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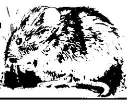

The Biology of the Vole *Clethrionomys rufocanus*: a Review

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Abstract. The biology of the gray-sided vole *Clethrionomys rufocanus* in Hokkaido, concerning taxonomy, morphology, phylogeny, distribution, and natural history, is reviewed. Applied issues in forest management (damage, control and census) are also mentioned. Although *Clethrionomys rufocanus* of Hokkaido was originally identified as a distinct species, *Evotomys* (=now *Clethrionomys*) *bedfordiae* Thomas, 1905, current literature generally refers to the gray-sided vole of Hokkaido as *Clethrionomys rufocanus* or as *C. rufocanus bedfordiae* (vernacular name, the Bedford's red-backed vole). The gray-sided vole is the most common small mammal in Hokkaido. It inhabits open areas as well as forests, and mainly feeds on green plants. The gray-sided vole has a high reproductive potential; litter size: 4–7; gestation period: 18–19 days; maturation age: 30–60 days old. Although spring-born individuals usually attain sexual maturity in their summer/fall of birth, their maturation is sometimes suppressed under high densities. The breeding season is generally from April to October, but with some regional variation. *Clethrionomys rufocanus* has a rather specialized diet (folivorous), particularly during winter when it feeds on bamboo grass. Many predators specialize on the grey-sided vole in Hokkaido; even the red fox, which is a typical generalist predator, selectively feeds on this vole. Damage by voles' eating bark used to be sever on forest plantations in Hokkaido. Censuses of small rodents have been carried out for management purpose since 1954.

Key words: biogeography, forest damage, life history, monitoring, taxonomy.

Introduction

Cyclic population fluctuations of the gray-sided vole *Clethrionomys rufocanus* (Sundevall, 1846) have fascinated many ecologists, both in Fennoscandia (Kalela 1957, 1971; Viitala 1977), in Siberia (Koshkina 1957, 1966; Semenov-Tjan-Shanskij 1970) and in Japan (Kinoshita 1928; Ota 1958a, 1968; Ota et al. 1959; Abe 1976a). This species has been intensively studied in Japan both from an applied perspective (forest damage) as well as from the perspective of basic ecology. Ueda et al. (1966) and Ota (1984) provided comprehensive reviews of the Japanese works. More recent studies on this species include Henttonen et al. (1977, 1987), Saitoh (1981, 1987, 1989, 1990, 1991, 1995), Nakata (1984, 1989), Kawata (1985, 1987, 1988, 1989), Ims (1987a, b, c, 1988, 1989, 1990), Ylönen and Viitala (1987), and Ishibashi et al. (1997). The volume edited by Stenseth (1985a) summarized much of what was known, particularly on the basis of the Western literature, at the time about this species and its congeners.

Besides providing a review of the Western literature on the species, the main purpose of this paper is to summarize the Japanese literature on the vole *Clethrionomys rufocanus* and to integrate it with other available studies on the species. Even though some of this literature pertaining to ecological issues have been summarized in English in two recent papers (Bjørnstad et al. 1998a; Saitoh et al. 1998a), we repeat some of this here in order to provide as complete as possible an account of the basic biology of the species

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and its ecological relationship to its environment. Besides providing a taxonomic account of *C. rufocanus* found in Hokkaido, we describe the initiation and basis for the monitoring program set up over the entire Hokkaido for the purpose of monitoring forest plantations against vole damage. For a review of social behavior and social organization, see Ishibashi et al. (1998a, b).

The genus *Clethrionomys*

Roughly speaking there are, within the family Muridae (Rodentia), three types of body shape: the mouse type which is small with a long tail, the rat type which also has a long tail but is larger than the mouse type, and the vole type which is small with a short tail. The red-backed voles (genus *Clethrionomys*) are of the vole type and belongs to the subfamily Arvicolinae including the genera *Microtus, Lemmus* and others (see e.g. Wilson and Reeder 1993). The genus *Clethrionomys* has rooted molar teeth which persist during adult life, being a primitive feature and differing from most other voles with rootless molar teeth, which continue to grow throughout their life. The red-backed vole is, therefore, thought to be less adapted to tough vegetation (Corbet and Harris 1991).

Species in this genus used to be listed under *Evotomys* (e.g. Hinton 1926) until Palmer (1928) established the priority of *Clethrionomys. Clethrionomys* is thought to be most closely related to *Eothenomys* (Iwasa 1998); some authors regard *Clethrionomys* as congeneric with *Eothenomys* (e.g. Corbet 1978; Corbet and Hill 1991).

Clethrionomys contains seven species (Table 1) found widely distributed throughout the Northern Hemisphere (e.g. Stenseth 1985b). These species show great karyotypic similarities (Gamperl 1982; Modi and Gamperl 1989; Yoshida et al. 1989; Obara et al. 1995); all have $2n=56$, with 26 pairs of acrocentric and one pair of metacentric.

Males and females of different species of *Clethrionomys* copulate readily when paired in the laboratory, although they exhibit a preference for conspecific mating when given the choice (Rauschert 1963). Experimental crosses of *C. rufocanus* of Hokkaido produced interspecific hybrids with *C. rex* (Tsuchiya unpublished), whereas the crosses failed to produce progeny between *C. rufocanus* and *C. rutilus* of Hokkaido (Tsuchiya personal communication). Experimental interbreeding of *C. glareolus* and *C. rutilus* from Eurasia (Zimmermann 1965) and of the English *C. glareolus* and the Canadian *C. gapperi* (Grant 1974) also produced interspecific hybrids. Female progeny from such crosses was fertile, but male progeny was sterile. However, experimental crosses between *C. rutilus* from North America and *C. gapperi* gave no progeny (Matthey 1953; Zimmermann 1965).

Most species of the *Clethrionomys* inhabit cold, mossy, rocky forests and woodlands in both dry and moist areas (Hansson 1985a,b); they also inhabit tundra and bogs. They are active during night and day, summer and winter, scurrying and climbing about stumps, fallen logs and rough-barked trees (e.g. Nowak and Paradiso 1983). They construct spherical nests of grasses, mosses, lichens, or shredded leaves. These nests are usually hidden under the roots of stumps, logs or brush piles. During winter, globular nests of grass may be placed directly on the ground under the snow, with tunnels radiating from the nest under and in the snow. The diet of *Clethrionomys* consists of tender vegetation, nuts, seeds, bark, lichens, fungi, and insects; they are usually found in forested habitats (Hansson 1985a, b). Food is often stored in the nest. When disturbed, red-backed voles may utter a chirplike bark that can be heard from one to two meters away, and they flee or freeze in position, depending on their location and preceding activity.

Taxonomy

The distribution of *C. rufocanus* is reported differently by authors coming from the Far East and Europe (Ognev 1950; Corbet 1978; Kaneko 1990, 1992, 1997). This is due to a rather confused situation in the Far East, especially in Korea and northeastern China (Fig. 1). More specifically this confusion is due to specimens from this region partly has been classified as *Clethrionomys rufocanus* by some workers (Hinton 1926; Ellerman 1941; Ognev 1950; Ellerman and Morrison-Scott 1951; see Kaneko 1990), whereas others have classified them as belonging to the genus *Eothenomys* (Corbet 1978; Kaneko 1990, 1992).

Corbet (1978) first designated the *Clethrionomys* species of the Far East as *Eothenomys shanseius, E. inez* and *E. eva* in northeast China and *E. regulus* in Korea; unfortunately he did not go into sufficient details, neither with respect to the description nor with respect to the published distribution maps. Kaneko (1990, 1992) carefully distinguished *Eothenomys* (without roots even during old age) from *Clethrionomys rufocanus* (with roots during old age) on the basis of detailed teeth examination, and clearly demonstrated the southern demarcation of the distribution for *C. rufocanus* (Kaneko 1990, 1992, 1997; Figs. 1 & 5).

What in much of the current ecological literature is referred to the gray-sided vole of Hokkaido, is identified as *Clethrionomys rufocanus* by some taxonomists (Corbet 1978; Corbet and Hill 1991; Musser and Carleton 1993; Abe et al. 1994) or as *C. rufocanus bedfordiae* (vernacular name, the Bedford's red-backed vole) by other taxonomists (Tokuda 1941; Imaizumi 1960; Abe 1984). It was originally named as a distinct species, *Evotomys* (=now *Clethrionomys*) *bedfordiae* by Thomas (1905a), who mentioned that it is allied to *Evotomys rufocanus*

Table 1. *Clethrionomys* species of the world. Primarily based on Corbet (1978), Hall (1981), Honacki et al. (1982), Gromov and Polyakov (1992), Wilson and Reeder (1993), and Abe et al. (1994) with respect to taxonomy and geographic distribution. Other sources are given as footnotes. Modified from Stenseth (1985b).

C. californicus (Merriam, 1890); California red-backed vole.

- Geographic distribution: Pacific coast coniferous forest from the Columbia River south through W. Oregon & N. California.
- Population dynamical pattern: unknown.
- Taxonomical comments: includes *C. mazama* & *C. obscurus*[1)]; population north of Columbia River are placed in *C. gapperi*.

C. centralis (Miller, 1906); Tien Shan forest vole.

- Geographic distribution: restricted to Tien Shan & Dzhungarsk, Altai Mts. (Russia & Singiang, China).
- Population dynamical pattern: unknown.
- Taxonomical comments: referred to in Russia as *C. frater* in current literature. Sometimes *C. centralis* is considered a synonym of *C. glareolus*.

C. gapperi (Vigors, 1830); Gapper's red-backed vole.

- Geographic distribution: Neoarctic. From Labrador to N. British Columbia (Canada), south in the Appalachians to N. Georgia; Great Lakes, Northern Plains, and Rocky Mts. (New Mexico & Arizona) to Columbia River in Washington (USA).
- Population dynamical pattern: non-cyclic throughout its range[2),3),4)].
- Taxonomical comments: includes *C. occidentalis* & *C. caurinus*; closely related to European *C. glareolus* - captive mating produced fertile hybrids but of reduced fertility[5)].

C. glareolus (Schreber, 1780); Bank vole.

- Geographic distribution: Palearctic. W. Eurasia, from Britain and Scandinavia south to Pyrenees, Italy, the Balkans, Transcaucasus, and east to central Siberia. Populations on exceptionally high altitude are found in S. Norway[6)], at 1400 m above sea level and in the French Alps[7)] at 2400 m above sea level.
- Population dynamical pattern: both stable and cyclic populations[4),8)].
- Taxonomical comments: see *C. gapperi* and *C. centralis*.

C. rex Imaizumi, 1971; Dark red-backed vole.

- Geographic distribution: restricted to Hokkaido, Japan & other adjunct islets (see Fig. 2).
- Population dynamical pattern: unknown.
- Taxonomical comments: includes *C. montanus*. Sometimes *C. rex* is considered a synonym of *C. rufocanus*.

C. rufocanus (Sundevall, 1846); Gray-sided vole.

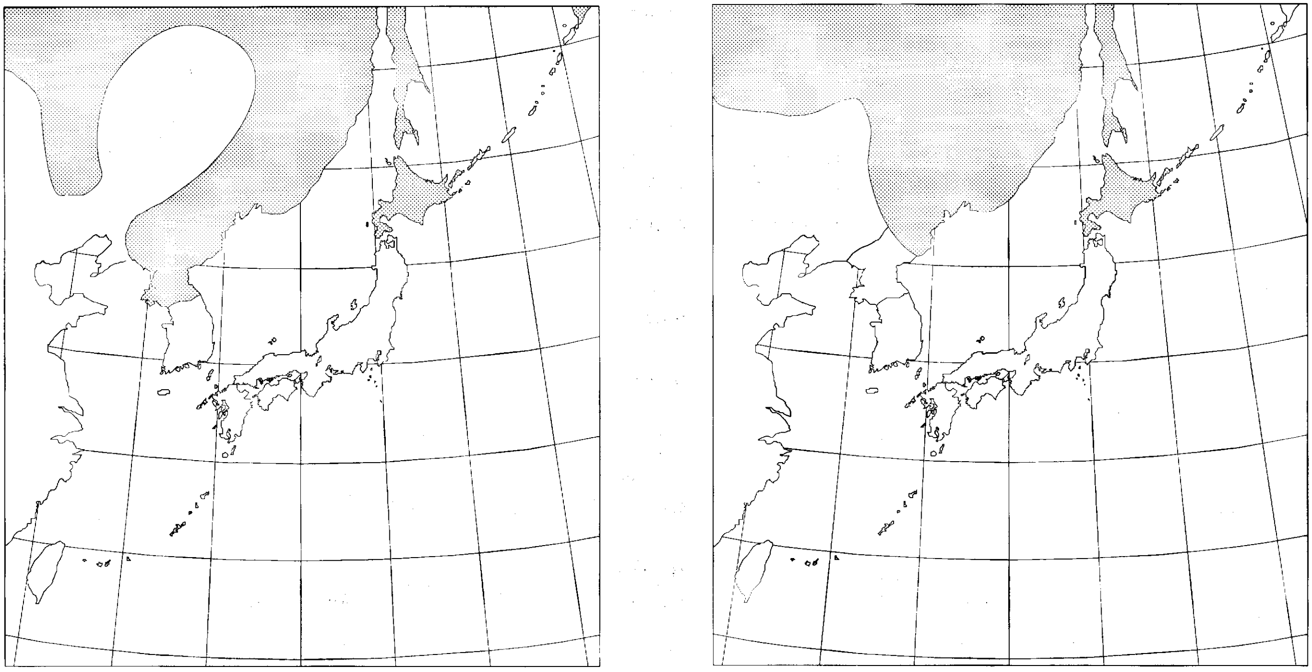
- Geographic distribution: Palearctic. N. Palearctic from Scandinavia to Chukchi pen. and Mongolia, Transbaikalia, N. E. China, Korea, Kamchatka, Sakhalin (Russia), Hokkaido, Japan & other adjunct islets (see Figs. 1, 2 & 5).
- Population dynamical pattern: both stable and cyclic populations in Hokkaido[4),9),10),11)]; cyclic in Fennoscandia[4),12)].
- Taxonomical comments: includes *C. bedfordiae* and *C. sikotanensis*; one or more separate species may occur in Japan, Korea & China (according to Honacki et al. 1982). Sometimes *C. rex* is considered a synonym of *C. rufocanus*.

C. rutilus (Pallas, 1778); Northern red-backed vole.

- Geographic distribution: Holarctic. N. Scandinavia east to Chukotka, south to N. Kazakhstan (Russia), Mongolia, Transbaikalia, N. E. China, Sakhalin and Hokkaido, St. Lawrence Isl. (Bering Sea), Alaska east to Hudson Bay, south to N. British Columbia and Manitoba (Canada).
- Population dynamical pattern: cyclic populations, at least, in Fennoscandia[3),4)] and non-cyclic, stable populations in Asia, N. America[3),4),13)] and W. Norway[14)].
- Taxonomical comments: *C. rutilus* and *C. gapperi* are sometimes considered conspecific.

1) Alexander and Verts 1992; 2) Merritt 1981; 3) Hansson and Henttonen 1985a, b; 4) Henttonen et al. 1985; 5) Grant 1976; 6) Skar et al. 1971; 7) Niethammer and Krapp 1982; 8) Hansson 1979; 9) Bjørnstad et al. 1996; 10) Stenseth et al. 1996; 11) Saitoh et al. 1998b; 12) Koshkina 1966; 13) Whitney 1977; 14) Hansson et al. 1978 (the Vesterålen site).

Sundevall, 1846 from Scandinavia, but that *bedfordiae* has a longer tail. Since the roots of the molars develop late in life in *Evotomys rufocanus*, Miller (1900) described the subgenus *Craseomys*. Referring to Miller (1900), Thomas (1905b) changed the name to *Evotomys* (*Craseomys*) *bedfordiae* for those specimens having less contrasted general color of red back and gray side, considerably longer tail, and broader and more powerful teeth



a. Corbet (1978)

b. Kaneko (1990, 1992)

Fig. 1. Distribution of *Clethrionomys rufocanus* in East Asia. a: Corbet (1978) revised the distribution map of *Clethrionomys rufocanus*, reidentifying specimens that were formerly treated as *Clethrionomys rufocanus* to the species of the genus *Eothenomys*. His examination was, however, insufficient. b: Kaneko (1990, 1992) re-examined the specimens and revised the distribution map referring to information from additional specimens.

than *Evotomys rufocanus*. In this paper we will, in order to avoid confusion, refer to this vole of Hokkaido as the Bedford's red-backed vole, whereas *C. rufocanus* of the continent is referred to as the gray-sided vole, though we recommend to consistantly use the Latin name.

Hinton (1926) arranged the gray-sided vole (then described as one *Evotomys*-species) as *rufocanus,* including *latastei, irkutensis,* and *bargusinensis* from Siberia, *shanseius, inez, nux, eva, aquilus,* and *alcinous* from northeast China, *regulus* from Korea, and *smithii, rufocanus, andersoni,* and *niigatae* from Japan. Then, he revised the vole from Sakhalin, Hokkaido, Honshu, Kyushu and Shikoku as a subspecies of *C. rufocanus smithii* due to the senior synonym. Howell (1929), Allen (1940), Ellerman (1941), Ognev (1950), Ellerman and Morrison-Scott (1951), Jones and Johnson (1965) and Zimmermann (1964) adopted this classification.

Kuroda (1931) disagreed in the classification of Hinton (1926) and classified the Bedford's red-backed vole of Hokkaido as *Evotomys* (=now *Clethrionomys*) *rufocanus bedfordiae*, since the Bedford's red-backed vole differs from forms described as *smithii* (*sensu stricto*), *andersoni* (*sensu stricto*), and *niigatae* (*sensu stricto*) in Honshu, Kyushu, and Shikoku on molar patterns and in the lengths of tail and molar. Since then Tokuda (1941), other Japanese taxonomists and Jameson (1961) followed Kuroda (1931); however, Imaizumi (1972), who did not do so, claimed the Bedford's red-backed vole of Hokkaido to be a distinct species of *C. bedfordiae* having a longer tail, greater skull, smaller auditory bullae, and less conspicuous contrasted color of skin.

Another taxonomic problem of the Bedford's red-backed vole, is that some different forms have been described on small islets off the coast of Hokkaido and alpine areas of Hokkaido. Tokuda (1935) described a new genus and species as *Neoaschizomys sikotanensis* from Shikotan, the southern part of Kurile Islands, as a larger form of the red-backed vole (Fig. 2); later he named this vole as *Clethrionomys sikotanensis* (Tokuda 1941). Imaizumi (1949) newly named *Neoaschizomys sikotanensis akkessi* from Daikoku Islet off Akkeshi, south-eastern Hokkaido; later he changed the scientific name of the vole from Daikoku and Rishiri Islets to *Clethrionomys sikotanensis* (Imaizumi 1960).

Ota (1956) disagreed with the classification of Imaizumi (1949) and demonstrated that one single and distinct species of *C. rufocanus bedfordiae* occurs in Hokkaido and on the Islets of Daikoku and Rishiri. Since rodents are likely to be larger on islands (see Foster 1964), Miyao (1968) followed Ota (1956).

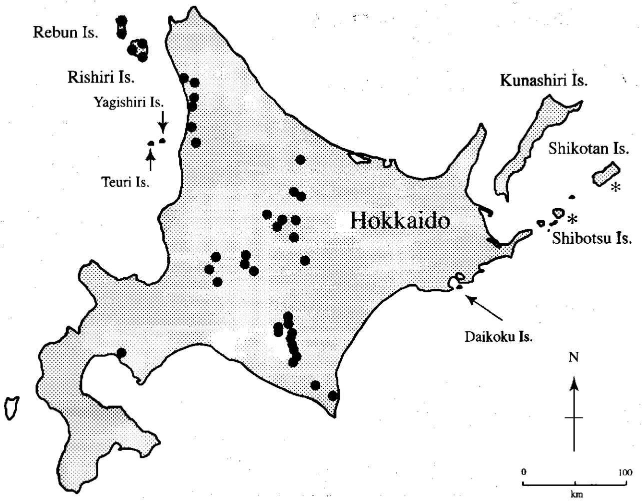


Fig. 2. Distribution of *Clethrionomys rufocanus* and *C. rex* in the island of Hokkaido and adjunct islets. Shaded areas represent the distribution of *C. rufocanus*. Dots indicate sampling places from which specimens are identified as *C. rex* from 1971 to 1996 (Nakata unpublished). The form of *C. rex* has been reported from Shikotan Is. and Shibotsu Is. shown by asterisks (Kostenko and Arrenoba 1978); however, its taxonomic status should be re-examined.

On Rishiri Islet, Imaizumi (1971) described a new form as *Clethrionomys rex* being different from *C. sikotanensis* (larger size, longer tail length and complex molar pattern on the third upper molar). Furthermore, Imaizumi (1972) described a new form of *Clethrionomys montanus* from the Hidaka Mountains, having a longer tail, complex molar pattern on the third upper molar with confluent dental spaces. Corbet (1978) listed *C. rex* as a distinct species from *C. rufocanus*, and considered *montanus* as a conspecific with *rex*. Aimi (1980), however, regarded *C. rex* as synonym with *C. rufocanus*, since the three diagnostic characters described by Imaizumi (1971, 1972) are not found in all specimens on Rishiri Islet. Abe (1984) objected to Aimi (1980) because of too small number of specimens and characters examined; Abe (1984) concluded that *C. montanus* is conspecific with *C. rex*.

Kaneko and Sato (1993) collected 57 specimens in sympatric distribution of *C. rufocanus* and *C. rex* in a small area of Rishiri Isl. *Clethrionomys rex* has a complex molar pattern on the third upper molar, where the width of salient triangles shows almost the same on both sides. *Clethrionomys rufocanus*, on the other hand, has a simple molar pattern on the third upper molar with a large second lingual salient angle shaped round on the molar, where the width of the salient triangle shows larger on the lingual side (Fig. 3). As the increase of CBL (condylobasal length), the molar pattern of *C. rex* gradually becomes simple due to smaller posterior loop and appears confluent dental isthmus as found in the holotype of *C. montanus*. They conclude that *Clethrionomys rex* is a distinct species being conspecific with *montanus*. A molecular study also identifies three distinct species of *Clethrionomys* in Hokkaido, namely *C. rufocanus*, *C. rex* and *C. rutilus* (Fig. 4; Wakana et al. 1996).

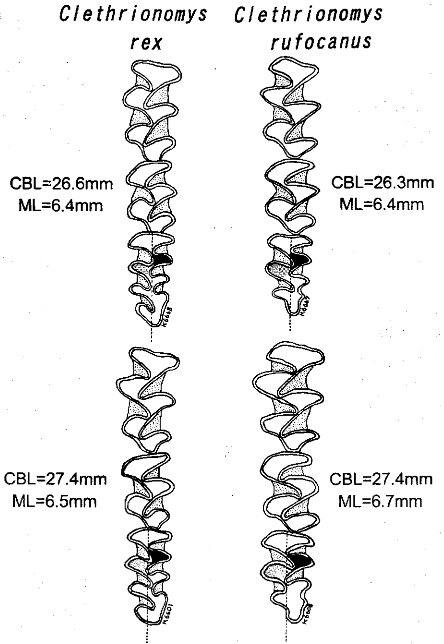


Fig. 3. Upper molar teeth patterns of *Clethrionomys rufocanus* and *C. rex* in a sympatric area of Rishiri Islet. A fine dotted dentine field on the second lingual side on the third upper molar is larger than a black one in *rufocanus*, whereas the size of corresponding areas is similar in *rex* (modified from Kaneko and Sato 1993). CBL: condylobasal length; ML: upper molars length.

Judging from the above morphological and molecular findings, we hereafter regard *C. rex* (the dark red-backed vole) as a distinct species differing from *C. rufocanus* (the gray-sided vole or the Bedford's red-backed vole).

Because the holotype of *Neoaschizomys sikotanensis* Tokuda, 1935 is lost and the picture of the holotype shows the simple form on the third upper molar (Tokuda 1935), the name of *sikotanensis* is considered to be a junior synonym of *rufocanus*. Therefore, the vole having the complex form on the third upper molar on Shikotan Island seems not to be *C. sikotanensis* (Kostenko and Arrenoba 1978) but *C. rex*. Further examination is needed for the specimens of Shikotan and Shibotsu, the southern part of Kurile Islands, and Sakhalin, where *C. sikotanensis* is distributed (Kostenko and Arrenoba 1978).

Scientific names of genera, species and subspecies related to *Clethrionomys rufocanus* are listed in historical order in Appendix.

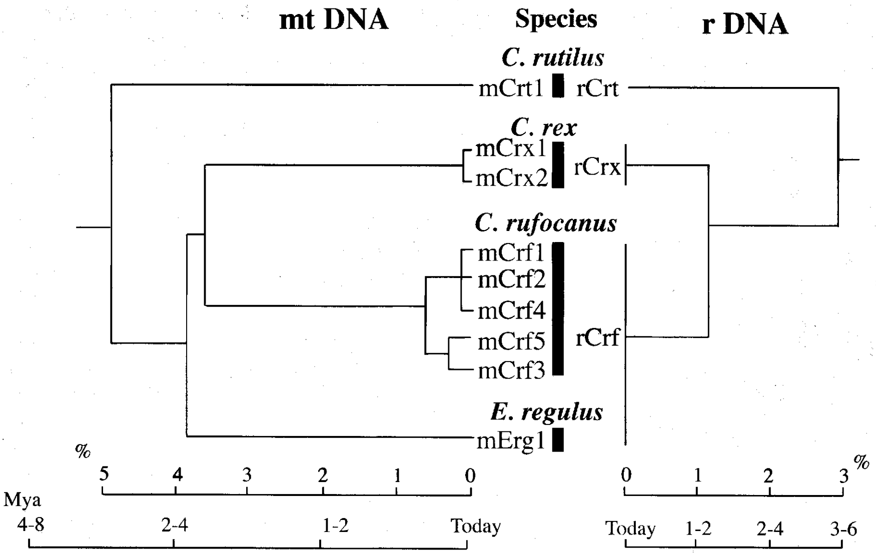


Fig. 4. Phylogenic trees for the mitochondrial DNA haplotypes and major ribosomal DNA repetypes (after Wakana et al. 1996). *Clethrionomys rufocanus* includes *C. sikotanensis*. *Clethrionomys rex* includes *C. montanus*. See the original paper for details.

Morphology

Clethrionomys rufocanus (Sundevall, 1846)

The vole *Clethrionomys rufocanus* found in Hokkaido is a small-sized and short-tailed (around 40% of body length) rodent. Data on external dimensions are as follows: head and body length = 107–126 mm, tail length = 44–57 mm, hind foot length = 18.2–20.8 mm, and body weight = 27–50 g (Abe et al. 1994). The sizes varies in Hokkaido and on islets off the coast of Hokkaido (Kaneko et al. unpublished). Males are generally larger than females, although no detailed data are available on sexual dimorphism. The fur is dense, long and soft in winter, but shorter and rougher in summer. The general coloration above is dark lead gray with a pronounced reddish wash. The wash becomes less prominent on the sides, which is beige. The underparts are dark slate gray to ivory white. The tail has a slight terminal pencile of hairs. The *C. rufocanus* of Hokkaido has a slightly longer tail than that in the Far East, but is almost the same as the hind foot length (Kaneko et al. unpublished).

The skull of adults is massive and angular. Interorbital region is moderately constricted, and parallel-sided. Braincase is large and rectangular. Pterygoid fossa is deep. Auditory bullae is moderately large. The size of adult skulls is larger in *C. rufocanus* from Hokkaido than in *C. rufocanus* from Finland. Data on skull dimensions are as follows: condylobasal length = 26.0–29.8 mm, zygomatic width = 15.0–17.1 mm, nasal length = 7.4–8.7 mm, interorbital width = 3.4–4.3 mm, palatine length = 12.3–13.5 mm, diastema = 7.5–9.2 mm, incisive foramen length = 5.2–6.2 mm, upper molars length = 6.5–7.5 mm, and the length of mandible = 16.8–18.9 mm (Abe 1984). The size varies between the main island of Hokkaido and adjunct islets (Kaneko et al. unpublished).

The size of I-M3 (the distance from the anterior point of incisor to the posterior edge of the third upper molar), where roots of the molars develop, is larger in the vole of Hokkaido (including adjunctive islets) than in the vole from the Eurasian continent (e.g. Finland, Mongolia, northeast China, North Korea, and Kamchatka), though the variation in size of I-M3 is overlapping in the vole from these regions (Kaneko et al. unpublished). The separate roots developed slightly earlier in Finland than in Hokkaido: 195 days in Finland (Viitala 1971) versus 200 days in Hokkaido (Abe 1976b). The interorbital width is almost the same in the voles of Hokkaido and the Far East (Kaneko et al. unpublished).

Clethrionomys rex and *C. rufocanus*

The dark red-backed vole *Clethrionomys rex* is dark yellow brown or dark brown on the dorsal side, differing from the red brown on the back of *C. rufocanus* from Hokkaido. External dimensions of *C. rex* are larger than those of *C. rufocanus* as follows: head and body length = 112–143 mm, tail length = 44–60 mm, hind foot length = 20–22.4 mm and body weight = 33–62 g (Abe et al. 1994). Data on skull dimensions are as follows: condylobasal length = 26.5–29.7 mm, zygomatic width = 15.0–17.4 mm, nasal length = 8.1–9.0, interorbital width = 3.8–4.5 mm, palatine length = 12.8–14.4 mm, incisive foramen length = 5.4–6.4 mm, upper molars length = 6.7–7.6 mm, and the length of mandible = 17.0–19.4 mm (Abe 1984). Males are generally larger than females in *C. rex*, although no detailed data are available on sexual dimorphism. The complicated pattern on the third upper molar is changed with the increase of CBL and the dentine spaces gradually develops (Kaneko and Sato 1993). The roots of molars develop slower in *C. rex* than in *C. rufocanus* (Abe 1973); molar roots of *C. rex* are not completely formed even in 250 age in days, whereas they are formed in 200 age in days in *C. rufocanus* (Onoyama et al. unpublished; see also Abe 1973).

Cytology

Even though various *Clethrionomys* species show great karyotypic similarities (Gamperl 1982; Modi and Gamperl 1989; Yoshida et al. 1989; Obara et al. 1995), there are at least two karyotypes. A reciprocal translocation between Nos. 1 and 9 chromosomes was first found using G-banding between *C. rufocanus* and *C. glareolus* (Gamperl 1982). Modi and Gamperl (1989) found the same translocation pattern in *C. glareolus* as in *C. rutilus, C. gapperi* and *C. californicus*. Although Yoshida et al. (1989) regarded the karyotypes of all species (or forms) of *Clethrionomys* in Hokkaido (*C. rufocanus, C. rex, C. montanus, C. sikotanensis,* and *C. rutilus*) as identical (i.e. *rufocanus*-type), the karyotype of *C. rutilus* in Hokkaido is suggested to be allocated into *glareolus*-type by Obara et al. (1995). Thus, karyotypes of species (or forms) of *Clethrionomys* in Hokkaido should also be classified to the two types; *rufocanus*-type: *C. rufocanus, C. rex, C. montanus*, and *C. sikotanensis*; *glareolus*-type: *C. rutilus.* According to Wakana et al. (1996), there is no difference in mtDNA between *C. rex* from Rishiri and *C. rex* from Teshio, the latter of which is named as *C. montanus* by the classification of Imaizumi (1972). The electrophoretic patterns of 14 different enzymes and general protein indicate that *C. rufocanus* from Hokkaido is conspecific with that from Rishiri, which Imaizumi (1971) named *C. sikotanensis* (Yoshida et al. 1989).

The chromosome number of *C. rufocanus* is 2N = 56 and the number of chromosome arms (FN) is 58. Autosomes are 26 pairs of acrocentric and one pair is metacentric. Several polymorphism were found for sex chromosomes both in the continent and in Hokkaido (Vorontsov et al. 1980; Tsuchiya 1981). The G-band patterns of *C. rufocanus* from Sweden are identical with those of Hokkaido (Mascarello et al. 1974; Gamperl 1982).

The karyotype of *Clethrionomys rex* is 2N = 56 and FN = 58. The autosomes are 26 pairs of acrocentrics and one pair of metacentric. The X- and Y-chromosomes are acrocentrics. The G-band patterns are similar between *C. rufocanus* from Hokkaido and *C. rex* from the Hidaka Mountains which is named *C. montanus* according to the classification of Imaizumi (1972) (Kashiwabara and Onoyama 1988). Polymorphisms in sex chromosomes, which is found in *C. rufocanus*, is not known in *C. rex*. However, that may not mean the absence of the polymorphisms in *C. rex*. Further reevaluation is needed in the karyotypes of these two species in comparison with those of other close related species and/or forms (e.g. voles in Shikotan Island).

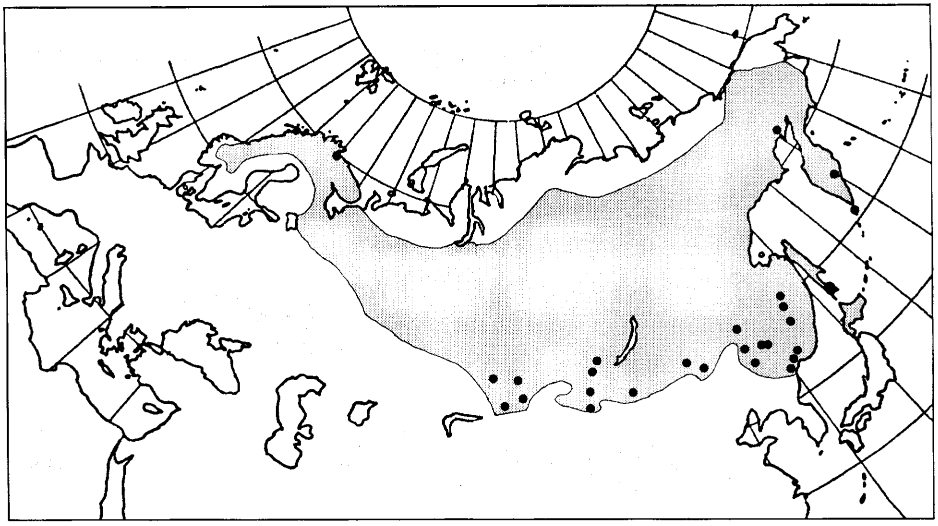


Fig. 5. Distribution of *Clethrionomys rufocanus* in the Holarctic (modified from Stenseth 1985). Shaded areas are the distribution formerly suggested, which is revised by Kaneko (1990, 1992). He confirmed the presence of *C. rufocanus* at the places indicated by dots.

Distribution

Clethrionomys rufocanus is distributed from Fennoscandia through Siberia (Fig. 5; where the northern Mongolia, northeast China and Kaima Plateau in North Korea are the southern boundary) to Kamchatka, Sakhalin and Hokkaido (Ognev 1950; Henttonen and Viitala 1982; Kaneko 1990, 1992, 1997; Fig. 5). *Clethrionomys rufocanus bedfordiae* is distributed in Hokkaido, on islets off Hokkaido such as Rishiri, Rebun, Daikoku, Teuri, and Yagishiri, and the southern part of Kurile Islands (i.e. Kunashiri, Shikotan, Shibotsu and others; Fig. 2; Ota 1956; Kostenko and Arrenoba 1978; Kaneko et al. unpublished).

Clethrionomys rex is distributed in Hokkaido (Daisetsu, Hidaka, Teshio, Kitami and Yubari Mountains, Abuta Town near Lake Toya; Fig. 2; Nakata unpublished), islets off Hokkaido such as Islets of Rebun and Rishiri (Abe et al. 1994), Shikotan and Shibotsu, the southern part of Kurile Islands, and Sakhalin (Kostenko and Arrenoba 1978).

The ecology of *Clethrionomys rufocanus* of Hokkaido

Growth and reproduction

The gestation period of the Bedford's red-backed vole is 18-19 days under laboratory conditions (Abe 1968). The litter size is typically 4–7 (Fig. 6; Kinoshita 1928; Fujimaki 1972, 1973, 1975, 1981; Kuwahata 1984; Nakata 1984; Saitoh and Ishibashi unpublished; see Table 1 in Ueda et al. 1966 for review). Newborns weigh about 2.0 g and grow fast; they wean after about 17 days and reach 22–23 g around an age of 30 days. Age of maturation is around 30–60 days under laboratory conditions (Abe 1968). Although females are generally becoming mature somewhat earlier (about 10 days) than males, maturation varies depending on conditions (e.g. population density, season and social interaction). Spring-born individuals grow faster and become mature earlier than fall-born ones (Kinoshita 1928; Ota 1984). Spring-born individuals attain sexual maturity in the year they are born. Fall-born voles remain reproductively inactive through the winter (Fujimaki 1975; Kuwahata 1984). The maturation of females is influenced by social interaction in natural conditions (Saitoh 1981, 1990). Spring populations are mainly composed of fall-born animals (Ota 1984; Ishibashi et al. 1998b). The proportion of this cohort declines to 10% or less by October/November (Fujimaki 1969a, b, 1975; Abe 1976a, b; Fujimaki et al. 1976; Kuwahata 1984). Generally, the lifetime of free ranging individuals is less than one year (Yoneda 1982).

The breeding season

The breeding season is generally from April to October. Although pregnant females are common between May and October, pregnancy rate is higher in spring and fall than in summer; the proportion of mature males is also low during the middle of the summer (Ota et al. 1959; Kinoshita and Maeda 1961; Kuwahata 1962). Thus, the breeding activity has two peaks (spring and fall) in a year. Most breeding females give birth to 2–4 litters through the breeding season (spring or fall) and post partum oestrous is frequently

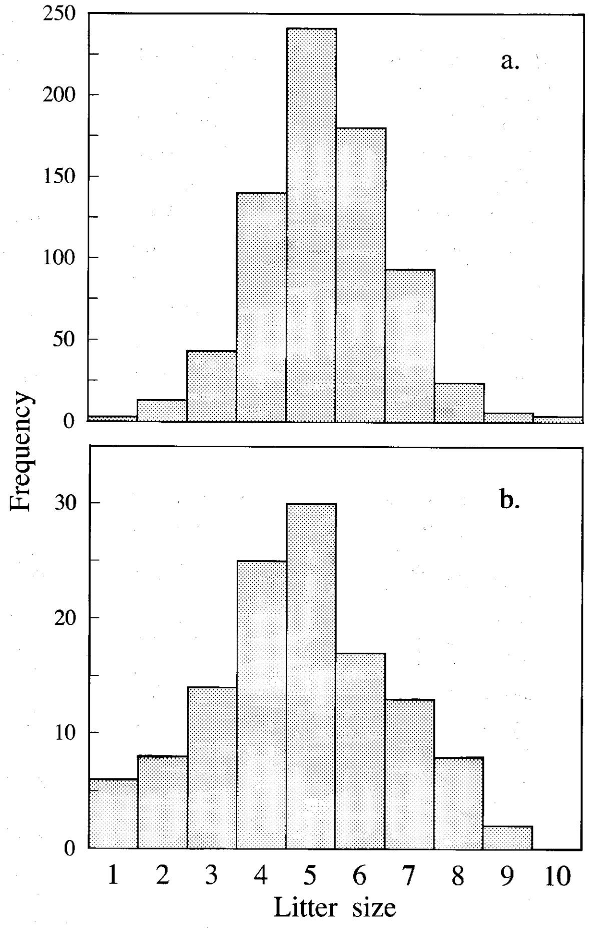


Fig. 6. Frequency distributions of litter size. a.: Frequency distribution of the number of embryos obtained from 747 pregnant females sampled at various sites in Hokkaido between 1967 and 1974 (Fujimaki 1981); average = 5.27. b.: Frequency distribution of the number of litter mates obtained from 123 litters in an experimental population in Sapporo, Hokkaido between 1992 and 1993 (Saitoh and Ishibashi unpublished data); average = 4.79. Litter mates were determined based on the following information: DNA analyses for parentage, reproduction career of a mother candidate, and date and site at the first capture of a juvenile.

observed in spring (Saitoh and Ishibashi unpublished data). Spring-born individuals typically mature during summer and comprise a major part of the breeding population in fall. Late summer- or fall-born individuals generally wait until the next spring.

In contrast to this general breeding pattern, populations in high elevation or in the eastern area, where temperature (particularly during summer) is lower than in the lowland, are reported to have higher pregnancy rates during summer than that during fall (Ueda 1961). This leads to a single peak in breeding activity through the season, rather than the two peaks described above. It appears, thus, that temperature influences the breeding activity. A single peak in the breeding pattern is also reported during periods of high densities in populations near Sapporo, where the two-peak pattern is the most common (Fujimaki 1969b; Abe 1976b).

There is also some other geographic variation in the breeding pattern. In the southern part of Hokkaido where temperature is higher and the snow disappears earlier, the breeding starts in the middle of March, and early spring-born individuals may attain maturity in June. In the colder northern and eastern parts of Hokkaido, the breeding starts in April (Fujimaki 1972). However, since voles in the northern or eastern areas become mature at a smaller size, fall breeding still tends to be more active in these areas (Fujimaki 1973).

Even though winter breeding is known to occur (Kaikusalo and Tast 1984; Nakata 1987; Saitoh 1989), it is not common (Ota 1984). There is no evidence suggesting it to be quantitatively important in Hokkaido.

Factors influencing breeding

Population density: High population density suppresses the maturation of young females (Saitoh 1981). Ota and Fujikura (1959) and Kuwahata (1966) reported low maturation rate of young individuals in high-density years. The breeding pattern with one peak a year near Sapporo (see above) may be caused by high population densities, and not by temperature (Abe 1976a). The breeding season is shorten in a high-density year and elongated in a low-density year (Nakata 1989). High densities may also lead to reduction of litter size (Nakata 1984).

Fluctuation phase: Even under similar densities, reproductive activity varies between different fluctuation phases. The proportion of breeding voles is higher during the increase phase than during the decline phase (Nakata 1989). Litter size also varies among phases with a similar pattern (Nakata 1984).

Food conditions: Breeding is usually more active in forest plantations than in natural forests, because the undergrowth in plantations is generally richer (Kinoshita and Maeda 1961; Maeda 1963). This is particularly so in young plantations, in which green plants are growing well owing to more sunlight as compared to those in mature natural forests. If provided *ad libitum* food, voles will breed in outdoor enclosure or cages in the winter (Haga 1954; Saitoh 1989). Thus, it is evident that quality and quantity of food greatly influence the breeding activity (see also Andreassen and Ims 1990).

Social interaction: Breeding females hold territories (Saitoh 1985). Sexual maturation of young females is inhibited when they fail to established a territory (Saitoh 1981, 1990), and females whose home ranges overlap with other females, fail to become pregnant (Kawata 1987). Such exclusiveness is relaxed during the non-breeding season (Ishibashi et al. 1998b).

Habitat and diet

The Bedford's red-backed vole is a habitat generalist in Hokkaido. Although the species of the genus *Clethrionomys* generally favor forests and woodlands, the vole inhabits open habitats as well as forests in Hokkaido, possibly because there are no *Microtus* (Ota and Jameson 1961). The Bedford's red-backed vole is the most strictly ground-dwelling among rodents in Hokkaido (Ota 1968; Abe 1986; Abe et al. 1989). That is, it is much more ground-dwelling than the three sympatric species of *Apodemus* (*A. argenteus, A. peninsulae* and *A. speciosus*). A dominant understory plant species in forests is the bamboo grass (*Sasa* spp.; Wada 1993). Vegetation cover and density of understory vegetation are well developed from mid June to October (Yoneda 1983). The snow rich period is associated with relatively high survival in *C. rufocanus* (Dewa 1975; see also Ishibashi et al. 1998b; Yoccoz et al. 1998). There is also some evidence (Yoneda 1983), that dense vegetation conveys some of the same protection against hostility factors such as predators or unfavorable weather conditions.

The Bedford's red-backed vole 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 food during winter, while various forbs and grasses are eaten during summer (Ota 1984). The diet is, thus, predominantly folivorous and subdominantly granivorous. The gray-sided vole is more folivorous than the other *Clethrionomys* species (cf. Hansson 1985a, b). This feeding habit of *C. rufocanus* is particularly prevalent in Hokkaido - possibly due to the absence of *Microtus*. However, acorns are also, to some extent, eaten in the fall while bark is taken during winter (Ota 1984).

Competitors and predators

Species of *Microtus* seem to be superior competitors for the gray-sided vole (*C. rufocanus*) in the Eurasian continent (Henttonen et al. 1977; Hanski and Henttonen 1996). However, there are no *Microtus* species in Hokkaido. Although two species of the wood mouse (*Apodemus argenteus* and *A. speciosus*) are common and sympatric with the Bedford's red-backed vole, there is no evidence of competition between *Clethrionomys* and *Apodemus* (Abe 1986). Interactions with the other rare species of the wood mouse (*A. peninsulae*) may be negligible. Congeneric interactions are, however, thought to occur (Ota 1968; Abe 1986; Nakata 1995). A possible competitor, the northern red-backed vole (*C. rutilus*) is inferior to the Bedford's red-backed vole in most habitats, except for in pure coniferous forests (Ota 1984). Habitat segregation is observed between *C. rufocanus* and *C. rex* (Kaneko and Sato 1993; Nakata 1995); *C. rex* is commoner than *C. rufocanus* in valley bottoms and on a lower half of slopes in a sympatric area of northern Hokkaido.

Three mustelid species are important predators for small rodents in Hokkaido (in assumed order of importance): *Mustela nivalis, M. itatsi,* and *M. vison. Martes zibellina* and *Mustela erminea* are certainly also present but there is little information about them. The red fox (*Vulpes vulpes*), two owls (*Strix uralensis* and *Asio otus*) and four species of snakes (*Elaphe climacophora, E. conspicillata, E. quadrivirgata* and *Agkistrodon blomhoffii*) are also important predators for rodents (Kadowaki personal communication). Predators prefer the Bedford's red-backed vole to the *Apodemus* species in Hokkaido; even the red fox, which is a typical generalist predator, selectively takes this vole (Yoneda 1979). The reported percentages of occurrence in dropping or stomach contents of the two genera are: 30.7% vs 0.3% in *M. vison* (Uraguchi et al. 1987), 30–60% vs 1% in *V. vulpes* (Abe 1975; Misawa 1979; Kondo et al. 1986), 25%–50% vs 5%–25% in *S. uralensis* (Matsuoka 1977; Yoneda et al. 1979) and 98–100% vs 0.8–3.7% in *A. otus* (Matsuoka 1974).

Although many parasites are known in *C. rufocanus* of Hokkaido, their influence on population dynamics is unclear (Yoneda and Nakata 1984; see also Saitoh and Takahashi 1998).

Forest management and rodent damage

Hokkaido is a forest-rich island: forests once covered about 70% of the island. Forestry plantations were started in 1886 and forest damage by voles' eating bark has occurred since around 1900 in Hokkaido (*Rodent Research Group* 1958; see also Ueda et al. 1966; Ueda 1977). Scientific investigations on both applied and basic questions pertaining to the ecology of the Bedford's red-backed vole in Hokkaido were initiated by Kinoshita (1928; see also Ueda et al. 1966). Thereafter, because of severe damage spreading all over Hokkaido (e.g. in 1937, 1942–43, and 1951), such studies were encouraged and have been followed up by researchers in *Hokkaido University, Forestry and Forest Products Research Institute,* and *Hokkaido Forestry Research Institute.*

The Forestry Agency of Japanese Government (FAJ) instigated forestry plantations since 1950s to transform natural forests into more productive plantations. Although forest planting followed various silvicultural

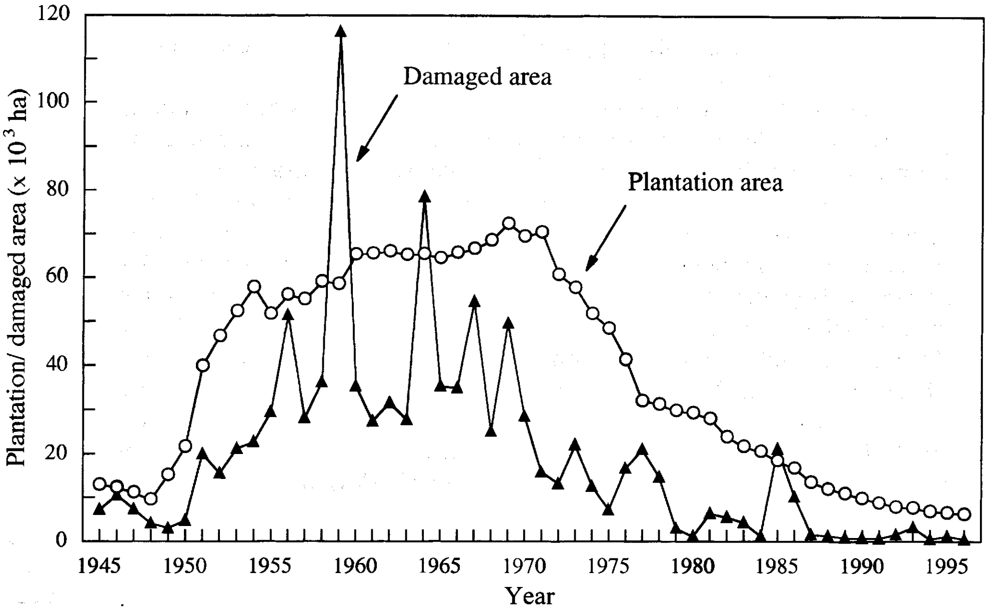


Fig. 7. Yearly changes in areas of forestry plantations and the damaged areas of the plantations by the vole in hectares.

procedures, the most common procedure which was adopted in Hokkaido, was the drastic method of transforming a natural system into an artificial one. After clearance of natural forests, weeds were removed from the clear-cut, then larch (*Larix kaempferi*) or todo fir (*Abies sachalinensis*) seedlings were planted densely. Because weeds grow thickly in young plantations and may suppress the growth of tree seedlings, the weeds are cut every summer for the next five to nine years after tree planting. This procedure have provided a favorable habitat for the Bedford's red-backed vole (Ota 1968; Saitoh and Nakatsu 1997), just like clearcutting appears to favor folivorous rodents elsewhere (Hansson 1992).

This forestry practice was implemented faithfully, all over Hokkaido. Considerable areas of natural forests were clear-cut and transformed into single species, largely coniferous, plantations (Fig. 7). During the peak of this development, more than one percent of natural forests were cut and transformed into coniferous plantations every year. Because this intensive planting increased the damage by the Bedford's red-backed vole, FAJ in Hokkaido and Hokkaido Government initiated a management-focused census program of small rodents, together with the *Rodent Research Group*, which was organized in 1953 by researchers in *Hokkaido University, Forestry and Forest Products Research Institute*, and *Hokkaido Forestry Research Institute*. After some preliminary work in the early 1950s aiming at developing an appropriate census method, census methods using snap traps were standardized in 1954. The methods were standardized again by using 50 snap traps at 10-m grid pattern in 1956, which have been used until the present (Fujimaki 1977; Nakata 1998; for details of methods, Saitoh et al. 1997, 1998a, b).

There are two census programs implemented by FAJ in Hokkaido and Hokkaido Government using the same trapping protocol; trapping three times a year (spring, summer and fall) in selected habitats in forests all over Hokkaido by foresters; both in young plantations (until about 15 years after planting) and in natural forests neighboring the plantations (Fig. 8). In the case of national forests managed by FAJ, Ranger Offices (which usually manage several thousands hectares of forests) constitute the unit of the census; e.g. a total of 433 Ranger Offices (which have at least two census sites in a plantation and in a natural forest) carried out censuses in 1992. The personnel of Ranger Offices, who were regularly trained by specialists, trapped and identified rodents. These are the data used for the spatio-temporal analysis reported by Saitoh et al. (1998b) and by Bjørnstad et

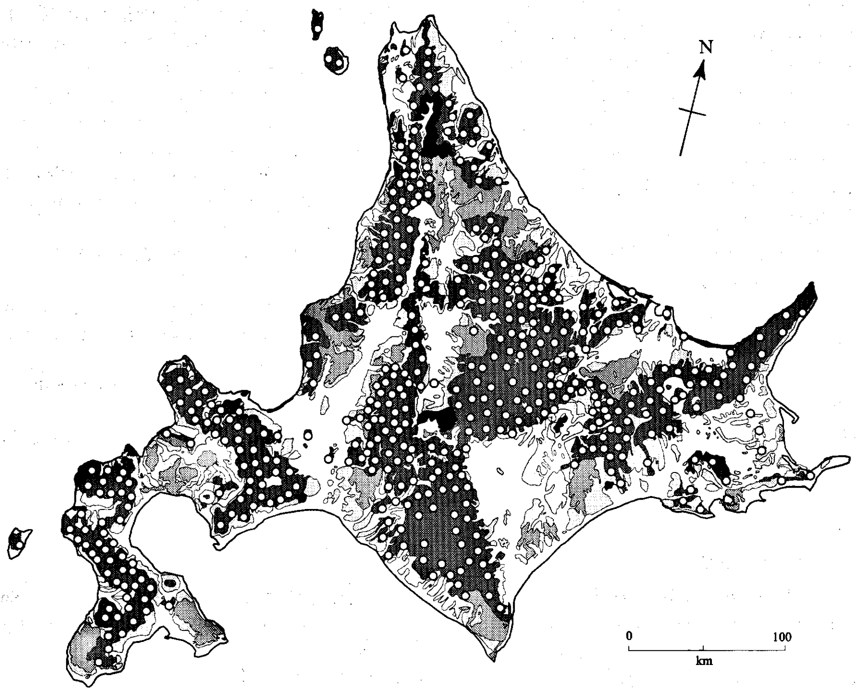


Fig. 8. Distribution of forests in Hokkaido and of census locations in national forests. Dense shaded areas: national forests managed by the Forestry Agency of Japanese Government (FAJ); slightly dense shaded areas; prefectural forest managed by Hokkaido Government; light shaded areas: private forests; solid areas: experimental forests of universities. Circles indicate locations of Ranger Offices in national forests, which carried out censuses of rodents.

al. (1998b) later in this *Special Feature*.

In private and prefecture's forests the Hokkaido Government has carried out three types of censuses. For private forests, there are furthermore two types; one is the census by designated trained specialists, whereas another is carried out by foresters. In prefecture's forests trained personnel of these offices perform the censuses. Most private forests are near suburban or cultivated areas ranging from lowland to mountainous areas, whereas most national and prefecture's forests are generally located in mountainous areas (Fig. 8).

Ota (1958b) first predicted, on the basis of the census data, a vole outbreak for the following year and the *Rodent Research Group* gave foresters a warning of damage. However, they were not able to check the unprecedented damage in 1959, when more than 60 million saplings were destroyed (Fig. 7). Thereafter, using the census data systematically, density in fall came to be estimated from the density in spring or summer. Based on these estimates and the past record on damages, the amount of poisonous baits to be scattered through forestry plantations was determined (Nakata 1986).

The census data has also proven invaluable for population ecological studies (Krebs 1997). Unfortunately, the census efforts of FAJ were greatly reduced during the middle of 1990s; this coincided with a reduction of the area with new forestry plantations, which began during late 1980s. This is caused mainly by the lack of appropriate land for such plantations, by economic hardship of forestry organizations and by public demands for less clearcutting; forestry plantations are usually made on areas where natural forests were clear-cut. However, data till 1992 have provided us with a most valuable set of data for describing and analyzing population fluctuations of the Bedford's red-backed vole. Parts of the census data, covering the northern national forests, have already been analyzed in some detail (Saitoh 1987; Bjørnstad et al. 1996, 1998a; Stenseth et al. 1996; Saitoh et al. 1997, 1998a, b). Saitoh et al. (1998b; see also Bjørnstad et al. 1998b) summarize and extend these analyses to the entire set of time series from the census program in the national forests surveyed by FAJ. This set of time series in Hokkaido certainly represents a gold mine for spatio-temporal analyses. Fluctuation patterns found using these data, together with the rich background information on the biology of the Bedford's red-backed vole reviewed in this *Special Feature*, provide a unique opportunity for understanding population fluctuations in rodents. Further work on the analysis of the monitoring data should be coupled with more detailed work on the demography and social organization of the Bedford's red-backed vole populations in the various regions of Hokkaido.

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Appendix. Chronology of scientific names of genera, species and subspecies in *Clethrionomys rufocanus.*

***1811**	*Hypudaeus* Illiger [Type: *Mus lemmus* Linnaeus, 1758; *Mus amphibius* Linnaeus 1758; and *Mus arvalis* Pallas, 1779] *Hypudaeus* is a synonym of *Lemmus* Link, 1795
***1846**	*Hypudaeus rufocanus* Sundevall [Type locality: Lappmark, Sweden]
1850	*Clethrionomys* Tilesius [Type: *Mus rutilus* Pallas, 1779]
***1874**	*Evotomys* Coues [Type: *Mus rutilus* Pallas, 1779]
***1881**	*Arvicola wosnessenskii* Polyakov [Type locality: Kamchatka, Russia]
***1881**	*Arvicola rufocanus* var. *sibirica* Polyakov [Type locality: Kamchatka, Russia]
1884	*Arvicola rufocanus* var. *kamtschaticus* Lataste [Type locality: Kamchatka, Russia] *nom. nud.*
1900	*Craseomys* Miller [Type: *Hypudaeus rufocanus* Sundevall, 1846]
1903	*Evotomys* (*Craseomys*) *latastei* Allen [Type locality: Gichiga, Kamchatka, Russia] Allen replaced *Arvicola rufocanus* var. *kamtschaticus* Lataste by this form, because *Arvicola kamtschaticus* (*nec.*) Polyakov was preoccupied as a primary homonym.
1905	*Evotomys bedfordiae* Thomas [Type locality: Shinshinotsu, near Sapporo, Hokkaido, Japan]
1917	*Evotomys* (*Craseomys*) *irkutensis* Ognev [Type locality: Irkutsk Province, Siberia, Russia]
1922	*Evotomys kolymensis* Ognev [Type locality: Berezova near Sredne Kolymsk, Russia]
1924	*Craseomys rufocanus bargusinensis* Turov [Type locality: Bargusin Reserve, northeastern shore, Lake Baikal, Russia]
1928	*Evotomys* (*Craseomys*) *arsenjevi* Dukelski [Type locality: Vladivostok, Ussuri Bay, Russia]
1930	*Clethrionomys rufocanus kurilensis* Kishida [Type locality: not described] *nom. nud.*
1932	*Clethrionomys rufocanus kurilensis* Tokuda [Type locality: Paramushir Island, Kuril Islands, Japan]
1935	*Neoaschizomys sikotanensis* Tokuda [Type locality: Shikotan Island, the southern part of Kuril Islands, Japan]
1949	*Neoaschizomys sikotanensis akkessi* Imaizumi [Type locality: Daikoku Islet, off Hokkaido, Japan]
***1984**	*Clethrionomys rufocanus bromleyi* Kostenko [Type locality: Sakhalin, Russia] *nom. nud.*
1993	*Clethrionomys rufocanus changbaishanensis* Jang, Ma and Luo [Type locality: Anty county, Jinlin Province, China]

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* not seen the original paper.