Effects of acorn abundance on density dependence in a Japanese wood mouse (*Apodemus speciosus*) population

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Abstract We analysed the effects of *Quercus crispula* acorn abundance on the density dependence of the large Japanese wood mouse *Apodemus speciosus* using time series data (1992–2007). The data were obtained in a forest in northern Hokkaido, Japan, by live-trapping rodents and directly counting acorns on the ground. Acorn abundance in one year clearly influenced the abundance of wood mice in the following year in all models examined based on the Gompertz and Ricker model; in addition, the abundance of wood mice had effects on the population. Acorn abundance influenced the strength of density dependence (intraspecific competition) of the wood mouse population. When the abundance of acorns was high, density dependence was relaxed and as a result the equilibrium density at which the population growth rate decreased to zero became higher. Those effects of acorn abundance were regarded as a nonlinear perturbation effect (sensu Royama 1992). The nonlinearity of density dependence was also detected; higher densities had stronger effects on population growth rates.

Keywords Dynamics · Intraspecific competition · Lateral perturbation effect · Masting · Nonlinear density dependence · Nonlinear perturbation effect

Introduction

Rodent population dynamics are a synergetic phenomenon, including effects of intraspecific competition, trophic interactions, weather, and disease (Batzli 1992), as well as other animal species (Royama 1992; Turchin 2003). Despite their complexity, some consensus has been reached among population ecologists regarding population cycles (periodic large-scale fluctuations with high amplitude) which have been reported for vole and lemming populations of northern Eurasia and North America. Trophic interactions may generate population cycles through delayed density dependence (Stenseth 1999; Klemola et al. 2003; Korpimäki et al. 2004), which may be due to interactions with food supply or natural enemies such as predators, parasites, and diseases. However, in populations that exhibit irregular outbreaks, density-independent factors may have more profound effects than in cyclic populations, and direct, rather than delayed, density dependence is predominant (Royama 1992; Saitoh et al. 1999; Lima et al. 2006).

Wood mice (genus *Apodemus*) appear to have dynamics dominated by irregular outbreaks related to years of abundant seed production (Flowerdew 1985; see also Montgomery 1989a, b). Masting of seeds (synchronous intermittent production of large seed crops) improves reproduction and survival of *Apodemus* (Montgomery et al. 1991: see Wilson et al. 1993 and Shimada and Saitoh 2006 for reviews) and often causes a high density of *Apodemus* populations (Jensen 1982; Miguchi 1988; Mallorie and Flowerdew 1994). Therefore, populations of *Apodemus* are likely to be influenced by seed production, in addition to direct density dependence (Saitoh et al. 1999).

Intraspecific competition for food or space is generally considered a mechanism of direct density dependence (Stenseth et al. 1996; Saitoh et al. 1997, 1999; Prévot-Julliard et al. 1999; Lima et al. 2001, 2002a, 2002b; Murúa et al. 2003), although generalist predators are considered a main agent for direct density dependence in Fennoscandia (Hansson and Henttonen 1988; Hanski et al. 2001; Turchin and Hanski 2001; Korpimäki et al. 2004). If intraspecific competition is a principle cause of direct density dependence, then density dependence could be influenced by the abundance of resources.

Royama (1992) suggests that resources which can be measured by a simple per-capita share of the resource (e.g., nests holes for birds) have linear effects on density dependence ("lateral perturbation effect"), while resources that are gradually depleted (e.g., crops for birds) have nonlinear effects on density dependence ("nonlinear perturbation effect"). A "lateral perturbation effect" shifts the equilibrium density at which population growth rate takes zero, but does not influence the strength of density dependence. In contrast, a "nonlinear perturbation effect", by altering the strength of density dependence, influences the equilibrium density. Yoccoz et al. (2001) examined the density-dependent structure of bank vole (*Clethrionomys glareolus*) populations, assuming that density dependence would be relaxed under conditions of abundant food resources; however, the effects of food addition on density-dependent structure were negligible. Food habits of the bank vole are intermediate between herbivorous and granivorous, and they consume a large variety of food items (Hanson 1985). Since they do not depend on a specific food resource, the interactions between food and rodents may be complex. Thus, the relationship is expected to be clearer in other rodent species that rely on a specific food resource.

The relationship between masting of the oak (*Quercus crispula* Blume) and population dynamics of the large Japanese wood mouse (*Apodemus speciosus* (Temmink, 1844)) is a suitable system with which to answer the question about the interaction between food and rodents. Acorns of *Q. crispula* are nutritionally rich (Shimada 2001), and *A. speciosus*, which is a small (40–60 g) mouse endemic to Japan, caches acorns (Miyaki and Kikuzawa 1988; Soné and Kohno 1996). The Field Science Centre of Hokkaido University has monitored the abundance of rodents and acorns from 1992 to the present, and Saitoh et al. (2007) have detected clear effects of acorn abundance on the population dynamics of *A. speciosus*.

Here, we analysed effects of acorn abundance on density dependence of a wood mouse population using time series data spanning the period from 1992 to 2007. We conclude that the strength of density dependence is altered by acorn abundance and that the nature of density dependence is essentially related to the interaction with resources.

Materials and methods

Study area

The study was conducted in the Uryu Experimental Forest (44°03’–29' N, 142°1’–20' E) of Hokkaido University in Horokanai, Hokkaido, Japan, located in the cool temperate wet climate zone. The yearly average temperature is 4.2°C (3.4 - 4.8°C between 1994 and 2006), annual precipitation is 1224.1 mm raging from 961.5 to 1540.5 mm in the same period, and the maximum depth of accumulated snow exceeds 200 cm every year.

Rodent abundance was investigated in two plots (see the map in Saitoh et al. 2007): one (A) was located in a forest plantation and the other (B) in a typical natural forest. The plantation was a 6.78-ha forest, where 4800 seedlings of Japanese ash (*Fraxinus mandshurica* var. *japonica*), 900 seedlings of Ezo spruce (*Picea glehnii*), and 350 seedlings of todo fir (*Abies sachalinensis*) were planted in 1985. Since that time, however, this forest has become a secondary forest with birch (*Betula ermani*) as a dominant species. The natural forest consisted 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.* The distance between the two plots was 970 m.

Acorn abundance was investigated at two other study sites in natural forests located 6300 m apart. The distance between the rodent plots and acorn count plots was approximately 5 km.

Large Japanese wood mouse

Although seven rodent species (*Apodemus speciosus*, *A. argenteus*, *A. peninsulae*, *Clethrionomys rufocanus*, *C. rutilus*, *Tamias sibiricus*, and *Rattus norvegicus*) were recorded in the study plots, we focused on the large Japanese wood mouse *A. speciosus* because this species is dominant in the study area, and a clear effect of acorn abundance on the mouse population has already been demonstrated (Saitoh et al. 2007).

Apodemus speciosus is a wood mouse that weighs 40–60 g and is endemic to Japan. The main reproductive season is from April/May to September/October in Hokkaido (Fujimaki 1969;

Murakami 1974; Kondo and Abe 1978). The main dietary items are seeds and invertebrates, mainly insects. There are no reports that green plants dominate over other food items in their diets in Hokkaido. The diet of wood mice is thus predominantly granivorous and subdominantly insectivorous. Caching behaviour is well developed (Miyaki and Kikuzawa 1988; Soné and Kohno 1996). Among the sympatric species that we recorded, there is no evidence of inter-generic competition (e.g., Abe 1986), although congeneric interactions are thought to occur (Ota 1968; Abe 1986). *Apodemus speciosus* is dominant over *A. argenteus* (Sekijima and Soné 1994).

Rodent abundance

Rodent abundance was recorded in the two study plots from 1992 to 2007. Trapping was carried out for 3 days each autumn (September or early October) at each plot 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 the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Acorn count

Acorn abundance was recorded from 1991 to 2006 in the two study sites (see the map in Saitoh et al. 2007). In total, 15 and 17 oak trees (*Q. 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 counts were adjusted to acorn abundance in a year; i.e., trees were more frequently investigated at shorter intervals in a high-abundance year. Although the selected trees were investigated continuously during the study period, four trees in Forest 422 were excluded in 2004 because they were heavily damaged by a typhoon in 2004.

In addition to the direct acorn counts, 50 seed traps with 0.5-m^2 aperture were set at 10-m intervals in a grid pattern in the rodent plot B in the natural forest. The seed traps were examined monthly from June to October between 1993 and 2005, and the number of collected 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 standardised methods, the study period was shorter than that for the direct counts in Forest 408 and Forest 422. Because the acorn abundance data from the two methods were highly correlated (Pearson's correlation coefficient $r_s = 0.825$), we used the data from Forest 408 and Forest 422 for the following analyses because of the longer study period.

Models

Although small rodent populations generally exhibit a second-order autoregressive structure on an annual basis (e.g., Bjørnstad et al. 1995; Stenseth 1999), in populations of the wood mouse *A. speciosus*, direct density dependence dominates over delayed density dependence, and there is no evidence for the effect of delayed density dependence (Saitoh et al. 1999). Thus, we considered only direct density dependence in a model to predict mouse abundance. The breeding season of the wood mouse is from spring to autumn. Because *Q. crispula* acorns

become available to rodents from late September, acorn abundance has little influence on
200 mouse reproduction in the current year and may have a minor effect on mouse populations in the current year. Acorn effects on mouse populations may appear in the next year through the
202 following process: in a mast year, mice may gain weight in autumn and cache acorns for the winter, which results in higher overwintering survival; more mice reproduce during the next
204 spring, and the population increases. Thus, letting x_t correspond to the log-transformed 'true' abundance of mice in year t, ignoring higher-order terms, the mouse abundance in year t may
206 be expressed using the density dependence parameter α_1 (the direct density dependence) together with effects of acorn abundance, α_2:

208 $$x_t = (1 + \alpha_1)x_{t-1} + \alpha_2 A_{t-1} + \varepsilon_t \qquad \text{(Model 1)},$$

where A_t is the log-transformed 'true' abundance of acorns in year t, and the process
210 stochasticity, ε_t, is assumed to be normally distributed with mean zero and a constant variance (σ^2). Since the term of $\alpha_2 A_{t-1}$ influences the equilibrium density, not altering the strength of
212 density dependence, this effect is conceptualised as "lateral perturbation effect" by Royama (1992).

214

By including the interaction term between mice and acorns (α_3; Model 2a) and modifying
216 Model 2a, we can analyse the relationship between direct density dependence and acorn abundance (Model 2b) :

218 $$x_t = (1 + \alpha_1)x_{t-1} + \alpha_2 A_{t-1} + \alpha_3 x_{t-1} A_{t-1} + \varepsilon_t \qquad \text{(Model 2a)},$$

$$x_t = (1 + \alpha_1 + \alpha_3 A_{t-1})x_{t-1} + \alpha_2 A_{t-1} + \varepsilon_t \qquad \text{(Model 2b)}.$$

220 Since Model 2a is identical to Model 2b, we focused on Model 2b. The term of $\alpha_3 A_{t-1}$ can alter the strength of density dependence and this effect is conceptualised as "nonlinear perturbation

effect" by Royama (1992).

In addition to the above models based on the Gompertz model, the following non-linear model based on the Ricker model was also examined:

$$x_t = x_{t-1} + \alpha_0 - \exp(\alpha_1 x_{t-1} + \alpha_2 A_{t-1}) + \varepsilon_t \qquad \text{(Model 3)}.$$

The discrete-time logistic model is a particular case of Model 3 (Royama 1992). Parameter-by-parameter comparison indicates that α_0 and $\alpha_2 A_{t-1}$ are equivalent to intrinsic rate of natural increase (γ) and $\log(\gamma/K)$, where K is the carrying capacity (Royama 1992).

Stenseth et al. (2003) explicitly accounted for sampling error 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 1.4.3 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; a program for WinBUGS 1.4.3 used in this study is available as Electronic Supplementary Material S1). Here, we used the minimum number alive (Krebs 1999) to represent mouse abundance and the number of trap-nights to represent trapping effort. Some of traps set in the field were sometimes disturbed by carnivores (e.g., red foxes). The number of disturbed traps were omitted from the trapping effort. Mouse 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 to represent acorn abundance and measurement effort, respectively. We used the mean of the posterior distributions as representatives of the coefficients.

246 **Results**

Acorn abundance (number per tree) fluctuated widely from 31.4 in 1994 to 3848.0 in 2006
248 (Fig. 1); the average for the study period was 1655.1, with a large standard deviation (1540.4). It was rare for the abundance to be high in two successive years, except for 2003 and 2004,
250 although low abundance was observed for several successive years.

252 Wood mouse abundance was represented by the minimum number alive in the two study plots. The average abundance was 30.2 (SD = 20.3; Fig. 1). Although there were some exceptions,
254 the wood mouse population increased following acorn masting. After the peak years of acorn abundance (1994, 1996, 1998, 2000, and 2003), the mouse population showed peaks in 1995,
256 1997, 1999–2000, and 2004.

258 Strong evidence for density dependence was found using Model 1 (Table 1). The mean coefficient (α_1) was around -1, which is consistent with the results of Saitoh et al. (1999). A
260 clear effect of acorn abundance was also found; the mean coefficient (α_2) was 0.366, and the lower limit of the 95% credible interval (CI) was positive (0.109).

262

An effect of the interaction between wood mice and acorn abundance was detected by Model
264 2b (Table 1). The mean α_3 was 0.287, and the lower limit of the 95% CI was positive (0.051). Density dependence (α_1 = -1.747) was considerably stronger than that in Model 1. The mean
266 of α_2 was similar to that obtained using Model 1, while the range of the 95% CI became narrower because of the smaller standard deviation. Model 2a provided results consistent with

268 those of Model 2b (Table 1).

270 The facts that α_3 was clearly positive and DIC indicates superiority of Model 2b over Model 1 (Table 1) indicate that acorn abundance had an effect which altered the strength of density
272 dependence (i.e., a nonlinear perturbation effect).

274 Observed population growth rates [$x_t - x_{t\text{-}1}$] were plotted against wood mouse abundance [$x_{t\text{-}1}$] in relation to acorn abundance [$A_{t\text{-}1}$] (Fig. 2). Population growth rates appeared to be inversely
276 related to wood mouse abundance, although there was some variation. Growth rates in poor years of acorn abundance (lighter circles) were scattered in lower positions of Fig. 2, whereas
278 growth rates in rich years of acorn abundance (darker circles) were scattered in upper positions.

280

Population growth rates could be predicted by Model 2b. By assigning the maximum acorn
282 abundance (A_{2006}), we obtained an equation representing density dependence [$x_t - x_{t\text{-}1} = (\alpha_1 + \alpha_3(A_{\mathrm{MAX}} - A_{\mathrm{AVERAGE}}))(x_{t\text{-}1} - x_{\mathrm{AVERAGE}}) + \alpha_2(A_{\mathrm{MAX}} - A_{\mathrm{AVERAGE}}) = -1.26x_{t\text{-}1} + 4.34$] for acorn-rich
284 years, whereas by assigning the minimum acorn abundance (A_{1996}), we obtained an equation representing density dependence [$x_t - x_{t\text{-}1} = (\alpha_1 + \alpha_3(A_{\mathrm{MIN}} - A_{\mathrm{AVERAGE}}))(x_{t\text{-}1} - x_{\mathrm{AVERAGE}}) +$
286 $\alpha_2(A_{\mathrm{MIN}} - A_{\mathrm{AVERAGE}}) = -2.64x_{t\text{-}1} + 6.83$] for acorn-poor years. Thus, when acorns were abundant, the slope of density dependence was less steep than in acorn-poor years (Fig. 2).
288 This means that high acorn production may relax the density dependence of wood mice.

290 The region contained by the two lines in Fig. 2 represents the variation in density dependence generated by acorn abundance. If the variation in density dependence is completely explained
292 by acorn abundance, observed growth rates should be included in this region contained by the two lines. Indeed, most observed growth rates were located in the region (Fig. 2), indicating
294 that these predictions of Model 2b are valid.

296 However, some unexpected predictions in this model were observed in the region to the left of the crossing point (Fig. 2). Assuming that acorn production was at its maximum and wood
298 mouse density (x_{t-1}) was extremely low (e.g., $x_{1996} = 0.003$), the model predicts the population growth rate to be 4.34. On the other hand, assuming minimum acorn production with an
300 extreme low density of wood mouse, the population growth rate was predicted to be 6.82. Higher population growth rates should be predicted when acorns are abundant, if the mouse
302 density is the same. However, because the two lines cross at the point $(\bar{x} - \frac{\alpha_2}{\alpha_3}, -\frac{\alpha_1\alpha_2}{\alpha_3})$, where $\bar{x}$ is the mean abundance of wood mice, Model 2b yields unrealistically high
304 population growth rates when acorn production is poor and mouse density is low.

306 To resolve these contradictory predictions, the nonlinear Ricker model (Model 3) was examined. Density dependence of wood mice and effects of acorn abundance were clearly
308 detected (Table 1). The mean α_1 was 0.890, and the lower limit of the 95% CI was positive (0.430). The mean α_2 was -0.199, and the higher limit of the 95% CI was negative (-0.041).
310 DIC indicates that Model 3 was the best model to represent wood mouse dynamics taking acorn effects in consideration.

312

Population growth rates predicted by Model 3 were plotted in Fig. 3. By assigning the maximum and the minimum acorn abundance, we obtained an equation representing density dependence [$x_t - x_{t-1} = \alpha_0 - \exp(\alpha_1(x_{t-1} - x_{\mathrm{AVERAGE}}) + \alpha_2(A_{\mathrm{MAX}} - A_{\mathrm{AVERAGE}})) = 1.94 - \exp(0.89x_{t-1} - 3.00)$] for acorn-rich years and [$x_t - x_{t-1} = \alpha_0 - \exp(\alpha_1(x_{t-1} - x_{\mathrm{AVERAGE}}) + \alpha_2(A_{\mathrm{MIN}} - A_{\mathrm{AVERAGE}})) = 1.94 - \exp(0.89x_{t-1} + 0.62)$] for acorn-poor years, respectively.

Both curves gradually sloped down until around $x_{t-1} = 2$, which was close to the crossing point of Model 2b, and when wood mouse density exceeded that density, the slopes of the curves became steeper. The curve for acorn-rich years was less steep than the curve for acorn-poor years and was always located above. This also indicates that high acorn production may relax the density dependence of wood mice and then enhance the equilibrium density: i.e., acorn abundance showed both “lateral” and “nonlinear perturbation” effects. In relation to the logistic model high acorn production enhances the carrying capacity (K).

In addition, these curves indicate that density effects are subtle at lower densities, while the effects are emphasised at higher densities. This non-linearity means that higher densities have stronger effects on population growth rates.

Discussion

A clear effect of acorn abundance was found consistently in all models that we examined (Table 1). Comparing Model 1 with Model 2b, it is noteworthy that the interaction term (α_3) between mice and acorns in Model 2b was clearly positive and that DIC indicated the

336 superiority of Model 2b over Model 1. These observations indicate that the interaction term is essential to describe the relationship between wood mice and acorn abundance. Moreover, the
338 fact that density dependence (α_1) was emphasised in Model 2b means that acorn abundance influences the strength of density dependence. This is also shown by the fact that α_3 can be
340 included in the term for x_{t-1} together with α_1 in Model 2b.

342 Royama (1992) conceptualised a density independent effect which shifts the equilibrium density to right or left, like the acorn effect in Model 1, as a "lateral perturbation effect" and a
344 different type of density independent effect which alters strength of density dependence, like the acorn effect in Model 2b as a "nonlinear perturbation effect". He adduces nest holes for
346 birds as an example of a "lateral perturbation effect" and crops for birds as a "nonlinear perturbation effect". Competition for nest holes can be characterised by a simple nest-to-bird
348 ratio, but consumption of crops cannot be measured by a simple crop-to-bird ratio, because the food is gradually depleted. Competition for crops may be more intense for the small
350 production of crops than for the large production. As a result the negative slope of population growth rates against density would become steeper for the small production than for the large
352 production. The present results based on Model 2b clearly demonstrate that acorn abundance acts as a "nonlinear perturbation effect" for density dependence of the wood mouse
354 population.

356 Direct density dependence (α_1) may be generated from intraspecific interactions for food or space in rodents. Although generalist predators are regarded as the main agents for direct
358 density dependence in Fennoscandia (Hansson and Henttonen 1988; Hanski et al. 2001;

Turchin and Hanski 2001; Korpimäki et al. 2004), this is not the case for the Japanese wood mouse because they are not preferred by predators in Hokkaido (Saitoh et al. 1999). There is some evidence suggesting intraspecific interactions in this species; density-dependent reduction in reproduction related to territoriality has been observed (Kondo and Abe 1978). We therefore suggest that self-regulation through competition for space or food is the most likely explanation of direct density dependence in the wood mouse in Hokkaido.

Density dependence (α_1) in Model 1 should be equivalent to [$\alpha_1 + \alpha_3 A_{t-1}$] in Model 2b. When acorn abundance is at maximum, [$\alpha_1 + \alpha_3 A_{t-1}$] is -1.26 in Model 2b. This value is very close to α_1 (-1.207) in Model 1. Thus, α_1 in Model 1 may show the strength of density dependence in a condition without constraints of acorn abundance. In other words, although wood mice may potentially be subject to very severe density dependence, density dependence is relaxed by an increase in acorn abundance.

Yoccoz et al. (2001) suggested that interactions between food and density may alter the density-dependent structure. Although they expected that food availability would modify the slope of the regression between population growth rate and rodent density, they failed to find such an effect of food availability on density dependence in bank vole (*Clethrionomys glareolus*) populations. Since bank voles are intermediate between herbivorous and granivorous, and they consume a large variety of food items (Hanson 1985), the interactions between food and their abundance may be more complex.

Though our time series was rather short (16 years), it clearly showed that the strength of density dependence of the wood mouse was altered by acorn abundance (Figs. 2 and 3). The diet of the wood mouse (genus *Apodemus*) is predominantly seeds and their abundance is affected by seed availability (Flowerdew 1985; see also Montgomery 1989a, b; Montgomery and Montgomery 1990). Masting seeding improves reproduction and survival of *Apodemus* (Montgomery et al. 1991; see Wilson et al. 1993 and Shimada and Saitoh 2006 for reviews).

The two lines in Fig. 2 represent the range of variation in population growth rates, which is generated by variation in acorn abundance. The region contained by the two lines covers the variation in the observed growth rates well when wood mouse density exceeds $\bar{x} - \frac{\alpha_2}{\alpha_3}$. Model 2b, however, yields unrealistic predictions under that density; population growth rates predicted under acorn-poor conditions exceed those under acorn-rich conditions (Fig. 2).

The nonlinear model (Model 3) resolves this problem (Fig. 3). The curve for acorn-rich years is always located above the curve for acorn-poor years and the fact that the curve for acorn-rich years is less steep also demonstrates that acorn abundance has a "nonlinear perturbation effect" on density dependence of the wood mouse population. In addition, both curves indicate that higher densities have stronger effects on population growth rates. This nonlinear nature of density dependence is also noteworthy.

Strong (1986) argued for the true existence of the nonlinearity of density dependence, and Stenseth (1999) encouraged the investigation of questions "relating to the extent of nonlinearity and where in the interacting system such nonlinearity is located" to understand

404 the rodent cycle. Stenseth (1999) showed that the density-dependent structure during the increase phase differs from that during the decrease phase in the grey-sided vole in Finland
406 (see also Framstad et al. 1997; Stenseth et al. 1998). Lima et al. (2002a) found that density effects could be negligible below a threshold density in a shrew population.

408

The density of wood mice at for $x_{t-1} = 2$, from which density effects were emphasised, is
410 equivalent to 7-8 individuals per hectare in the study population. Home ranges of adult females of the wood mouse are spaced apart, and the home range size is 604–962 m^2 during
412 the breeding season; in contrast, those of adult males overlap with each other and with those of females, and are 858–1853 m^2 during the breeding season (Oka 1992). Since 1 ha (10,000
414 m^2) is sufficiently large for 7-8 females to establish exclusive home ranges, intraspecific competition may be minor below this density level.

416

We have found that the strength of density dependence was altered by acorn abundance, and
418 we have demonstrated the nonlinearity of density dependence of the wood mouse population. We make the following suggestions for further studies on density dependence in rodent
420 populations, dynamics of wood mouse populations, and rodent-seed interactions:

1. In contrast to our results, Yoccoz et al. (2001) concluded that the effects of food on
422 density dependence are negligible in the bank vole (*Clethrionomys glareolus*). Our results suggest that wood mice compete for acorns, whereas direct density dependence
424 of bank vole populations may not be generated by competition for food, but for other resources. Generalist predators may be agents for direct density dependence of the

bank vole. Comparative studies on density-dependent mechanisms between *Apodemus* and *Clethrionomys* would therefore be of interest.

2. We have demonstrated nonlinearity in density dependence. Density effects are minor at low-density levels. We recommend comparing space use and dispersal patterns of wood mice between low- and high-density conditions.
3. The nonlinear model in Fig. 3 does not perfectly represent the observed variation in population growth rates. Since the model consists of variables in the previous year (t - 1), the variation that derives from effects in the current year (t) is not covered. Studies on food resources or other factors in the current year that influence the reproduction of the wood mouse should be conducted. In addition information under low density conditions which is scarce in this study should be accumulated. The model would be revised using such information.

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566

568

570 Table 1. Estimated coefficients of each model. Density effects of wood mice (α_1), direct effect of acorn abundance (α_2), interaction between wood mice and acorns (α_3), and a constant (α_0) are shown. SD and 95% CI indicate standard deviation and 95% credible interval, respectively.
572 DIC (Deviance Information Criterion) is a Bayesian method for model comparison.

	α_0			α_1			α_2			α_3			
	mean	SD	95% CI	mean	SD	95% CI	mean	SD	95% CI	mean	SD	95% CI	DIC
Model 1				-1.207	0.233	[-1.662, -0.738]	0.366	0.132	[0.109, 0.635]				339.4
Model 2a				-1.739	0.335	[-2.466, -1.127]	0.342	0.099	[0.150, 0.544]	0.288	0.124	[0.050, 0.546]	337.8
Model 2b				-1.747	0.359	[-2.543, -1.119]	0.342	0.103	[0.148, 0.555]	0.287	0.124	[0.051, 0.544]	334.7
Model 3	1.944	0.741	[0.355, 3.343]	0.890	1.130	[0.430, 2.954]	-0.199	0.232	[-0.644, -0.041]				321.3

574

576 Figure legends

578 Fig. 1 Annual changes in acorn and wood mouse abundance. Acorn abundance is represented by the number of acorns per oak tree (upper panel). Wood mouse abundance is represented by 580 the minimum number alive per one ha (lower panel). The numbers in the two study sites were summed. Note that wood mouse abundance lags one year behind acorn abundance.

582

Fig. 2 Observed (circles) and predicted (triangles) population growth rates of the wood mouse 584 against density based on Model 2b. The darkness of the circles indicates the relative abundance of acorns; darker circles indicate richer acorn production. Predicted population 586 growth rates were obtained using Model 2b: $x_t - x_{t-1} = (\alpha_1 + \alpha_3(A_{t-1} - A_{\mathrm{AVERAGE}}))(x_{t-1} - x_{\mathrm{AVERAGE}}) + \alpha_2(A_{t-1} - A_{\mathrm{AVERAGE}})$. By assigning the maximum acorn abundance (A_{2006}), an equation 588 representing density dependence ($x_t - x_{t-1} = -1.26x_{t-1} + 4.34$) was obtained for an extreme case of acorn-rich years, whereas by assigning the minimum acorn abundance (A_{1996}), an equation 590 representing density dependence ($x_t - x_{t-1} = -2.64x_{t-1} + 6.83$) was obtained for an extreme case of acorn-poor years. The two lines cross at the point $(\bar{x} - \frac{\alpha_2}{\alpha_3}, -\frac{\alpha_1\alpha_2}{\alpha_3})$.

592

Fig. 3 Observed (circles) and predicted (triangles) population growth rates of the wood mouse 594 against density based on Model 3. The darkness of the circles indicates the relative abundance of acorns; darker circles indicate richer acorn production. Predicted population growth rates 596 were obtained using Model 3: $x_t - x_{t-1} = \alpha_0 - \exp(\alpha_1(x_{t-1} - x_{\mathrm{AVERAGE}}) + \alpha_2(A_{t-1} - A_{\mathrm{AVERAGE}}))$. Two curves were obtained for an extreme case of acorn masting: $x_t - x_{t-1} = 1.94 - \exp(0.89x_{t-1} + 0.62)$ 598 for acorn-poor years and $x_t - x_{t-1} = 1.94 - \exp(0.89x_{t-1} - 3.00)$ for acorn-rich years.

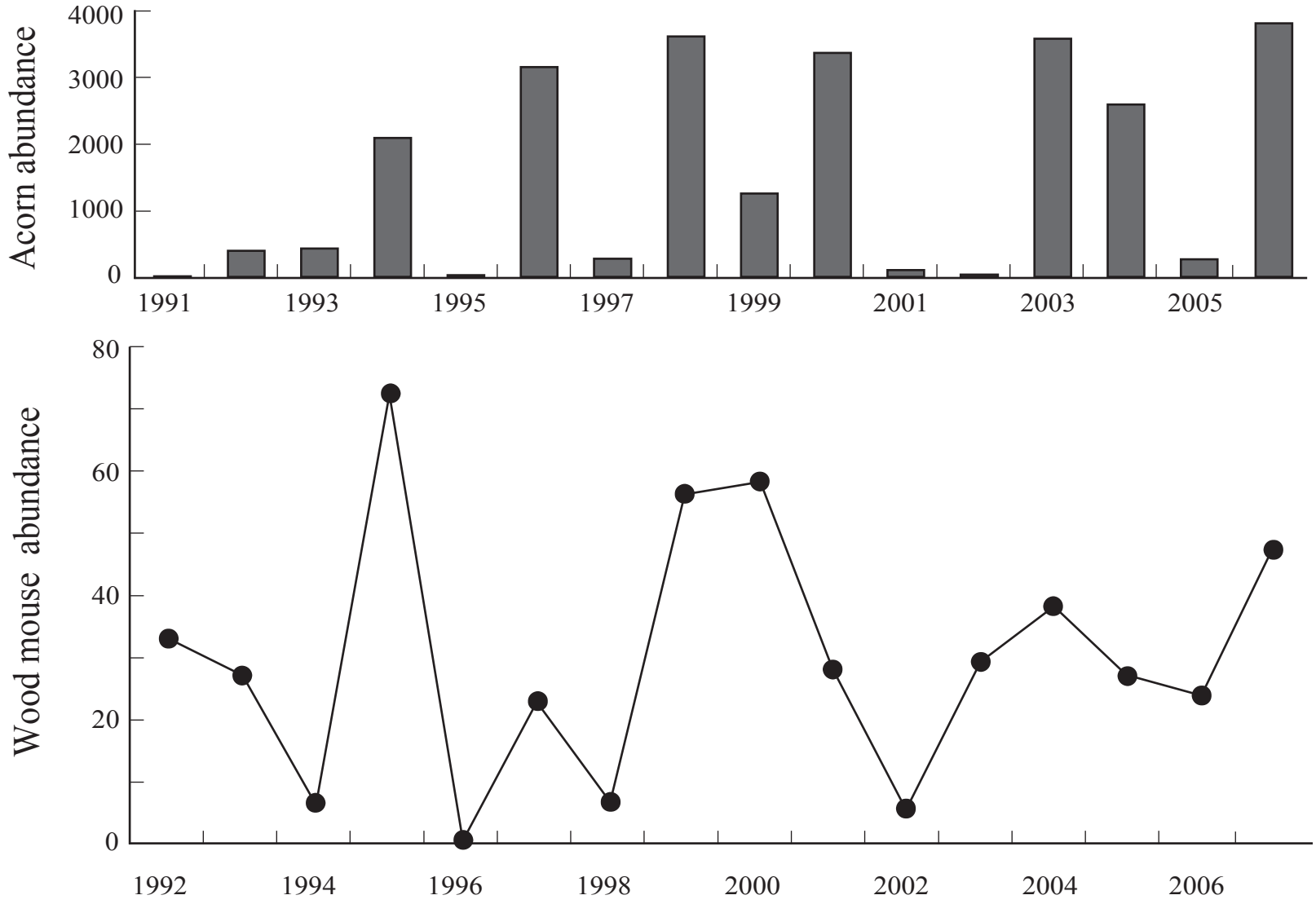
Acorn abundance
4000
3000
2000
1000
0
1991
1993
1995
1997
1999
2001
2003
2005
Wood mouse abundance
80
60
40
20
0
1992
1994
1996
1998
2000
2002
2004
2006

Figure 1

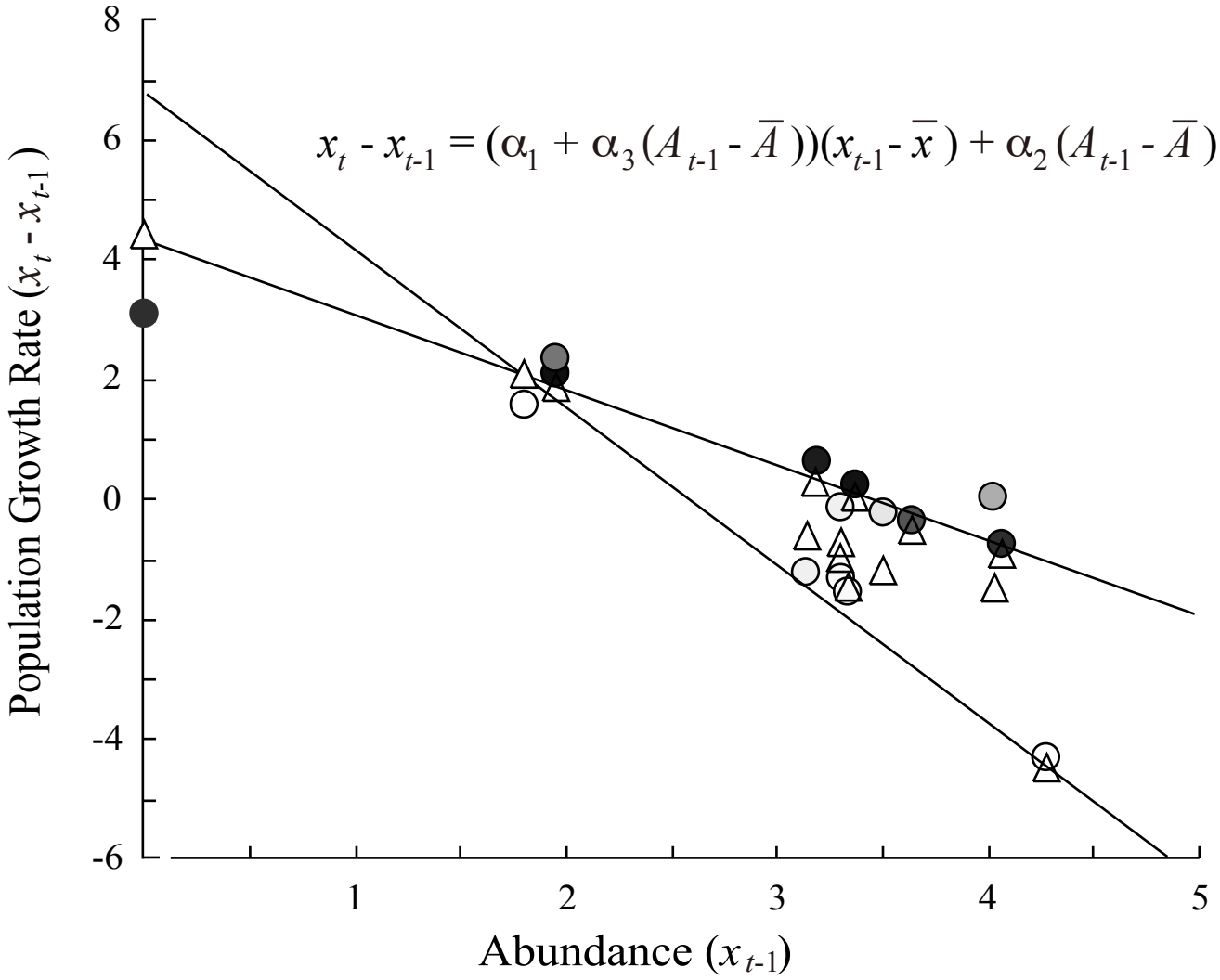
$x_t - x_{t-1} = (\alpha_1 + \alpha_3 (A_{t-1} - \bar{A}))(x_{t-1} - \bar{x}) + \alpha_2 (A_{t-1} - \bar{A})$
Population Growth Rate ($x_t - x_{t-1}$)
Abundance (x_{t-1})
8
6
4
2
0
-2
-4
-6
1
2
3
4
5

Figure 2

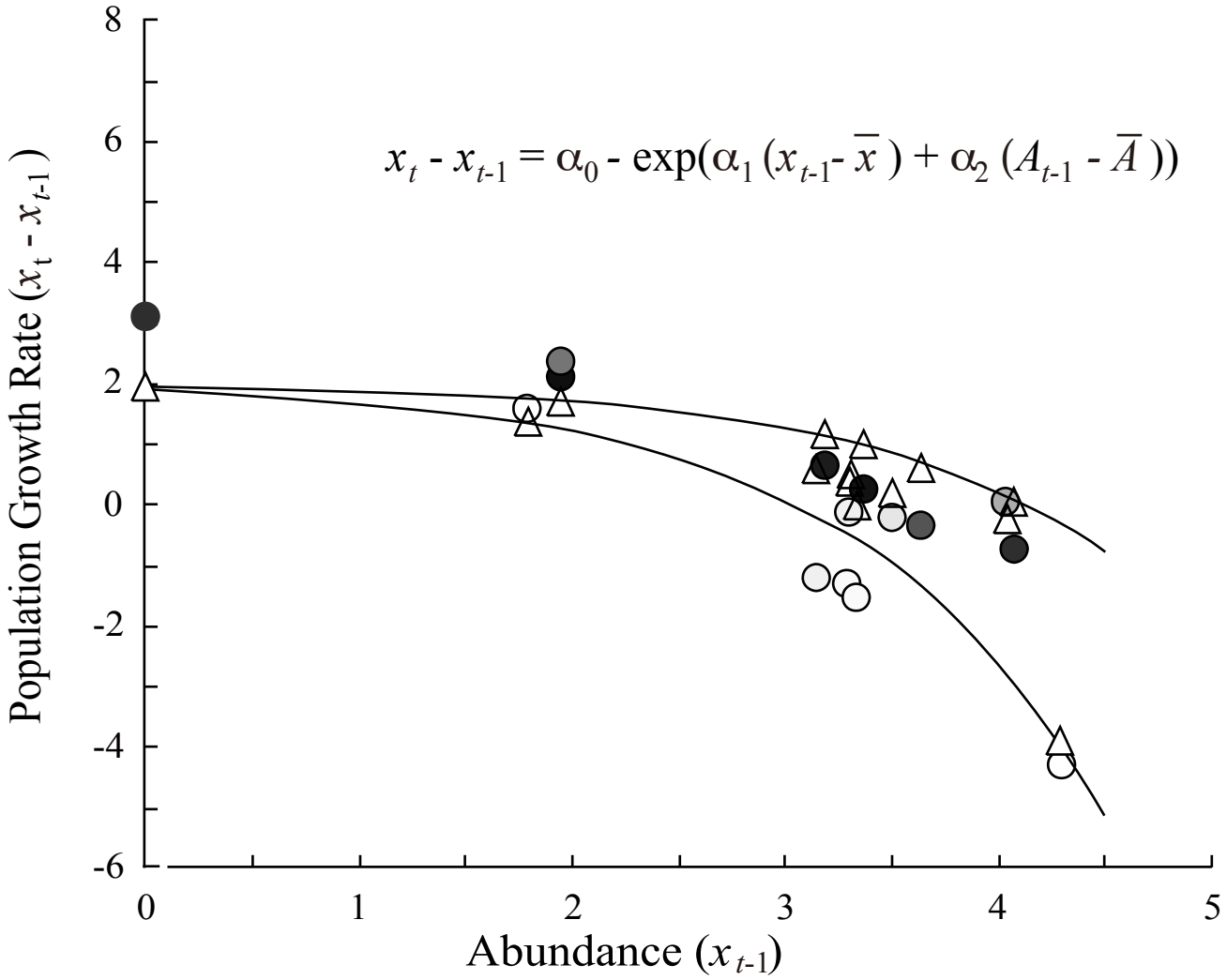
$x_t - x_{t\text{-}1} = \alpha_0 - \exp(\alpha_1 (x_{t\text{-}1} - \bar{x}) + \alpha_2 (A_{t\text{-}1} - \bar{A}))$
Population Growth Rate ($x_t - x_{t\text{-}1}$)
Abundance ($x_{t\text{-}1}$)
8
6
4
2
0
-2
-4
-6
0
1
2
3
4
5

Figure 3