The impact of forestry on the small rodent community of Hokkaido, Japan

Takashi SAITOH¹ and Atsushi NAKATSU²

Hokkaido Research Centre, Forestry and Forest Products Research Institute, Hitsujigaoka 7,
Toyohira, Sapporo 062, Japan

Fax. +81-11-851-4167, ¹e-mail. bedford@ffpri-hkd. affrc. go. jp

²e-mail. nakatsua@ffpri-hkd. affrc. go. jp

Abstract. The structure of small rodent communities, in both natural forests and young plantations, in the Asahikawa region of Hokkaido, Japan, in relation to the effects of long-term and large-scaled forestry, was analyzed using census data spanning the 31 years from 1962 to 1992. Rodent communities in both natural forests and plantations consisted largely of four species: *Clethrionomys rufocanus*, *C. rutilus*, *Apodemus argenteus*, and *A. speciosus*. *Clethrionomys rufocanus* was found to be dominant in both habitats, however the relative abundance of species differed significantly between habitats. Although the dominance of *C. rufocanus* was most obvious in forestry plantations, the proportion it contributed to the community decreased during the 1980s. Conversely, *Apodemus* species have increased in both habitats over the same period. Rodent species diversity has increased in the last decade. The decline in the proportion of *C. rufocanus* has occurred in parallel with the decrease in the area of land under forestry plantation, which is the preferred habitat for *C. rufocanus*. These findings indicate that monocultural habitats, such as forestry plantations, may support super dominant species such as *C. rufocanus*, which results in an impoverished rodent community, in terms of species diversity.

Key words: *Apodemus*, *Clethrionomys*, forest structure, species diversity.

Intensive silvicultural practices including site preparation, removal of potentially competing species, replacement of naturally occurring diversity with single species, and extensive use of herbicides, fertilizer and pesticides, transform natural ecosystems into a timber production system. Monotonous forestry plantation is, in other words, an artificially transformed, and greatly simplified habitat for animals. The faunas of such artificial forests have been intensively investigated for comparison with those of natural forests, and the effects of the introduction of monoculture on faunas have been widely discussed. Most previous studies have, however, been of a short-term nature, and on a limited spatial scale.

Bird densities and species diversity are, for example, generally lower in plantations, especially in young plantations, than in natural forests (Fujimaki

1970, Ishigaki and Matsuoka 1972, Ishigaki *et al.* 1973, Kobayashi and Fujimaki 1985, Yui and Suzuki 1987; see also Murai and Higuchi 1988 for a review). Small mammal faunas also differ between natural and planted forests. Even when the species composition remains similar, the dominance of the predominant species, for example, is enhanced in forestry plantations (Ota *et al.* 1977, see also Ota 1984 for a review). Increases in the abundance of specific vertebrate species have also been observed on areas of forest clear-cuts (Hansson 1994). Thus, a forest managed for maximum timber yield may be best regarded as analogous, in ecosystem terms, to a monocultured wheat field (Meffe and Carrol 1994). If the scale of operation was extended, so that the landscape became thoroughly transformed over several decades, then the effects of the plantation would be likely to become profound. Little is known, however, about such effects, because study on them requires wide-ranging long-termed investigation.

In the 1950s, the Japanese Forestry Agency investigated a policy to transform natural forests into more productive plantations. As a consequence of this policy, considerable areas of natural forests were clear-cut and transformed into single species, largely coniferous, plantations. In Hokkaido, Japan's northernmost island, this policy was implemented faithfully and extensively. During the peak period, more than one percent of natural forests were cut and transformed into coniferous plantations each year.

Because young plantations were frequently damaged by the grey-sided vole, *Clethrionomys rufocanus* Sundevall, the Forestry Agency has, since 1954, carried out censuses of small rodents, for management purposes, in forests all over Hokkaido. That census data have proven invaluable. It has enabled us to describe, in this paper, changes in the structure of small rodent communities, in both natural forests and young plantations in Hokkaido over three decades from 1962 to 1992, and to analyze the effects of long-term, large-scaled plantations on small rodent communities.

MATERIALS AND METHODS

1. Study area and census methods

Since 1954 the Forestry Agency has carried out censuses of rodent populations at approximately 1,000 sampling locations all over the 78,073 km² island of Hokkaido (41°24'–45°31'N, 139°50'–145°49'E). The forests under Forestry Agency Management cover 28,300 km² (21,500 km² of natural forests, and 6,800 km² of plantations). In 1990, these forests were managed by 81 District Offices, which were subdivided into Ranger Offices. The censuses were carried out by each individual Ranger Office. The data analyzed for this paper come from 8,034 km² of northern Hokkaido (corresponding to about 10% of the island's total area) under the supervision of the Asahikawa Sub-regional Office. Our study areas included 22 District Offices, which consisted of 113 Ranger Offices in 1990. Most of the natural forests in this area are classified as "pan mixed forests" with needle and broad-leaved trees, in what is regarded as a transition

zone between the temperate and boreal zones (Tatewaki 1958). The dominant tree genera here are: *Abies*, *Acer*, *Betula*, *Picea* and *Quercus* (Tatewaki 1958).

Trapping was carried out three times a year, in spring (May or June), summer (July or August) and autumn (September or October). Ranger Offices set 50 snap traps, at 10 m intervals on 0.5 ha (50 × 100 m) grids, over either three or five consecutive nights. Since rodent abundance in Hokkaido usually reaches its peak in autumn, and because autumn populations are known to reflect accurately annual variation in populations (Saitoh 1987), we used autumn census data in our analyses.

Four rodent species, *C. rufocanus*, *C. rutilus* (Pallas), *Apodemus speciosus* (Temminck), and *A. argenteus* (Temminck) were recorded during the censuses. *C. rex imaizumi*, *A. peninsulae* (Thomas), and several species of shrew, *Sorex* spp., also occur in the region and may have been caught occasionally. These less common species were, however, not reported officially.

Each Ranger Office censused 2–6 separate sites. Census grids were usually located in selected habitats (young plantations, and natural forests neighbouring plantations) which together constituted a unit. Census sites were sometimes relocated within the area of a given Ranger Office, and methods have changed over the period of study. From 1962 to 1976, for example, traps were set for five nights, whereas from 1977 to 1992 a three-night trapping scheme was employed. To make these two data sets compatible for time-series analyses, the data from the first 15 years were transformed to three-night equivalents (*i.e.*, 150 trap nights), using the regression of the three-night (*y*) on the five-night (*x*) captures ($y = 0.68066x + 0.18127$, $r^2 = 0.935$).

For the purposes of this study, rodent abundance is defined as the number of individuals caught per 150-trap-nights. Species diversity and species ratios were calculated based on the data from the four main rodent species. The Shannon-Wiener function (index of evenness, J') was used as an index for species diversity (Krebs 1989). As data for 1970 and 1974 have been lost (except for on *C. rufocanus*), values have been calculated excluding the data from these two years. Moving averages, for each three year period, were used to smooth annual variation. For the calculation of moving averages, for periods including the years 1962, 1970, 1974, and 1992, values were obtained from the data for the associated two years.

2. Forest management

Forest planting follows several silvicultural procedures. For this paper we focused on the most drastic method of transforming a natural system into an artificial one; that is young plantations grown on clear-cuts. After clearance of natural forest, weeds are removed from the clear-cut, then larch, *Larix kaempferi* (Lambert) or fir, *Abies sachalinensis* Fr. Schmidt seedlings are planted densely. Because weeds grow thickly in young plantations and may suppress the growth of tree seedlings, the weeds are cut every summer until between five and nine years after tree planting. Censuses were carried out in such young plantations until ten years after planting.

3. The voles and mice

The grey-sided vole, *Clethrionomys. rufocanus*, is common in both open fields and in natural forests and plantations in Hokkaido. This species is well known for exhibiting a wide spectrum of population dynamics ranging from stable to cyclic (Saitoh 1987, Bjørnstad *et al.* 1996, Stenseth *et al.* 1996, Saitoh *et al.* 1997). This small (30–40 g), short-tailed (around 40% of head and body) rodent is more folivorous than other *Clethrionomys* species (Hansson 1985). This feeding habit is particularly prevalent in Hokkaido, possibly due to the absence of *Microtus* spp. This is consistent with its wider habitat preference from open fields to natural forests in Hokkaido. During winter, *C. rufocanus* eats mainly leaves and shoots of bamboo grass, and some shrub/tree bark. During summer it eats various forbs and grasses, and in autumn, acorns are eaten to some extent (Ota 1984).

The red-backed vole, *C. rutilus*, is a short-tailed, forest-dwelling rodent. Its body shape is similar to that of *C. rufocanus*, though at 20–30 g, it is smaller. Although *C. rutilus* is essentially granivorous (Hansson 1985), it also eats, to some extent, insects year around (Ota 1984). Its abundance is usually low in Hokkaido, though it sometimes dominates in mature coniferous forests (Ota 1984).

The Japanese wood mouse, *A. argenteus*, is endemic to Japan (though ecologically equivalent to *A. sylvaticus* of Eurasia). It is small, weighing just 15–20 g, and has a relatively long tail which is longer than its body length. At a weight of 40–60 g, *A. speciosus*, another Japanese endemic mouse, is the largest of the four species analyzed here. Its tail is relatively short (77–99% of body length) for a mouse-shaped rodent. These two *Apodemus* species are both largely granivorous, though they also eat a considerable amount of insects (Ota 1984). The larger species *A. speciosus* prefers larger seeds such as acorns, walnuts, or pine nuts, whereas *A. argenteus* eats smaller seeds and berries.

The main habitats of these two species include various forest types. The two species are usually dominant in natural forests, though *A. speciosus* is also found in open fields.

RESULTS

1. Species composition

The total of 223,663 rodents were trapped during the 31 year study period ; 122,653 of these were from 6,438 census grids in natural forests, and 101,010 were from 5,222 grids in young plantations. The average number per trapping grid in the two types of forests were very similar : 19.1 for natural forests and 19.3 for plantations.

The proportion of *Clethrionomys rufocanus* to the total number of rodents captured, exceeded 50% in both natural forests and plantations (Fig. 1).

Although the order of dominance (*C. rufocanus* > *A. argenteus* > *A. speciosus* > *C. rutilus*) was the same in natural forests and in plantations, relative proportions of each species differed significantly between them (*G*-test, $G_{adj}=449.3$,

Fig. 1. The proportion of rodent species in natural forests and plantations in the Asahikawa region, Hokkaido, Japan. Figures in parentheses indicate the total number of rodents caught during the 31 year census.

$p < 0.001$, Sokal and Rolf 1995). The dominance of *C. rufocanus* was particularly obvious in plantations. Because *C. rutilus* was very uncommon, our main analyses are of the other three species.

2. Variation in species abundance

Rodent abundance fluctuated greatly from year to year, particularly at two to four year intervals, both in natural forests and in plantations (Figs. 2a, 2b). This pattern may be led by the demographic features of the dominant species, *Clethrionomys rufocanus*. Basic statistics of population dynamics are given in Table 1. Note that values indicating variability (*i.e.*, CV, *s*-value, and Max/Min ratios) were moderated owing to averaging the abundance of rodents on more than 100 census grids.

The relative proportion of *C. rufocanus* was correlated with its abundance, whereas this relationship was not found in other species, with the exception of *A. speciosus* in plantations (Table 2). These vague relationships among *Apodemus* species, attributed to the positive correlation in abundance with *C. rufocanus*, which was most influential on the proportions of the various species (Table 3). Even when the abundance of an *Apodemus* species increased, it still did not represent a large proportion of the community because *C. rufocanus* was always even more abundant. The abundances of the three main species were generally correlated with each other in both natural forests and plantations (Table 3).

Table 1. Basic statistics for rodent abundance. Data on *C. rutilus* was eliminated because of its scarcity. Note that values indicating variability (i.e., CV, Max/Min ratio and s-value) were moderated owing to averaged figures.

	<i>C. rufocanus</i>	<i>A. argenteus</i>	<i>A. speciosus</i>
Natural forests			
Average	9.49	5.16	3.55
CV (%)	51.90	41.30	62.20
Max.	19.28	10.21	10.40
Min.	1.49	1.25	0.67
Max./Min.	12.95	8.16	15.42
s-value	0.29	0.21	0.28
Plantations			
Average	10.69	4.87	3.11
CV (%)	53.30	44.10	62.40
Max.	22.52	10.92	9.80
Min.	1.31	1.14	0.63
Max./Min.	17.24	9.59	15.55
s-value	0.31	0.22	0.29

Table 2. Relationships between abundance and proportion in the three species are given using Kendall rank-order correlation coefficient τ ($n=29$). Figures in parentheses are probabilities of a Type I error for Kendall's τ .

	<i>C. rufocanus</i>	<i>A. argenteus</i>	<i>A. speciosus</i>
Natural forest	0.468 (0.000)	0.094 (0.476)	0.217 (0.099)
Plantations	0.429 (0.001)	0.244 (0.063)	0.274 (0.037)

Species proportions were, however, negatively correlated between *C. rufocanus* and the two *podemus* species, whereas a positive relationship was found between the two *Apodemus* species (Table 3). Positive correlations between the two *Apodemus* species, both in abundance and species proportion, indicate that competition between them is probably not severe. Species proportions fluctuated from year to year with some clear patterns revealed by moving averages (Figs. 2a, 2b). *C. rufocanus* seemed to have gradually lost its dominance in both natural forests and plantations since the 1980s (Fig. 3a, 3b). In contrast to the decline in *C. rufocanus*, *Apodemus* species contributed a steadily increasing proportion of the community in the later years of the study.

3. Species diversity

Species diversity values in natural forests fluctuated around 0.7 during the 1960s and early 1970s, increased from the late 1970s to the early 1980s, and thereafter attained relative stability at 0.8. The change in species diversity in plantations exhibited a very similar pattern to that in natural forests, although

Fig. 2. Fluctuation of rodent abundance in: a. natural forests and b. new plantations. Abundance is shown as the number of rodents caught per 150-trap night. Lozenge: the total number, solid circle: *C. rufocanus*, triangle: *A. argenteus*, square: *A. speciosus*, and open circle: *C. rutilus*.

Fig. 3. Changes in rodent species ratios in: a. natural forests, and b. new plantations. Species proportions are shown with moving averages for each three year period. Solid circle: *C. rufocanus*, triangle: *A. argenteus*, square: *A. speciosus*, open circle: *C. rutilus*.

Table 3. Relationships of abundance and proportion between the three species of rodents (*C. rufocanus* [*Cr*], *A. argenteus* [*Aa*], and *A. speciosus* [*As*]) in the two types of forests are given using Kendall rank-order correlation coefficient τ ($n=29$). Figures in parentheses are probabilities of a Type I error for Kendall's τ . Upper matrix for natural forests, lower matrix for plantations.

	Abundance			Proportion		
	<i>Cr</i>	<i>Aa</i>	<i>As</i>	<i>Cr</i>	<i>Aa</i>	<i>As</i>
<i>Cr</i>	—	0.301 (0.022)	0.281 (0.032)	—	-0.709 (0.000)	-0.668 (0.000)
<i>Aa</i>	0.222 (0.091)	—	0.655 (0.000)	-0.778 (0.000)	—	0.387 (0.003)
<i>As</i>	0.266 (0.043)	0.640 (0.000)	—	-0.699 (0.000)	0.478 (0.000)	—

the species diversity in plantations was almost always lower than that in natural forests (Fig. 4, Wilcoxon signed-ranks test, $Z = -4.249$, $p < 0.0001$). Species diversity in natural forests during the latest ten years averaged 0.8, which was significantly higher than during the first ten years (0.7, Random permutation test, $p = 0.001$). A similar significant pattern was also observed in plantations, where species diversity averaged 0.6 in the first decade, and 0.8 in the latest (Random permutation test, $p = 0.0012$).

4. Species diversity and forestry

Extensive forest planting took place during the 1960s and early 1970s in Hokkaido. More than one percent of natural forests (more than 7,000 ha) were felled, and coniferous seedlings were planted on the clear-cuts within a year. Since the 1970s, however, planting effort has decreased (Fig. 4). The pattern of planting has been closely followed by the proportion of the small rodent community contributed by *C. rufocanus* (Fig. 3). The proportion of *C. rufocanus* was highly correlated with the area of new plantations (Kendall's $\tau = 0.897$, $p < 0.001$ for natural forests; $\tau = 0.566$, $p < 0.001$ for plantations).

DISCUSSION

The gray-sided vole, *C. rufocanus*, was found to be the most abundant small rodent in both natural forests and plantations (Fig. 1). Its dominance was most obvious in plantations. The young plantations, where the censuses were carried out, were open and herb-dense habitats and the preferred habitat of *C. rufocanus* in Hokkaido (Ota 1984). Thus, the dominance of *C. rufocanus* in plantations is consistent with previous studies (Ota *et al.* 1977, Ota 1984). The present results, indicating that *C. rufocanus* contributed over 50% of small rodent communities even in natural forests, should, however, be noted. Previous studies have indicated that either *A. argenteus*, or *A. speciosus* is usually

Fig. 4. Changes in rodent species diversity and in the area of new plantations. The Shannon-Wiener function (index of evenness, J') was used as an index for species diversity. Species diversity is shown with moving averages for each three year period. Circle: species diversity in natural forests, triangle: species diversity in plantations, square: new plantation area.

dominant in mature natural forests, even though *C. rufocanus* is also common there (Ota *et al.* 1977, Ota 1984). The extensive areas of plantation contiguous with the natural forests studied here may have led to the increased proportion of *C. rufocanus* in natural forests.

The prominent dominance of *C. rufocanus* caused species diversity to be low during the 1960s and early 1970s (Figs. 3, 4). Thereafter, as the proportion of *C. rufocanus* decreased, species diversity increased. These changes were consistent with changes in forestry planting effort. These findings suggest that monocultural habitats, such as forestry plantations, may support a super dominant species (in this case *C. rufocanus*), which suppresses species diversity in the rodent community.

The censuses were carried out continuously on the same types of habitats (on young plantations and on natural forests neighbouring plantations) throughout the study period. Thus the decrease in the relative proportion of *C. rufocanus* was not caused by environmental changes on census grids. The present results should, therefore, reflect changes in rodent communities in more extensive areas than just on census grids; thereby indicating that long-term, extensive forestry practices may simplify the rodent community not merely in the plantations themselves but also in the natural forests surrounding large scale plantations.

Nakatsu (1988, 1992) has also reported changes in species proportion based

on the same census data that we analyzed; he did not analyze the data as a time-series, but his data set, however, covered all regions of Hokkaido. Although Nakatsu (1988, 1992) also found a significant reduction in the proportion of *C. rufocanus* in the Asahikawa region, he did not find such a reduction in either Kitami or Obihiro regions, where planting efforts were also decreasing during the 1980s.

A clear relationship between rodent communities and forestry plantations was revealed in this study. We do not think that this relationship is superficial, and believe that extensive forestry planting may simplify the rodent community on a large scale. The present analyses are not robust enough, however, to prove this, because different types of rodent population fluctuations were pooled in this study (see Bjørnstad *et al.* 1996), and because this study tells nothing about the regional differences in species proportion that Nakatsu (1988, 1992) observed. To resolve these problems more detailed analyses are required.

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