiological tolerance to tannins.

Keywords: *Apodemus argenteus* · *Apodemus speciosus* · *Clethrionomys rufocanus* · Density dependence · *Quercus crispula*

Introduction

Various aspects of the relationship between acorns (seeds of oak trees) and forest-dwelling rodents have been studied, particularly, seed dispersal (see review by Vander Wall 2001) and acorn masting on rodent population dynamics (see review by Shimada and Saitoh 2006).

Because acorns contain high levels of calories (Shimada 2001a; Vander Wall 2001; Shimada and Saitoh 2006), they are thought to be important food items for rodents, as "acorns are the ecological equivalent of manna from heaven" (McShea and Healy 2002). Indeed, various species of rodents collect and feed on various species of acorn (Vander Wall 1990).

However, acorns of some oak species accumulate considerable amounts of tannins (red oak group 5.7–8.8% per dry seed weight, Ofcarcik and Burns 1971; Shimada 2001a), which potentially have severe detrimental effects on herbivores (Fowler and Richards 1965; Robbins et al. 1987; Blytt et al. 1988; Bernays et al. 1989; Chung-MacCoubrey et al. 1997). Shimada and Saitoh (2003) demonstrated the toxic effects of acorns containing tannins on the Japanese large wood mouse *Apodemus speciosus*; 75% of mice fed solely *Q. crispula* acorns in the laboratory died within 15 days. However, *A. speciosus* may reduce the damage caused by acorn tannins through acclimation, which can be achieved by a gradual increase in tannin intake (Shimada et al. 2004). Tannin-binding salivary proteins (proline-rich proteins: PRPs) and tannase-producing bacteria (TPB) may play an important role in this acclimation (Shimada et al. 2006).

Because not all rodent species have PRPs and TPB, tolerance to the toxic effects of tannins may vary among species. Shimada and Saitoh (2006) examined studies on the effects of acorn

masting on rodent population dynamics and found that *Apodemus* and *Peromyscus* species respond positively to acorn masting in general, whereas *Clethrionomys* species do not exhibit a clear response to acorns containing large amounts of tannins. The response of rodent populations to acorn masting may be determined by the tolerance of rodents to tannins and the quality of acorns (nutritional richness and tannin content). A species with higher tolerance to tannins may increase in abundance following masting of various types of acorns, whereas a species with lower tolerance cannot use acorns with high tannin content and does not increase in abundance. The oak *Quercus crispula* is a representative oak in north East Asia and provides large amount of acorns every few years. Because these acorns contain a high percentage of tannins (Shimada 2001a; Shimada and Saitoh 2003), different responses to acorn masting by different rodent species are expected. However, few studies have examined the effects of this key species on rodents (Shimada and Saitoh 2006).

Recent advances in the analysis of population dynamics reveal that density dependence is an essential driving force for population fluctuations in many species of rodent (Saitoh et al. 1997, 1999; Stenseth 1999). Because direct density dependence may emerge through intraspecies competition for various resources, density dependence should be taken into consideration when examining the effects of acorn abundance on rodent populations. However, studies which considered simultaneously the effects of both acorn and rodent density on population dynamics in their analytical models are limited (Elkinton et al. 1996; Elias et al. 2004, 2006).

The aim of this study was to characterize the numerical response of three species of forest-

dwelling rodents, *A. speciosus*, *A. argenteus*, and *Clethrionomys rufocanus*, to the fluctuation of acorn (*Q. crispula*) abundance, taking density dependence of rodents in consideration.

Through those analyses we will evaluate the prediction that rodent species with different food habits and different tolerance to acorn tannins may respond differently to acorn masting (Shimada and Saitoh 2006).

Materials and Methods

Study area

The study was conducted at the Uryu Experimental Forest of Hokkaido University (44°03'–29' N, 142°1'–20' E) in Horokanai, Hokkaido, Japan, which is located in the cool temperate wet climate zone. The yearly average temperature is 3.5°C, annual precipitation is 1410 mm, and maximum snow depth is 275 cm. One site (6.78 ha) was a plantation forest comprising 4800 seedlings of Japanese ash (*Fraxinus mandshurica* var. *japonica*), 900 seedling of Ezo spruce (*Picea glehnii*) and 350 seedling of todo fir (*Abies sachalinensis*) planted in 1985. However, this forest has changed to a secondary forest with birch (*Betula ermani*) as a dominant species. The other site was a natural forest of broad-leaved trees and conifers. Dominant species were *Acer mono*, *Q. crispula*, *Betula ermani*, *Sorbus commixta*, *Abies sachalinensis*, and *Picea glehnii*. The undergrowth of the natural forest was dominated by dwarf bamboo, *Sasa senanensis* and *S. kurilensis*.

Rodent abundance was assessed out in two plots (Fig. 1); one (A) was located in the plantation and the other (B) in the natural forest. The distance between these plots was 970 m. Acorn abundance was investigated at two study sites (plot 408 and 422, Fig. 1) located 6300

m apart. The distance between the rodent and acorn plots was approximately 5 km.

Rodent species

The following seven rodent species were recorded in the study plots: *Apodemus speciosus*, *A. argenteus*, *A. peninsulae*, *Clethrionomys rufocanus*, *C. rutilus*, *Tamias sibiricus*, and *Rattus norvegicus*. Because the abundances of *A. peninsulae*, *C. rutilus*, *T. sibiricus*, and *R. norvegicus* were very low, these species were excluded from analyses.

The gray-sided vole, *C. rufocanus*, is a small-sized (30–40 g), short-tailed (around 40% of head and body) rodent. It is distributed widely from Fennoscandia to eastern Asia (e.g., Stenseth 1985; Kaneko et al. 1998). 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 weight of 40–60 g, it is the largest of the three species examined here.

The main reproductive season for the three species is from April/May to September/October in Hokkaido (Fujimaki 1969a, b, 1972, 1973, 1975; Murakami 1974; Kondo and Abe 1978; Kuwahata 1984; Nakata 1987, 1998). The wood mice (*Apodemus* spp.) tend to cease reproduction earlier than the vole (*C. rufocanus*, Fujimaki 1969a, b; Nakata 1998).

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 more than 50% of its diet (Ota et al. 1959; Ota 1984).

Leaves and shoots of bamboo grass dominate the diet during winter, whereas 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 than *A. speciosus* (Ota et al. 1959). The diets of the wood mice are thus predominantly granivorous and subdominantly insectivorous. 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 1985a, b).

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 possible 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). Because other rodents were rare in the study area, their influences on the three species of concern were likely to be negligible.

Rodent abundance

Rodent abundance was assessed in the two plots from 1992 to 2006. Trapping was carried out for three consecutive days in every autumn (September or early October) at each plot (0.5 ha) using 50 Sherman-type live traps baited with oats and placed at 10 m intervals in a grid pattern. All rodents were identified by toe clipping upon first capture. Species, location,

identity, sex, body weight (once or more per trapping session), and reproductive status were recorded upon capture. The methods of animal handling conformed to guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Acorn count

Acorn abundance was investigated from 1991 to 2005 at the two study sites. A total of 15 and 17 oak trees (*Quercus crispula*) were selected for investigation in Forest 408 and Forest 422, respectively. All acorns found on the ground within a 10-m radius of a selected tree were counted. This direct count was carried out three or four times at 2- to 20-day intervals every autumn (September–November). The frequency and interval of the direct count were adjusted to acorn abundance in a year; i.e., trees were more frequently investigated at a shorter interval in a high abundance year. Acorns were collected at the study sites and counted in the research station of the experimental forest. Although the selected trees were investigated continuously during the study period, four trees from Forest 422 were excluded in 2004 and thereafter, because they were severely damaged by a typhoon.

Fifty seed traps with 0.5 m² aperture were set at 10-m intervals in a grid pattern on the rodent plot B in the natural forest. The seed traps were examined every autumn from 1993 to 2005 and the number of captured seeds was counted for each tree species. Although data from the seed traps are preferable because the investigation was performed in the rodent plot using the standardized method, the study period was shorter than that for the direct count at Forest 408 and Forest 422. Because the acorn abundance data were highly correlated with each other (Pearson's correlation coefficient $r = 0.847$, $P = 0.0003$), we used data from Forest 408 and

Forest 422 for the following analyses because of the longer study period.

Models

Typically, small rodent populations exhibit no higher than an order-two autoregressive structure on an annual basis (e.g., Bjørnstad et al. 1995; Stenseth 1999). For populations of the gray-sided vole (*C. rufocanus*) and the two species of wood mouse (*A. speciosus* and *A. argenteus*) in this study area, direct density dependence dominates over delayed density dependence, and there is no evidence of an effect of delayed density dependence (Saitoh et al. 1997, 1999). Thus, we included only direct density dependence in a model to predict rodent abundance. The breeding season of the three species of rodents is from spring to autumn (Ota 1984). Because *Q. crispula* acorns become available to rodents in late September, acorn abundance hardly influences rodent reproduction in the current year and may have a minor effect on rodent abundance in the current year. Acorn effects on rodent populations may appear in the next year through the following process: in a mast year, rodents may gain their weight in autumn and cache acorns for winter, which results in higher overwinter survival; more rodents reproduce in the next spring, and the population increases. Thus, letting x_t correspond to the log-transformed ‘true’ abundance of rodents in year t , ignoring higher-order terms, the rodent abundance in year t may be expressed using the density dependence parameter α_1 (the direct density dependence) together with effects of acorn abundance α_2 :

$$x_t = (1 + \alpha_1)x_{t-1} + \alpha_2 A_{t-1} + \varepsilon_t \quad (\text{Model 1}),$$

where A_t is the log-transformed ‘true’ abundance of acorns in year t and the process stochasticity, ε_t , is assumed to be normally distributed with mean zero and a constant variance (σ^2). We also examined the following model for comparison:

$$x_t = \alpha_2 A_{t-1} + \varepsilon_t \quad (\text{Model 2}).$$

Previously (Stenseth et al. 2003), sampling error was explicitly accounted for by incorporating both an ecological process model and an observation model (i.e., a state-space model; see de Valpine and Hastings 2002; Viljugrein et al. 2005). Using the WinBUGS 1.4.1 software package (Spiegelhalter et al. 2003), a Bayesian approach was taken to estimate coefficients for density dependence and effects of acorn abundance (for detailed methodology, see Stenseth et al. 2003). Here, we used the minimum number alive (Krebs 1999) as rodent abundance and the number of trap-nights as trapping effort. Rodent abundance from the two study plots was pooled for each year. The total number of counted acorns and the number of investigated trees were used as acorn abundance and measurement effort, respectively (see Spiegelhalter et al. 2003 for technical problems). The mean of the posterior distributions was used for representatives of the coefficients.

Results

Acorn abundance (given as the number per tree) fluctuated widely, from 31.4 in 1995 to 3603.6 in 1998 (Fig. 2); the average for the study period was 1509.2, with a large standard deviation (1470.6). It was rare for the abundance to be high in two successive years, except for 2003 and 2004, although low abundance occurred for several years following.

Apodemus speciosus was the most common rodent. Its average abundance (minimum number alive) was 29.1 (SD = 20.5). *Apodemus argenteus* and *C. rufocanus* followed the dominant species; their average abundance was 16.7 (SD = 12.3) and 10.2 (SD = 10.7), respectively.

These populations fluctuated greatly, but without any significant correlation between the species (Pearson's correlation coefficient $r = 0.263$, $P = 0.344$ between *A. speciosus* and *A. argenteus*; $r = 0.285$, $P = 0.303$ between *A. speciosus* and *C. rufocanus*; $r = 0.385$, $P = 0.157$ between *A. argenteus* and *C. rufocanus*; Fig. 2).

Apodemus speciosus increased in abundance following acorn masting. After the peak years of acorn abundance (1994, 1996, 1998, 2000, and 2003), *A. speciosus* population showed peaks in 1995, 1997, 1999–2000, and 2004. One exception was observed in 2000–2001; *A. speciosus* population decreased after the mast year. A simple correlation between logarithmic abundance of acorns and *A. speciosus* was high (Pearson's correlation coefficient $r = 0.506$, $P = 0.054$). Although *A. argenteus* population did not showed clear peaks except for 2000, it appeared to fluctuate following acorn abundance. A correlation with acorn abundance was highest ($r = 0.604$, $P = 0.017$). No clear relationship was found between abundance of acorns and *C. rufocanus* ($r = 0.319$, $P = 0.246$).

Strong evidence for density dependence was found for all three species using Model 1 (Table 1). The mean coefficients (α_1) were around -1 , which is consistent with the results of Saitoh et al. (1999).

A clear-cut effect of acorn abundance was found only for *A. speciosus* (Table 1). The mean coefficient of acorn effects (α_2) was 0.345, and the lower limit of the 95% credible interval was positive (0.072) in Model 1. That effect was also evident in Model 2. In contrast to *A. speciosus*, an effect of acorn abundance was not detected for *C. rufocanus*. Although the mean

α_2 was relatively high (0.369), the lower limit of the 95% credible interval was negative (-0.271) because of high deviation in Model 1. The results of Model 2 were consistent with those of Model 1 (Table 1). An effect of acorn abundance was marginal for *A. argenteus*. The mean α_2 was low (0.203) but the lower limit of the 95% credible interval was close to zero (-0.007) in Model 1, while the lower limit in Model 2 was positive (0.008).

Discussion

A clear-cut effect of acorn abundance was found for *A. speciosus*, but not for *A. argenteus* and *C. rufocanus* in this study (Table 1; Fig. 2). There were no large difference in the results on acorn effects between the two models; one (Model 1) includes density dependence of rodents and the other (Model 2) consists of an acorn effect alone. Although a model including density dependence is recommended, a simple model like Model 2 could provide consistent results. It is known that sampling errors cause overestimate of the degree of density dependence owing to bias (see Freckleton et al. 2006 for a recent review). The autoregressive approach ignoring sampling errors may provide somewhat inflated estimates for density dependence and that may result in underestimation of an acorn effect. The Bayesian state-space models, used in this study, which take sampling errors in consideration, reduce the bias of density dependence compared to that of the autoregressive approach ignoring sampling errors (Viljugrein et al. 2005). Thus the present results are robust in both examinations of effect combination and sampling errors.

The two species of wood mouse (*A. speciosus* and *A. argenteus*) are granivorous (Ota 1984), taking various types of seeds including acorns. However, *A. speciosus* prefers larger seeds,

whereas *A. argenteus* selectively uses smaller seeds (Shimada 2001b). Because the size of *Q. crispula* acorns is very large (5–10 g), they may not be preferable for *A. argenteus*. Saitoh et al. (2000) investigated which species is responsible for taking artificially buried *Q. crispula* acorns in the ground using a large outdoor enclosure (3 ha). They found that *A. speciosus* collected many acorns, whereas *A. argenteus* left many buried acorns. The gray-sided vole (*C. rufocanus*), which exhibits food habits intermediate to herbivore and granivore (Ota 1984), also took acorns, although at a lower rate than *A. speciosus* (Saitoh et al. 2000).

The rodent species also might differ with respect to their tolerance to the toxic effects of acorn tannins. Acorns of *Q. crispula* contain 6–12% tannins (Shimada 2001a), which potentially have detrimental effects on wood mice (Shimada and Saitoh 2003). However, *A. speciosus* can reduce the damage caused by acorn tannins through acclimation, which could be achieved by a gradual increase in tannin intake (Shimada et al. 2004). PRPs and TPB may play an important role in this acclimation (Shimada et al. 2006). Thus, *A. speciosus* can use acorns due to these countermeasures against tannins. In contrast, *A. argenteus* and *C. rufocanus* may have weaker or no countermeasures against tannins, although the tannin tolerance of the two species are unknown.

In a forest of Maine, USA, differences in response to mast were found between *Peromyscus leucopus* and *C. gapperi* (Elias et al. 2004, 2006). Population increases in *P. leucopus* followed large acorn crops produced mainly by *Quercus rubra*, whereas *C. gapperi* was influenced by the seed abundance of *Pinus strobus*. The red oak *Q. rubra* produces nutritious acorns with high tannin content (Shimada and Saitoh 2006). *Peromyscus leucopus* may be able to use the

acorns, whereas *C. gapperi* may not. *Clethrionomys gapperi* can eat the seeds of *Pinus strobus*, which are generally thought to be important food for various species. The tannin tolerance of *P. leucopus* and *C. gapperi* is unknown. We can, however, predict that *P. leucopus* could reduce the toxic effects of *Q. rubra* acorns by physiological and/or behavioral countermeasures against tannins, as does *A. speciosus*. In contrast, *C. gapperi*, like *A. argenteus* and *C. rufocanus*, may have weaker or no countermeasures against tannin. The tannin tolerance of these species should be evaluated in future studies.

Shimada and Saitoh (2006) reviewed studies of the effects of acorn masting on rodent population dynamics. They stressed the importance of studying acorns that contain a high percentage of tannins and are relatively nutritionally poor (type 2 after Shimada and Saitoh 2006) because the effects of tannins may become conspicuous and different effects on different rodent species are expected in type 2 species, whereas the effects of tannins may be masked by a high nutritive value in oak species whose acorns contain a lot of protein and fat. *Quercus crispula* is a representative type 2 oak and provides a large amount of acorns every few years.

As a follow-up, nutritional constituents of shelled acorns from tree No. 212 in Forest 422 were measured (Table 2). Although these acorns showed high caloric content, resembling those in previous studies (Shimada 2001a; Shimada and Saitoh 2003), the percentage of total phenolics, which is generally regarded as an index of tannins, was smaller than that in previous studies, in which the total phenolics were measured as 11.7% in acorns collected in Miyama, Kyoto Prefecture. Because the amount of tannins contained in acorns varies greatly

among individual trees (Sork et al. 1983; A. Takahashi and T. Shimada personal communication), we may have accidentally selected acorns that contained less tannin, and because of regional variation in tannin content, acorns in this area may contain less tannin than those in other areas. Nevertheless, the total phenolics observed, at 6.1%, could be regarded as enough to potentially harm rodents (see Shimada and Saitoh 2003).

Meeting our expectations, we found a difference in the effects of acorn masting on population dynamics among the three rodent species; acorn effects were clearly demonstrated for *A. speciosus*, but not for *A. argenteus* or *C. rufocanus*. However, this is not a conclusive answer for *A. argenteus* and *C. rufocanus*. Long-term data are required to examine some ecological effects. Saitoh et al. (1998) demonstrated that data sets covering more than 20 years are needed to conclusively detect density dependence (see also Hanski 1990). This study (15 years) may not have been long enough to obtain a conclusive answer, particularly for *A. argenteus*, in which the probability that the coefficient (α_2) was positive was high. We have, however, no doubt that *A. speciosus* populations are more strongly influenced by *Q. crispula* acorn abundance than *A. argenteus* and *C. rufocanus*, and this difference can be interpreted by differences in their food habits and tannin tolerance.

Acknowledgements. We are indebted to the Uryu Experimental Forest, Field Science Center, Hokkaido University, for providing support for the investigation. Takuya Shimada critically read the manuscript and provided valuable comments. The manuscript was improved by helpful comments of the editor and reviewers. This study was supported in part by a Grant-in-

Aid for Scientific Research (B) No. 17370006 from the Ministry of Education, Science, Sports and Culture to TS.

References

- Abe H (1986) Vertical space use of voles and mice in woods of Hokkaido, Japan. *J Mammal Soc Japan* 11: 93-106
- Animal Care and Use Committee (1998) Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *J Mammal* 79: 1416-1431
- Bernays EA, Driver GC, Bilgener M (1989) Herbivores and plant tannins. *Adv Ecol Res* 19: 263-302
- Blytt HJ, Guscar TK, Butler LG (1988) Antinutritional effects and ecological significance of dietary condensed tannins may not be due to binding and inhibiting digestive enzymes. *J Chem Ecol* 14: 1455-1465
- Bjørnstad ON, Falck W, Stenseth NC (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proc R Soc Lond B* 262: 127-133
- Chung-MacCoubrey AL, Hagerman AE, Kirkpatrick RL (1997) Effect of tannins on digestion and detoxification activity in gray squirrels (*Sciurus carolinensis*). *Physiol Zool* 70: 270-277
- de Valpine P, Hastings A (2002) Fitting population models incorporating process noise and observation error. *Ecol Monogr* 72: 57-76
- Elias SP, Witham JW, Hunter MLJ (2004) *Peromyscus leucopus* abundance and acorn mast: 10 population fluctuation patterns over 20 years. *J Mammal* 85: 743-747

- Elias SP, Witham JW, Hunter MLJ (2006) A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in Maine. *J Mammal* 87: 440-445
- Elkinton JS, Healy WM, Buonaccorsi JP, Boettner GH, Hazzard AH, Smith HR (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* :2332-2342.
- Fowler ME, Richards WPC (1965) Acorn poisoning in a cow and a sheep. *J Am Vet Med Assoc* 147: 1215-1220
- Freckleton RP, Watkinson AR, Green RW, Sutherland WJ (2006) Census error and the detection of density dependence. *J Anim Ecol* 75: 837-851
- Fujimaki Y (1969a) Reproductive activity in *Apodemus argenteus* Temminck. *J Mammal Soc Japan* 4:74-80 (in Japanese with English summary)
- Fujimaki Y (1969b) The fluctuations in the number of small rodents. *Bul Hokkaido Forest Exp Stn* 7:62-77 (in Japanese with English summary)
- Fujimaki Y (1972) Reproductive activity in *Clethrionomys rufocanus bedfordiae* 1. Regional differences in spring reproductive activity. *Bul Hokkaido Forest Exp Stn* 10: 59-67 (in Japanese with English summary)
- Fujimaki Y (1973) Reproductive activity in *Clethrionomys rufocanus bedfordiae* 2. Regional differences in summer reproductive activity. *Bul Hokkaido Forest Exp Stn* 11: 122-131 (in Japanese with English summary)
- Fujimaki Y (1975) Reproductive activity in *Clethrionomys rufocanus bedfordiae* 3. Regional differences in autumn reproductive activity. *Bul Hokkaido Forest Exp Stn* 13: 38-45 (in Japanese with English summary)
- Hanski I (1990) Density dependence, regulation and variability in animal populations.

- Regulation and Relative Abundance of Plants and Animals* (eds R. M. May & M. P. Hassell), pp.140-150. The Royal Society, London.
- Hansson L (1985a) *Clethrionomys* food: generic, specific and regional characteristics. *Ann Zool Fen* 22:315-318.
- Hansson L (1985b) The food of bank voles, wood mice and yellow-necked mice. *Symp Zool Soc London* 55: 141-168
- Kaneko Y, Nakata K, Saitoh T, Stenseth NC, Bjørnstad ON (1998) The biology of the vole *Clethrionomys rufocanus*: a review. *Res Popul Ecol* 40: 21-37
- Kondo N, Abe H (1978) Reproductive activity of *Apodemus speciosus ainu*. *Memoirs of the Faculty of Agriculture, Hokkaido University* 11: 159-165 (in Japanese with English summary)
- Krebs, CJ (1999) *Ecological methodology*. Benjamin/Cummings, Menlo Park. 620pp.
- Kuwahata T (1984) Studies on reproduction and population dynamics of the red-backed vole, *Clethrionomys rufocanus bedfordiae* (Thomas). *Bul Forestry & Forest Products Res Inst (Ibaraki, Japan)* 327: 1-81 (in Japanese with English summary)
- McShea WJ, Healy WM (2002) Oaks and acorns as a foundation for ecosystem management. In: McShea WJ, Healy WM (eds) *Oak forest ecosystems*. The Johns Hopkins University Press, 5 Baltimore, pp 1-12
- Miyaki, M., and K. Kikuzawa (1988) Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest. 2. Scatterhoarding by mice. *Forest Ecology and Management* 25: 9-16.
- Murakami O (1974) Growth and development of the Japanese wood mouse (*Apodemus speciosus*). I. The breeding season in the field. *Japanese J Ecol* 24: 194-206 (in Japanese)

- with English summary)
- Nakata K (1987) Effects of spring-removal on the populations of small rodents. Japanese J Appl Entomol Zool 31: 97-91 (in Japanese with English summary)
- Nakata K (1995) Microhabitat selection in two sympatric species of voles *Clethrionomys rex* and *Clethrionomys rufocanus bedfordiae*. J Mammal Soc Japan 20: 135-142.
- Nakata K (1998) Regulation of reproduction in a natural population of the small Japanese field mouse, *Apodemus argenteus*. Mammal Study 23: 19-30
- Ofcarcik RP, Burns EE (1971) Chemical and physical properties of selected acorns. J Food Sci 36: 576 - 578
- Ota K. (1968) Studies on the ecological distribution of the murid rodents in Hokkaido. Res Bul College Experiment Forests (Faculty of Agriculture, Hokkaido University) 26:223-295 (in Japanese with English summary)
- Ota K.(ed.) (1984) Study on wild murid rodents in Hokkaido. Hokkaido University Press, Sapporo. (in Japanese)
- Ota K, Takatsu S, Abe, H (1959) Fluctuations of numbers in small mammals at Mt. Moiwa, Sapporo. I. Seasonal fluctuations of small mammal populations. Memoirs of the Faculty of Agriculture, Hokkaido University 3: 49-69 (in Japanese with English summary)
- Robbins CT, Hanley TA, Hagerman AE, Hjeljord O, Baker DL, Schwartz CC, Mautz WW (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98-107
- Saitoh T, Stenseth NC, Bjørnstad ON (1997) Density dependence in fluctuating grey-sided vole populations. J Anim Ecol 66: 14-24
- Saitoh T, Stenseth NC, Bjørnstad ON (1998) The population dynamics of the vole

- Clethrionomys rufocanus* in Hokkaido, Japan. Res Popul Ecol 40: 61-76
- Saitoh T, Bjørnstad ON, Stenseth NC (1999) Density-dependence in voles and mice: a comparative study. Ecology 80: 638-650
- Saitoh T, Kawaji N, Kudo T (2000) Who takes artificially buried acorns in a forest? Hoppou Ringyo 52: 215-218 (in Japanese)
- Saitoh T, Nakatsu A (1997) Impact of forest plantation on the community of small mammals in Hokkaido, Japan. Mammal Study 22: 27-38.
- Sekijima T, Soné K (1994) Role of interspecific competition in the coexistence of *Apodemus argenteus* and *A. speciosus* (Rodentia: Muridae). Ecol Res 9: 237-244.
- Shimada T (2001a) Nutrient compositions of acorns and horse chestnuts in relation to seed-hoarding. Ecol Res 16: 803-808
- Shimada T. (2001b) Hoarding behaviors of two wood mouse species: Different preference for acorns of two Fagaceae species. Ecol Res 16: 127-133
- Shimada T, Saitoh T (2003) Negative effects of acorns on the wood mouse *Apodemus speciosus*. Popul Ecol 45:7-17
- Shimada T, Saitoh T (2006) Re-evaluation of the relationship between rodent populations and acorn masting: a review from the aspect of nutrients and defensive chemicals in acorns. Popul Ecol 48: 341-352
- Shimada T, Saitoh T, Matsui T (2004) Does acclimation reduce the negative effects of acorn tannins in the wood mouse *Apodemus speciosus*? Acta Theriol 49:203-214
- Shimada T, Saitoh T, Sasaki E, Nishitani Y, Osawa R (2006) The role of tannin-binding salivary proteins and tannase-producing bacteria in the acclimation of the Japanese wood mouse to acorn tannins. J Chem Ecol 32: 1165-1180

- Soné K, Kohno A (1996) Application of radiotelemetry to the survey of acorn dispersal by *Apodemus* mice. *Ecol Res* 11: 187-192
- Sork VL, Stacey P, Averett JE (1983) Utilization of red oak acorns in non-bumper crop year. *Oecologia* 59:49-53
- Spiegelhalter DJ, Thomas A, Best NG, Lunn D (2003) WinBUGS user manual (version 1.4).
MRC Biostatistics Unit, Institute of Public Health, Cambridge
- Stenseth NC (1985) Geographic distribution of *Clethrionomys* species. *Ann Zool Fen* 22:215-219
- Stenseth NC (1999) Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87: 427-461
- Stenseth NC, Viljugrein H, Saitoh T, Hansen TF, Kittilsen MO, Bølviken E, Glöckner F.
(2003) Seasonality, density dependence and population cycles in Hokkaido voles. *Proc Natl Acad Sci USA* 100: 11478-11483
- Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago
- Vander Wall SB (2001) The evolutionary ecology of nut dispersal. *Botanical Rev* 67: 74-117
- Viljugrein H, Stenseth NC, Smith GW, Steinbakk GH (2005) Density dependence in North American ducks. *Ecology* 86: 245-254

Table 1. Estimated coefficients for Model 1 for the three rodent species. Density effects of rodents (α_1) and the direct effect of acorn abundance (α_2) are shown. SD and 95% CI indicate standard deviation and 95% credible interval, respectively.

Species	α_1			α_2		
	mean	SD	95% CI	mean	SD	95% CI
<i>A. speciosus</i>						
Model 1	-1.220	0.237	[-1.686, -0.747]	0.345	0.139	[0.072, 0.625]
Model 2				0.372	0.145	[0.086, 0.667]
<i>A. argenteus</i>						
Model 1	-0.899	0.304	[-1.493, -0.279]	0.203	0.106	[-0.007, 0.415]
Model 2				0.201	0.098	[0.008, 0.398]
<i>C. rufocanus</i>						
Model 1	-1.228	0.347	[-1.866, -0.475]	0.369	0.343	[-0.271, 1.104]
Model 2				0.317	0.325	[-0.305, 0.990]

Table 2. Nutritional constituents of *Quercus crispula* acorns as percent content on a dry weight basis* .

Crude protein	Crude fat	Crude fiber	Crude ash	MME ¹ (kJ/g)	Total phenolics ²
5.1	2.0	1.8	2.6	14.05	6.1

*Nutritional constituents were measured by the Japan Food Research Laboratory.

¹MME: modified metabolizable energy. This value was obtained following Shimada and Saitoh (2006).

²Total phenolics were measured using the Folin-Denis method. The values are expressed as tannic acid equivalent.

Figure legends

Fig. 1. Map of the study sites. Rodent abundance was investigated out in two plots: one (A) located in a secondary forest with birch (*Betula ermani*) as the dominant species and the other (B) in a natural forest. Acorns on the ground were counted in two plots (Forests 408 and 422).

Fig. 2. Annual changes in acorn and rodent abundance. Acorn abundance is represented as the number of acorns per oak tree, in the upper panel. Rodent abundance is represented as the minimum number alive, in the lower panel. The numbers at the two study plots were summed. Solid circle: *Apodemus speciosus*; triangle: *Apodemus argenteus*; open circle: *Clethrionomys rufocanus*. Note that rodent abundance lags one year behind acorn abundance.

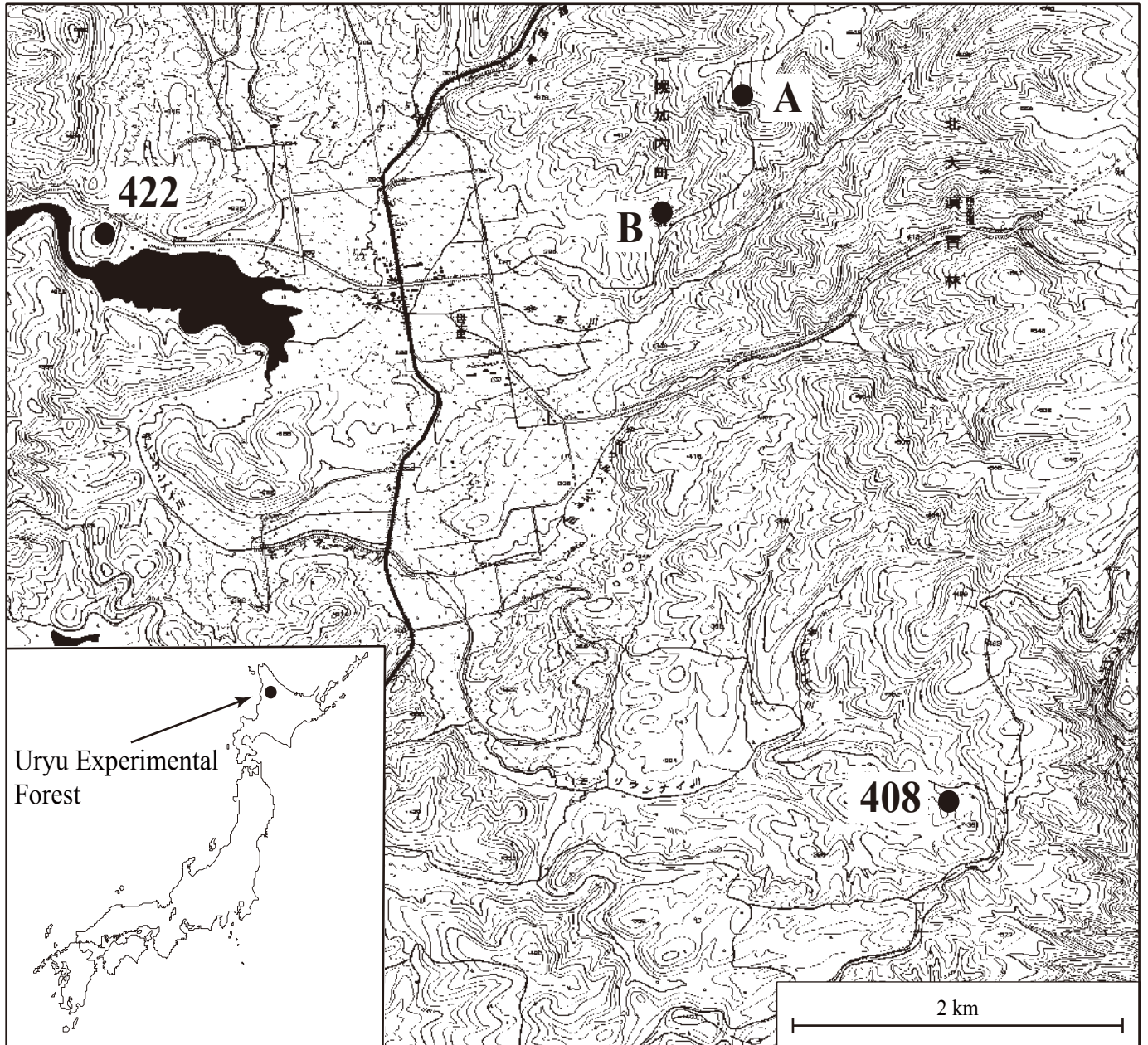


Figure 1

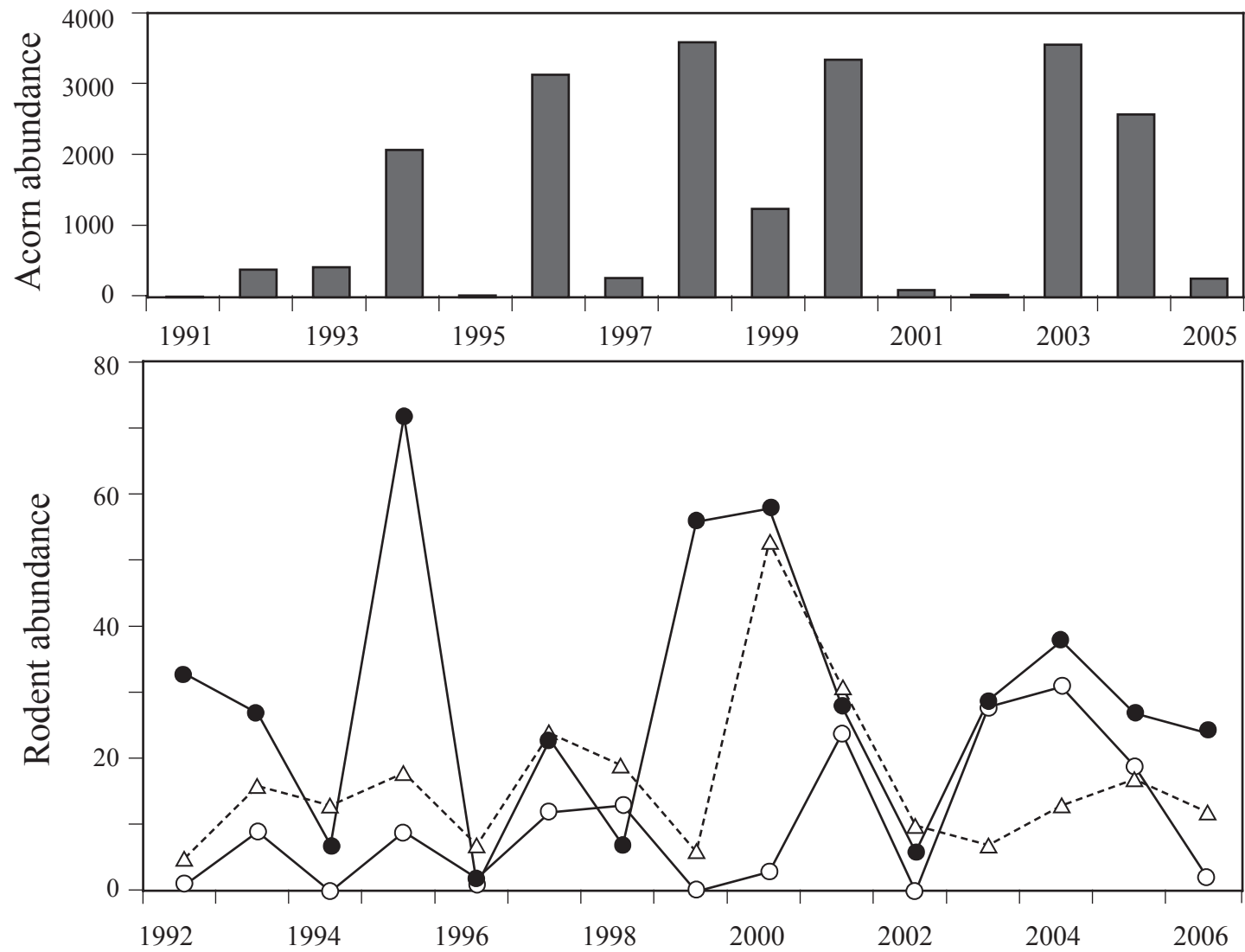


Figure 2