

Phylogeography of the root vole *Microtus oeconomus* in Russian Far East: A special reference to comparison between Holarctic and Palaeartic voles

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Abstract. The phylogeography of the Holarctic *Microtus oeconomus* in Russian Far East, near the Beringia, was studied using mitochondrial cytochrome *b* (*Cytb*) gene sequences. In comparison with the *Cytb* data of the Holarctic *Myodes rutilus* and the Palaeartic *My. rufocanus* previously studied by us, those of *Mi. oeconomus* showed similar local differentiation patterns to those of *My. rutilus* and obviously differed from those of *My. rufocanus*. Further, the current and previous *Cytb* data indicated that the genetic distances of specimens between the Magadan and Kamchatka/Kuril Archipelago regions were clearly higher in *Mi. oeconomus* and *My. rutilus* and lower in *My. rufocanus*. On the basis of the genetic distances and the geological splitting time between Kamchatka and Kuril Archipelago as 10,000 years ago previously reported, we could estimate the divergence time between the two region populations of Holarctic arvicolid as a few ten thousand years at most. Namely, in the Russian Far East, a past geographic and/or environmental barrier seemed to have appeared and to have inhibited genetic communication between the Magadan and Kamchatka/Sakhalin/Kuril Archipelago regions in *Mi. oeconomus* and *My. rutilus*, before *My. rufocanus* had expanded its distribution there.

Key words: Holarctic, Kuril Archipelago, *Microtus oeconomus*, Palaeartic, phylogeography.

Phylogeographic analysis using molecular markers is valuable for understanding intraspecific local differentiation and colonization history (Morrone and Crisci 1995; Patterson 1999). The phylogeographies of local differentiation in Palaeartic and Nearctic small rodents have been studied in many species (Hayes and Harrison 1992; Fedorov et al. 1996; Jaarola and Tegelström 1996; Conroy and Cook 2000; Iwasa et al. 2000; Cook et al. 2001; Frisman et al. 2002, 2003; Iwasa and Suzuki 2002, 2003; Jaarola and Searle 2002; Serizawa et al. 2002). However, there are only several phylogeographic studies on intraspecific differentiation for Holarctic small rodents using biochemical analysis (Nadler et al. 1978; Lance and Cook 1998; Frisman et al. 2003) and molecular analysis (Iwasa et al. 2002; Brunhoff et al. 2003; Galbreath and Cook 2004). Taking into consideration the phylogeography and evolution of Holarctic rodents, an interspecific comparison of local differentiation patterns should be conducted among those that are distributed sympatrically, particularly in areas of the Russian Far East and Western Alaska (Lance and Cook 1998;

Iwasa et al. 2002; Brunhoff et al. 2003).

We previously studied intraspecific local differentiation in two red-backed vole species occurring sympatrically in the Russian Far East, the gray red-backed vole, *Myodes* (formally *Clethrionomys*) *rufocanus* (Palaeartic species), and the northern red-backed vole, *My. rutilus* (Holarctic species) (Musser and Carleton 1993, 2005; Kaneko et al. 1998; Shenbrot and Krasnov 2005), on the basis of the mitochondrial and nuclear gene sequences (Iwasa et al. 2000, 2002). Our previous results revealed the presence of local-specific haplotypes of the mitochondrial gene with a considerable extent of sequence divergences, which suggests the local differentiation of this species on Sakhalin and Hokkaido as well as in the continental Russian Far East (Iwasa et al. 2000, 2002). However, these sympatric species, *My. rutilus* and *My. rufocanus*, showed different patterns in intraspecifically phylogenetic relationships among the local mitochondrial haplotype groups (Iwasa et al. 2000, 2002). For example, the genetic distances between individuals from the Magadan region and the Kamchatka region in the Rus-

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sian Far East were obviously higher in *My. rutilus* than in *My. rufocanus*. This suggests that they have experienced different processes in lineage differentiation and/or geographic separation during the Quaternary period.

The root vole, *Microtus oeconomus*, together with *My. rutilus*, inhabits areas of Europe, Siberia, and Alaska, while *My. rufocanus* inhabits Eurasia (Paradiso and Manville 1961; Gromov and Polyakov 1977; Musser and Carleton 1993, 2005; Shenbrot and Krasnov 2005). As mentioned above, according to Iwasa et al. (2000, 2002), *My. rufocanus* and *My. rutilus* show different intraspecific phylogeography, and it would be interesting to study the intraspecific genetic diversity of *Mi. oeconomus* in northeastern Asia, particularly in the Russian Far East. *Myodes rutilus* had a boundary to discriminate two major haplotypes of the mitochondrial gene between the Magadan and the Kamchatka regions but *My. rufocanus* did not show such phylogeographic pattern (Iwasa et al. 2002). Thus, the Magadan-Kamchatka relationship of *Mi. oeconomus* would contribute to the elucidation of the relationship between biological and

geographic historical events, as shown in *My. rufocanus* and *My. rutilus* (Iwasa et al. 2000, 2002). Recently, Brunhoff et al. (2003) and Galbreath and Cook (2004) revealed the Holarctic phylogeography of *Mi. oeconomus* in detail using specimens from the Beringian areas, but they did not include samples from Kuril Archipelago.

In this study, we collected *Mi. oeconomus* samples from Magadan, Kamchatka, and Kuril Archipelago and examined the extent of the local differentiation in mitochondrial gene sequences. To understand evolutionary processes of Holarctic and Palaearctic arviculids, we traced the intraspecific phylogeography of *Mi. oeconomus* and compared its genetic divergence with those of *My. rutilus* and *My. rufocanus* previously reported.

Materials and methods

Fifteen individuals of *Mi. oeconomus* were collected from six localities from three distinct regions, Magadanskaya region (MAG), Kamchatkaya region (KAM), and Kuril Archipelago (KUR), as shown in Table 1 and

Table 1. The root vole, *Microtus oeconomus*, samples used in this study

Collection locality*	Specimen code	<i>Cytb</i> type	Accession No.
Magadanskaya region			
1. Magadan	IK57-96	Magadan (MAG)	AB372195
	IK59-96	Magadan (MAG)	AB372193
	IK86-96	Magadan (MAG)	AB372196
	IK87-96	Magadan (MAG)	AB372194
	RUS-10	Magadan (MAG)	AY305205***
Kamchatkaya region			
2. Milkovo	IK109-97	Kamchatka (KAM)	AB372197
3. Elisovo	IK120-97	Kamchatka (KAM)	AB372198
	IK121-97	Kamchatka (KAM)	AB372199
	IK122-97	Kamchatka (KAM)	AB372200
Sakhalinskaya region and Northern Kuril Archipelago			
4. Paramushir Island	VK6.05	Kuril Archipelago (KUR)	AB372202
	VK6.15	Kuril Archipelago (KUR)	AB372201
5. Onkotan Island	VK6.41	Kuril Archipelago (KUR)	AB372203
	VK6.42	Kuril Archipelago (KUR)	AB372204
6. Kharimkotan Island	VK6.51	Kuril Archipelago (KUR)	AB372205
7. Shiashkotan Island	VK6.59	Kuril Archipelago (KUR)	AB372206
	VK6.69	Kuril Archipelago (KUR)	AB372207
8. Rasshua Island	HEH40	Kuril Archipelago (KUR)	AF163902**
Kolyma region			
9. Chukotka	RUS-11	Kolyma (KOL)	AY305091***
	RUS-12	Kolyma (KOL)	AY305090***
Alaska region			
10. St. Lawrence Island	USA-1	Alaska (ALK)	AY305167***
	USA-2	Alaska (ALK)	AY305171***
11. Pilgrim Springs	USA-3	Alaska (ALK)	AY305133***

*Collection locality numbers are identical to those in Fig. 1.

**Conroy and Cook (2000).

***Galbreath and Cook (2004).



Fig. 1. Collection localities of *Microtus oeconomus* samples examined in this study. Samples from localities indicated with asterisks are referred from databases (see text). Black colored areas roughly indicate distribution of *Mi. oeconomus* (Shenbrot and Krasnov 2005). Collection locality numbers are (1–11) identical to those of Table 1.

Fig. 1. All the voucher specimens are preserved at the authors' laboratory. Furthermore, *Cytb* data of *Mi. oeconomus* in the DNA databases were also used for the present analysis: AF163902 from Rasshua Is. (Conroy and Cook 2000), Kuril Archipelago, Russia (KUR); AY305205 from Magadan, Magadanskaya region, Russia (MAG); AY305090 and AY305091 from Chukotka, Kolyma region, Russia (KOL); AY305167 and AY305171 from St. Lawrence Is., Alaska region, USA (ALK); and AY305133 from Pilgrim Springs, Alaska region, USA (ALK) (Galbreath and Cook 2004). We chose the sampling localities mentioned above from the data in Conroy and Cook (2000), and Galbreath and Cook (2004), considering the sampling localities of *My. rutilus* and *My. rufocanus* in Iwasa et al. (2000, 2002).

The total DNA was extracted from liver tissue by the conventional phenol-chloroform method. According to Iwasa et al. (2000), a fragment of the *Cytb* of mtDNA was amplified with polymerase chain reaction (PCR), using universal primers (L14724 and H15915; Irwin et al. 1991). Both DNA strands of the PCR products were directly sequenced (1,143 bp) by an automated method using the Big Dye Terminator Cycle Sequencing Kit (ABI) and an automated sequencer (model 3100, ABI).

We constructed a phylogenetic tree by the neighbor-joining (NJ) method (Saitou and Nei 1987) and per-

formed bootstrap analysis (1,000 replications); the genetic distances were computed with Kimura's two-parameter method (Kimura 1980) using the MEGA ver. 2.1 program (Kumar et al. 2001) for the *Cytb* sequences considering all substitutions at all codon positions. A *Cytb* sequence of *Mi. montebelli* from the DNA databases (accession No.: AB163900) was used as an outgroup (Conroy and Cook 2000).

The local differentiation of the *Cytb* data in *Mi. oeconomus* was assessed by pairwise genetic distances against the geographic distances (< 1,500 km distribution area) in the Russian Far East in comparison with our previous data: *My. rutilus* ($n = 27$) and *My. rufocanus* ($n = 29$), respectively (Iwasa et al. 2000, 2002). The statistical significance of the relationships was determined using a Mantel permutation test (Mantel 1967; Hutchison and Templeton 1999).

Results

A total of 20 haplotypes for the complete sequences of *Cytb* of 1,143 bp in length were compared, including the sequences from the DNA databases (Conroy and Cook 2000; Brunhoff et al. 2003). The Kimura distances (D) in the intraspecific comparison ranged from 0.0000 to 0.0371. The NJ tree with the calculation indices revealed

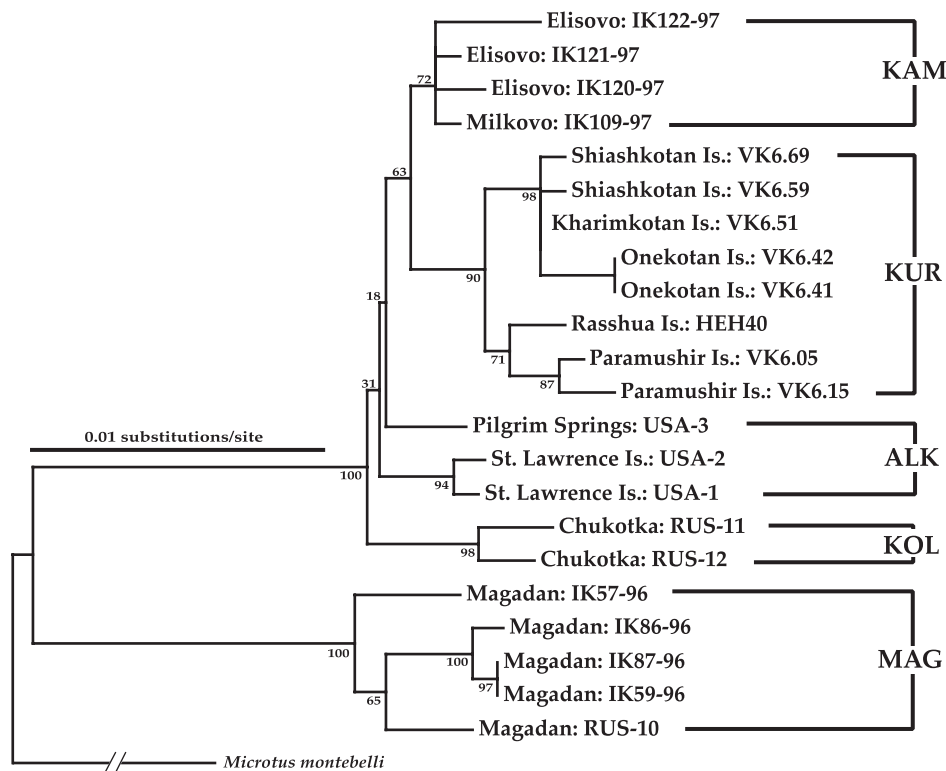


Fig. 2. A neighbor-joining tree of the *Microtus oeconomus* constructed considering all substitutions at all codon positions of the mitochondrial cytochrome *b* gene (1,143 bp). Numbers near nodes of the tree are bootstrap values to assign the confidences of nodes.

two clusters with the highest bootstrap values (100%), representing both the MAG region (locality No. 1) and KAM/KUR/KOL/ALK regions (locality Nos. 2–11) (Fig. 2). Regarding the two major clusters, there was substantial differentiation between both clusters with *D*, which ranged from 0.0288 to 0.0371, as well as those in *My. rutilus* (Iwasa et al. 2002).

The relationship of the genetic distances against the geographic distances in *Mi. oeconomus* was compared with those in *My. rutilus* and *My. rufocanus* (Iwasa et al. 2002) through scatter plots using Kimura's calculation indices (Fig. 3). In the scatter plots, each species showed a significant correlation ($P < 0.01$) between both distances (Fig. 3). However, the pairwise genetic distances between the "MAG region" and "KAM/KUR/KOL/ALK regions" in *Mi. oeconomus* ($D > 0.0288$) and *My. rutilus* ($D > 0.0251$) were significantly ($P < 0.05$) higher than those in *My. rufocanus* ($D < 0.0120$) (solid circles in Fig. 3; Iwasa et al. 2002). The relationships of the transition/transversion ratio against all substitutions in the three species were plotted to visualize the levels of genetic differentiation among the local regions (Fig. 4). The scatter plots in Fig. 4 show the highest frequency of transversions within *Mi. oeconomus*, the second highest

within *My. rutilus*, and the lowest within *My. rufocanus* between haplotypes from the MAG and KAM/KUR regions (solid circles in Fig. 4).

Discussion

The local differentiation in *Cytb* of *Mi. oeconomus* was similar to that of *My. rutilus*, but not similar to that of *My. rufocanus* (Figs. 3 and 4). In addition, the present results also essentially resemble the allozyme patterns in both Holarctic vole species reported by Nadler et al. (1978), Lance and Cook (1998), and Frisman et al. (2003), whereas *Mi. oeconomus* in Siberia and Alaska shared resemblance of gene frequencies in several loci. Furthermore, as Iwasa et al. (2000) used, on the basis of the splitting time between Hokkaido and Sakhalin as 15,000 years ago (Ohshima 1990) in *My. rufocanus*, the isolation time between the MAG region and the KAM/SAK/KUR regions was estimated to be $< 13,000$ years ago using the scale of the genetic distances, which is smaller than that of Frisman et al. (2003) (Fig. 3). It is well known that the KAM and KUR regions were bound to Alaska through a land bridge during the Quaternary glacial periods (Frenzel et al. 1992) and the data in

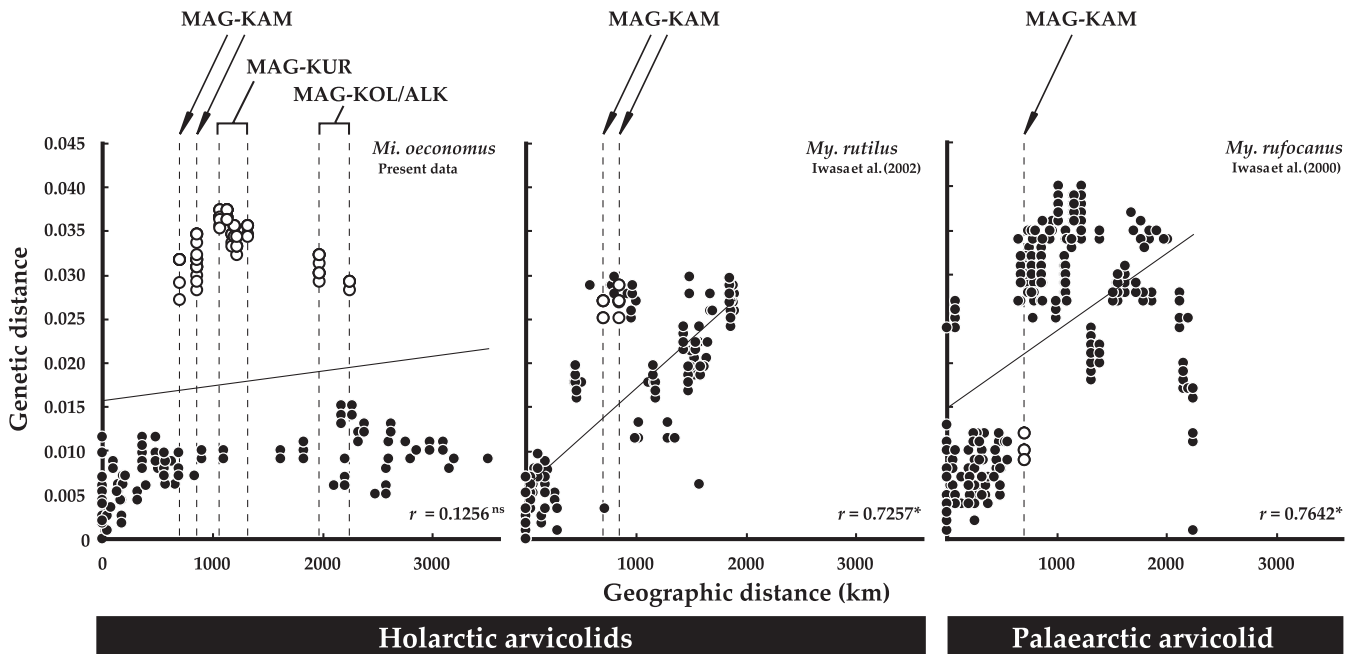


Fig. 3. Comparison of relationship of genetic distance against geographic distance in *Microtus oeconomus*, *Myodes rutilus* and *My. rufocanus*, the latter two data are according to Iwasa et al. (2000, 2002). Open circles indicate the Magadan region versus Kamchatska/Sakhalin/Kuril Archipelago regions (see text for abbreviations).

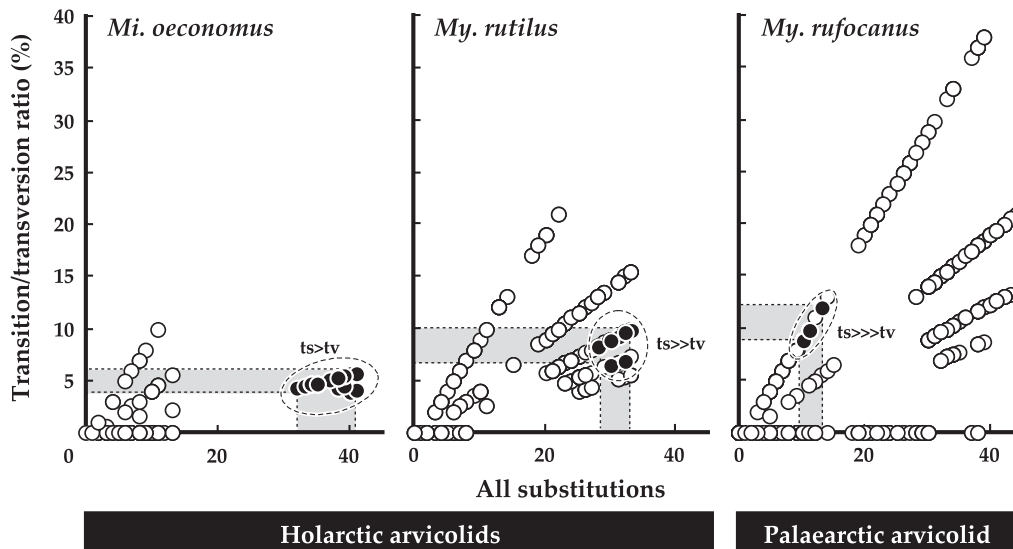


Fig. 4. Scattergrams of relationships between all substitutions and transition (ts)/transversion (tv) ratio within *Microtus oeconomus*, *Myodes rutilus* and *My. rufocanus*, the latter two data are according to Iwasa et al. (2000, 2002). Dotted lines surrounding solid circles indicate the Magadan region versus Kamchatska/Sakhalin/Kuril Archipelago regions.

Nadler et al. (1978) and Lance and Cook (1998) were also acceptable considering the geographical history. In contrast, the local differentiation in the *Cytb* haplotypes between the MAG and KAM/KUR/KOL/ALK regions substantially differ between the Holarctic species and the Palearctic *My. rufocanus* (Fig. 3; Iwasa et al. 2000; Frisman et al. 2002). Notably, a Palearctic species of

insectivores, *Sorex caecutiens* (Ohdachi et al. 2001), also showed low genetic divergences between the MAG and KAM/KUR regions, similarly to *My. rufocanus*. On the other hand, the genetic similarities at Berigian areas for phylogeographic relationships are observed in the *Sorex cinereus* group, which consists of taxa of closely related species (Ivanitskaya 1989; Demboski and Cook 2003).

All of these considerations suggest that the Holarctic vole species have differentiated through similar evolution and radiation patterns in synchronic periods in the late Quaternary (e.g., Hoffmann and Koepl 1985; Lance and Cook 1998).

The present result provides valuable information for the possible association of geological and environmental changes and microevolution of small rodents in East Asiatic regions. Taking into account an important geological event, the formation of the Soya Strait splitting Hokkaido and Sakhalin, which is thought to have occurred 15,000 years ago (Ohshima 1990), this geological time would be converted with a time scale of the average genetic distance of individuals between Hokkaido and Sakhalin, 0.039 ± 0.009 , in *My. rufocanus* (Fig. 3; Iwasa et al. 2000). If we apply this time scale of the genetic distance, the genetically splitting time between the MAG and KAM populations in *My. rutilus* (0.0251–0.0288) and *Mi. oeconomus* (0.0270–0.0343), and that in *My. rufocanus* (0.009–0.012) are estimated to be approximately 10,000–13,000 years ago and 3,000–4,000 years, respectively, at least under the assumption of a constant divergence rate of the *Cytb* (Fig. 3; Iwasa et al. 2000, 2002). However, these times are considered as an under estimation based on the previous biogeographic opinions (e.g., Demboski and Cook 2003; Galbreath and Cook 2004). Therefore, we used the separation time between the KAM and KUR regions has been estimated to be 10,000 years by Veliganin (1976) geologically. If the geo-historical separation time is applied for our mtDNA divergence data, the splitting time between the MAG and KAM regions in *My. rutilus* and *Mi. oeconomus* is estimated to be 25,000–55,000 years ago (Fig. 3). Thus, we can conclude that the splitting time between the MAG and KAM populations in the Holarctic arviculids is considered within a few ten thousand years ago at most.

Lance and Cook (1998), Brunhoff et al. (2003) and Galbreath and Cook (2004) analyzed the intraspecific genetic variation of *Mi. oeconomus* in Alaska and the Russian Far East. A specimen of this species from the Russian Far East (locality: Chuan Bay area, see Fig. 1 in Lance and Cook 1998) showed no genetic differentiation with those from Alaska. Similarly, previous mtDNA analysis also revealed a close relationship between specimens from Alaska and the Russian Far East (Brunhoff et al. 2003). In addition, these studies suggested that the colonization of *Mi. oeconomus* in North America might have occurred in the late Quaternary as well as in a previ-

ous zoogeographical issue (Hoffmann and Koepl 1985). Thus, our molecular data support the conclusion of these studies. Furthermore, Repenning et al. (1990) reported that the *Mi. oeconomus* invasion might have occurred from the Russian Far East to North America during the Quaternary on the basis of paleontological data (Kurtén and Anderson 1980; Zakrzewski 1985; Kordos 1990). However, our results were not able to refer the invasion direction of *Mi. oeconomus*. On the basis of the karyological relationships using G-band patterns among the Palaearctic, Nearctic, and Holarctic arviculids, the genera *Myodes* (= *Clethrionomys*), *Eothenomys*, and *Alticola* (Iwasa 1998) carry two cytotypes, so-called “*glareolus*-cytotype” and “*rufocanus*-cytotype” (Gamperl 1982; Iwasa 1998). Considering the distribution patterns of vole species carrying both cytotypes in the Northern hemisphere, alternative possibilities for the direction of invasion of the Holarctic species, from Siberia to Alaska or vice versa, should be reevaluated (Iwasa 1998).

On the basis of the description of Klumov (1960), the KUR’s *Mi. oeconomus* populations are regarded as artificially introduced ones. Moreover, Voronov (1974) also reported that native populations of *Mi. oeconomus* were limited in Paramushir, Atlasova, and Shumshu Islands. Our current data of the mtDNA showed slight genetic distances (0.0000–0.0088) among the KUR samples, but the present sequences apparently differed between the islands. Likewise, Han et al. (2002) and Ohdachi et al. (2004) revealed the low level of the genetic distances (0.0000–0.0090) in *Crocidura dsinezumi* specimens from northeastern Honshu of Japan and regarded them as artificially introduced samples. The mtDNA data of *C. dsinezumi*, however, showed no local specificity among artificially introduced specimens and differed from the tendency of our current data of *Mi. oeconomus*, which showed island specificity. Therefore, we thought that the present *Mi. oeconomus* specimens might be indigenous; however, we do not dispute the idea that the voles may have been introduced from island to island because there is poor for geological findings about Kuril Archipelago. The insular peculiarity may be result as founder effect.

Our present and previous data (Iwasa et al. 2000, 2002) are contributed to elucidate evolutionary processes in phylogeographically related species of voles. These data facilitate our understanding of the roles of geographical and environmental factors during recent glacial times in the context of phylogeographic standpoints (Brown and Lomolino 1998; Avise 2000). The present data support the formation of land bridges that connected

the KAM and KUR regions during the glacial periods of the Quaternary (< one million years), as suggested by geohistorical studies (e.g., Frenzel et al. 1992). Furthermore, our data also illustrate the role of a certain geographic barrier that would have appeared between the MAG and KAM/KUR regions in the late Quaternary and only had an effect on the Holarctic species. The fact that the Palaeartic *My. rufocanus* was not affected by this barrier suggests that the Palaeartic vole species experienced different evolutionary forces that resulted in its own phylogeographic structure. The difference suggests that the KAM population of *My. rufocanus* was newly established in the last interglacial period, while, in populations of the Holarctic species, the regional populations are independent and have a long-term colonizing time (Fig. 3). The presence of the “ALK” population may have taken place due to persistence of the KAM haplotype group in *Mi. oeconomus*.

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