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Colonization history of the sable *Martes zibellina* (Mammalia, Carnivora) on the marginal peninsula and islands of northeastern Eurasia

Gohta Kinoshita,* Jun J. Sato, Ilya G. Meschersky, Sofiko L. Pishchulina, Leonid V. Simakin, Vyacheslav V. Rozhnov, Boris A. Malyarchuk, Miroslava V. Derenko, Galina A. Denisova, Lyubov V. Frisman, Alexey P. Kryukov, Tetsuji Hosoda, and Hitoshi Suzuki

Laboratory of Ecology and Genetics, Graduate School of Environmental Earth Science, Hokkaido University, N10W5, Kita-ku, Sapporo 060-0810, Japan (GK, HS)
Laboratory of Animal Cell Technology, Department of Biotechnology, Faculty of Life Science and Technology, Fukuyama University, Higashimura-cho, Aza, Sanzo 985, Fukuyama 729-0292, Japan (JJS)
Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskiy pr. 33, Moscow 119071, Russia (IGM, SLP, VVR)
Pechoro-Ilychskii Biosphere Reserve, Laninoy str. 8, Yaksha, Komi Republic 169436, Russia (LVS)
Genetics Laboratory, Institute of Biological Problems of the North, Far East Branch of Russian Academy of Sciences, Portavaya str. 18, Magadan 685000, Russia (BAM, MVD, GAD)
Institute for Complex Analysis of Regional Problems, Far Eastern Branch Russian Academy of Science, Sholom-Aleihem str. 4, Birobidzhan 679016, Russia (LVF)
Laboratory of Evolutionary Zoology and Genetics, Institute of Biology & Soil Science Far East Branch Russian Academy of Sciences, Stoletija str. 159, Vladivostok 690022, Russia (APK)
Kansai University, International Education, 1-2-20 Satake-dai, Suita-shi, Osaka 565-0855, Japan (TH)

* *Correspondent: gohta_kinoshita@ees.hokudai.ac.jp*

We examined the nucleotide sequences of the mitochondrial NADH dehydrogenase subunit 2 gene (976 base pairs) for 279 individuals of the sable *Martes zibellina* (Carnivora, Mustelidae), derived from diverse areas throughout the regions of the Ural Mountains to the Russian Far East on the Eurasian continent and the peripheral peninsula (Kamchatka) and islands (Sakhalin, Hokkaido, and southern Kurils). The demographic history of the sable and its migration history to the eastern peripheral peninsula and islands were inferred using phylogeographic approaches. The analyses confirmed the previously found major lineages for the examined sables and further identified novel sublineages. Our data also support that a lineage, which is endemic to the eastern marginal islands (Sakhalin, Hokkaido, and southern Kurils), was produced by the demographic expansion of an ancestral lineage in the Eurasian continent. The most recent common ancestor of the Sakhalin, Hokkaido, and southern Kuril sables was estimated to exist during the Late Pleistocene. We also determined that another lineage exists on Sakhalin and is shared by the Far East Primorsky population. Our results indicate multiple migration events onto Sakhalin from the continent and suggest the importance of the formation of several straits to the distribution of sable lineages. Meanwhile, Kamchatka is dominated by a sole lineage which would also have followed the demographic expansion on the Eurasian continent. The Russian Far East was indicated as the source area for lineage diversifications; in this region, genetic diversity was relatively high, which is consistent with previous studies.

Key words: Hokkaido, mitochondrial DNA, *Nd2*, phylogeography, sable, Sakhalin

Climate oscillations during the Pleistocene imposed enormous constraints on boreal species, causing the reformation of their distributions and population genetic diversity (Hewitt 1996, 2000). Intensive glaciation forced boreal species to retreat from areas of high latitude, especially in northern parts of Europe and North America (Stewart and Lister 2001; Hewitt 2004; Lister 2004). Previous studies have presented plausible evidence of southern refugia in Europe and North America based on paleontological data and signatures of past demographic history left behind on the phylogeographic structure of

present-day species (e.g., Fedorov and Stenseth 2002; Waltari et al. 2007; Provan and Bennett 2008). On the other hand, the majority of northeastern Eurasia was not covered by ice sheets during glacial periods (Grosswald 1980, 1998; Svendsen et al. 2004). Instead, the cold and dry climate led to coverage by tundra steppe-like vegetation; therefore, taiga forests have been fragmented as small patches in mainly southern Siberia (Abbott and Brochmann 2003; Semerikov et al. 2007; Binney et al. 2009). Many phylogeographic studies of boreal species in northeastern Eurasia have generally suggested the contraction of the ranges of boreal species into several refugia (e.g., southern Ural Mountains or southeastern Siberia) during glacial periods, followed by demographic expansion to form present-day distributions (Kvist et al. 2001, 2003; Oshida et al. 2005; Goropashnaya et al. 2007; Fedorov et al. 2008; Poyarkov and Kuzmin 2008; Korsten et al. 2009; Hope et al. 2010; Sakka et al. 2010; Davison et al. 2011; Malyarchuk et al. 2011; Kryukov et al. 2012; Ohdachi et al. 2012; Todisco et al. 2012; Malyarchuk et al. 2013). However, how climate changes during the Pleistocene period influenced the demographic history of boreal species in northeastern Eurasia, particularly compared to Europe and North America, remains to be precisely determined.

Meanwhile, recent phylogeographic studies have shown that peripheral populations of Eurasian boreal mammals in areas such as the Kamchatka Peninsula and on Sakhalin, Hokkaido, and the southern Kuril Islands possess characteristic genetic structures compared to mainland populations (Iwasa et al. 2000; Matsuhashi et al. 2001; Inoue et al. 2007; Iwasa et al. 2009; Korsten et al. 2009; Bannikova et al. 2010; Davison et al. 2011; Malyarchuk et al. 2011; Abramson et al. 2012; Kinoshita et al. 2012; Ohdachi et al. 2012; Yu et al. 2012; Gus'kov et al. 2013; Hirata et al. 2013; Ishida et al. 2013; Malyarchuk et al. 2013). However, the unique colonization histories of these peripheral populations have not been sufficiently discussed in combination with the demographic population expansions that occurred on mainland Eurasia, with the exception of studies on a limited number of species (Iwasa et al. 2000; Poyarkov and Kuzmin 2008; Korsten et al. 2009; Davison et al. 2011; Abramson et al. 2012; Ohdachi et al. 2012; Hirata et al. 2013). Thus, the specific process involved in the formation of these peripheral populations is not well understood.

The sable *Martes zibellina* (Mammalia, Carnivora, Mustelidae) is an arboreal species that is intimately associated with forest habitats in northern Eurasia; its distribution ranges widely from the Ural Mountains to the Russian Far East, and isolated populations occur on Sakhalin, Hokkaido, and the southern Kuril Islands along the coast of northeastern Eurasia (Murakami 2009). Its distribution includes the taiga forest zone in Siberia and extends to southern areas where coniferous and deciduous forests occur. Therefore, the population dynamics of the sable may have been synchronized with the repeated vegetational shifts in northern Eurasia during Pleistocene glacial periods. Because the sable exhibits substantial morphological variation across its distribution and because its population structure may have been affected by the many artificial translocations (augmentation, introduction, and/or reintroduction) since the early 20th century (Monakhov 2011; Powell et al. 2012), phenotypic analyses to classify local races and clarify the demographic history are difficult. In contrast, previous genetic analyses using mitochondrial DNA (mtDNA) sequences have revealed several patterns of intraspecific variation. In general, 3 major lineages have been recognized for most continental sables from Ural to Russian Far East populations (Petrovskaya 2007; Malyarchuk et al. 2010; Sato et al. 2011; Li et al. 2013; Rozhnov et al. 2013); these lineages are estimated to have diverged from each other during the late Middle Pleistocene (Sato et al. 2011; Li et al. 2013).

On the other hand, the Kamchatka population has been shown to possess only one of these 3 major lineages, and this population exhibits much lower genetic diversity compared to other continental populations (Petrovskaya 2007; Malyarchuk et al. 2010; Rozhnov et al. 2013). Similarly, lower genetic diversity has also been observed in the Hokkaido population (Sato et al. 2011; Ishida et al. 2013). However, neither the source area nor the exact process of these migrations has been clarified to date. To elucidate the colonization history of the eastern marginal peninsular and insular populations and the related demographic history of the sable in continental Eurasia, more comprehensive sampling from both mainland and peripheral regions as well as in-depth analyses of population genetic structure are required.

The present study examines the comprehensive range of sables including mainland populations from the west (Ural), central (Krasnoyarsk), and east (Russian Far East) as well as most peripheral peninsular and insular populations from Kamchatka, Sakhalin, Hokkaido, and southern Kuril (Fig. 1). The examination of the Sakhalin and Kuril samples is a novel aspect of this study. We used mitochondrial NADH dehydrogenase subunit 2 (*Nd2*) gene sequences in the phylogeographic analyses to address the following issues: how marginal peninsular and insular populations were established in combination with the demographic history of mainland Eurasian populations and how the migration history of the peripheral peninsular and insular sable have been synchronized with other boreal species in northern Eurasia since the Pleistocene.

Materials and Methods

A total of 279 individual sables were analyzed, as listed in Supporting Information S1. We determined partial nucleotide sequences of the mitochondrial *Nd2* gene (976 bp) for 209 individuals; homologous sequences for an additional 70 individuals were downloaded from the DDBJ/EMBL/GenBank international DNA database with accession numbers AB455741 and AB625980–626048 derived from Sato et al. (2009, 2011). Novel sequences were deposited in the DNA databases with accession numbers AB908319–AB908369 (Supporting Information S1). Sequences for other *Martes* species, including *M. americana* (AY598546), *M. foina* (AB564140), *M. martes* (AB564141), and *M. melampus* (AB455709), were also downloaded from the database and examined in this study. In the phylogeny (topology) inferences, *M. foina* was used as an outgroup according to the phylogenetic hypothesis that this

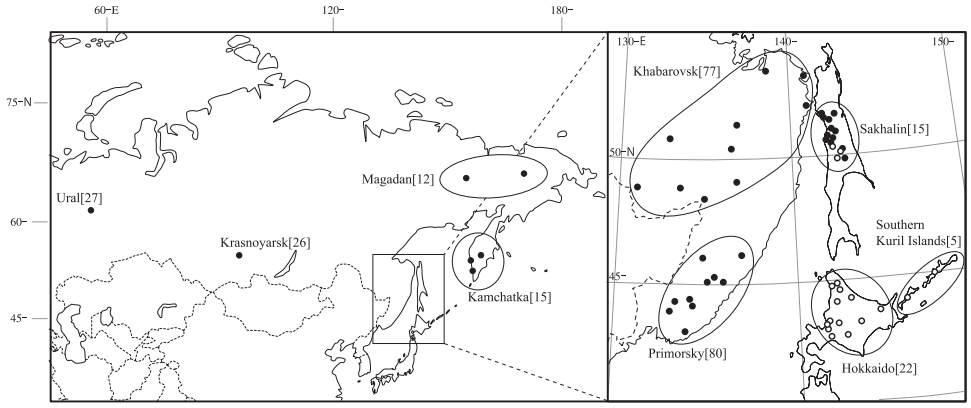

Fig. 1.—Sampling localities for sables examined in this study. The map on the left gives a continental-scale view. The square indicates the inset shown on the right, the area of the southern Russian Far East and marginal islands. The numbers in square brackets after the name of a region indicate the number of examined individuals. We present each population in the text based on these sampling localities: Ural, Krasnoyarsk, Magadan, Kamchatka, Khabarovsk, Primorsky, Sakhalin, Hokkaido, and southern Kuril Islands. Open circles represent localities that only possess H1 lineage haplotypes.

species is the most closely related to the clade of "true martens," which includes *M. americana*, *M. martes*, *M. melampus*, and *M. zibellina* (e.g., Wolsan and Sato 2010; Sato et al. 2012).

PCR amplification and sequencing strategy.—Total genomic DNA was extracted from tissues preserved in ethanol using the conventional phenol–chloroform method (Sambrook and Russell 2001). Polymerase chain reaction (PCR) was performed in a final volume of 20 µl, which consisted of 1 µl template DNA, 2.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.05 µM each primer, 1 × *Taq* polymerase buffer, and 0.5 units AmpliTaq Gold DNA polymerase (Applied Biosystems [ABI], Foster City, California). Thermal cycling parameters were as follows: one cycle of denaturation at 95°C for 2 min, 35 cycles of denaturation at 95°C for 30 s, annealing at 50°C for 30 s, extension at 72°C for 1 min, and a final cycle of extension at 72°C for 10 min. The primers used to amplify the *Nd2* gene were ND2-FelF (Yu and Zhang 2006) and ND2-melExtR (Sato et al. 2009). A negative control sample replacing DNA templates with a corresponding volume of water was also prepared for each PCR reaction. We did not observe any amplification in our negative control PCR analyses. The sequence reaction of the PCR products was conducted using the BigDye Terminator Cycle Sequencing kit v3.1 (ABI) and the primers ND2-FelF and ND2-CarF (Yu and Zhang 2006), followed by automated sequencing on an ABI3130 Genetic Analyzer (ABI). The *Nd2* sequences generated in this study and collected from the DNA database were aligned by eye using ProSeq ver. 2.91 (Filatov 2002), as the absence of insertions and deletions made the alignment straightforward.

Phylogenetic and chronological analyses.—Reconstruction of the phylogenetic tree using the maximum likelihood (ML) criterion (Felsenstein 1981) was conducted using the program MEGA ver. 5.05 (Tamura et al. 2007). The best-fit substitution model (TN93+I) was selected using the Bayesian Information Criterion (BIC) implemented in MEGA. Trees were obtained from heuristic searches using as-is sequence addition and nearest-neighbor interchange (NNI) branch swapping; otherwise, default settings were used. Clade support was assessed using nonparametric bootstrap analyses (Felsenstein 1985) with 1,000 replicates with the same settings as the above ML heuristic search.

Reconstruction of the phylogenetic tree and estimation of divergence times by Bayesian inference were conducted using the program BEAST ver. 1.4.8 (Drummond and Rambaut 2007). The model test function in MEGA was used to choose an appropriate substitution model (TN93+I) with the BIC. The dataset was analyzed in a Bayesian uncorrelated log-normal relaxed-clock model using the coalescent model with constant population size as tree prior on phylogeny. We considered rate variation among different branches, where the rates on each branch were independently drawn from a log-normal distribution and were uncorrelated (Drummond et al. 2006). We used the program BEAUti, ver. 1.6.1 (provided in the BEAST package) to generate the input file for the BEAST program, using the substitution model for the sequence evolution, priors, and conditions of the Markov Chain Monte Carlo (MCMC) approach for estimating posterior distributions of the time to the most recent common ancestor (MRCA) of individual sables. Three independent MCMC analyses were run for 50×10^6 generations with trees sampled every 5,000 generations. Each log file was checked to confirm convergence to the stationary posterior distribution and sufficient effective sample size (ESS) of each parameter using the program Tracer ver. 1.6 (Rambaut and Drummond 2007). Then the log files of 3 independent runs were combined to provide each parameter estimate, with the first 25% of the sampled parameters discarded as burn-in. We obtained sufficient ESS values exceeding 200 for all parameters. A calibration point was set on the basis of the time estimate for the divergence between *M. foina* and the other *Martes* species in Sato et al. (2012). We adopted a normal distribution with a mean of 3.045 million years ago (mya) and *SD* of 0.3555 to the basal divergence of the examined taxa, such that the 95% confidence intervals (*CI*s) ranged from 2.46 to 3.63 mya as shown in Sato et al. (2012). This calibration was also consistent with the estimate of Koepfli et al. (2008).

Network and phylogeographic analyses.—To infer the relationships of the obtained haplotypes, the median-joining

network was reconstructed using the program Network ver. 4.6 (Bandelt et al. 1999). For the lineages inferred from the phylogenetic analysis, estimation of nucleotide diversity (π), analysis of mismatch distribution (Li 1977; Harpending 1994; Rogers 1995), and the neutrality test (Tajima 1989; Fu 1997) were conducted using the program ARLEQUIN ver. 3.5.1.3 (Excoffier et al. 2005). In the mismatch distribution analysis, the goodness-of-fit of the observed distribution to the expected distribution under the sudden expansion model (Rogers 1995) was tested by computing the sum of squares deviation (*SSD*) and the raggedness index. In the same program, haplotype diversity (h) and π were evaluated for each population defined geographically as in Fig. 1. We explored population structure using the program SAMOVA (spatial analyses of molecular variance—Dupanloup et al. 2002) to infer the genetic barriers within the distribution of the sable. This method implements a simulated annealing approach to define groups of populations that are geographically homogeneous and maximally differentiated from the other populations. In this analysis, the number of groups (K) was a priori determined to range from 2 to 8. For each K value, 10,000 simulated annealing steps were performed starting from each of 200 sets of initial conditions, searching for the largest F_{CT} values (proportion of total genetic variance due to differences among groups of populations) as a predictor of the best grouping of populations (Dupanloup et al. 2002). In addition, we estimated pairwise fixation index (Φ_{ST}) values among populations in ARLEQUIN and constructed a neighbor-joining (NJ) tree using these values in MEGA.

Results

Sequence variation and phylogenetic inference.—In total, 51 haplotypes were identified in the 976 bp mitochondrial *Nd2* gene sequences among the 279 individual sables. Haplotypes (Hap) 1–13 have been described previously (Sato et al. 2011), whereas Hap 14–51 were newly identified in the present study (74.5% [38/51] haplotypes are novel). Among the 51 haplotypes, we found 61 segregating sites, of which 36 were singleton sites and the remaining 25 were parsimony informative sites.

We constructed the ML phylogenetic tree (Fig. 2) and recognized 3 major lineages (R1 + H1, R2, and R3) within the sable clade, as reported in Sato et al. (2011). We do not present the Bayesian tree here, as it is the same as the ML tree; thus, we only present the posterior probabilities (Fig. 2). In the topology, the R3 lineage initially branched off from the other lineages, followed by R2 from the remainder. The R1 + H1 lineage consisted of 3 sublineages (R1a, R1b + H1, and R1c), of which the R1b and R1c haplotypes were newly found in this study. The H1 lineage was exclusively composed of insular individuals from Sakhalin, Hokkaido, and the southern Kuril Islands. The range of each group of haplotypes is depicted in Fig. 3.

Statistical indices for genetic diversity and the demography are shown in Table 1. For all groups of haplotypes, except R1c, H1, and R3, at least one of the neutrality tests indicated negative values that significantly deviated from 0, implying rapid population growth (Table 1). In addition, the mismatch distribution for most groups of haplotypes, except R1, did not reject the sudden expansion model (Table 1).

Chronological inference.—The divergence times for each major node of the phylogenetic tree, estimated using BEAST, are shown in Fig. 2. The lineages of *M. martes* and *M. zibellina* were estimated to have diverged 0.54 mya, with a 95% *CI* of 0.27–0.80 mya. The MRCA for the sable clade was estimated to have existed 0.22 mya (*CI* = 0.12–0.34 mya), which corresponds to the divergence time of the R3 lineage from the other sable lineages. Subsequent divergence of the R2 lineage from the R1 + H1 clade occurred 0.20 mya (*CI* = 0.10–0.30 mya). The dates for the MRCA of each major lineage, R1 + H1, R2, and R3, were estimated to be within 0.09–0.14 mya from the latter part of the Middle Pleistocene (0.126–0.781 mya) to the Late Pleistocene (0.01–0.126 mya). The MRCA of the R1b + H1 lineage was dated at 0.09 mya (*CI* = 0.04–0.15 mya). The MRCAs of the other R1 sublineages, R1a and R1c, and H1 were inferred to be around 0.02–0.06 mya, corresponding to the Late Pleistocene.

Geographic trends of the sable lineages.—The haplotype network was constructed to represent the locality compositions in each haplotype and their relationships (Fig. 4). The observed haplotypes in the continental lineages were widespread, from eastern to western regions of the sable distribution in Eurasia. However, only 13 of 46 continental haplotypes were shared among populations. Furthermore, 28 of 33 continental-tip haplotypes were unique to each population.

We also calculated the compositional variability of each group of haplotypes among local populations (Table 2). All individuals from Hokkaido and the southern Kuril Islands were of the H1 lineage, whereas Sakhalin individuals harbored 5 haplotypes; 1 was included within the H1 lineage and the other 4 were in the R2 lineage (Fig. 4; Table 2). Three R1 sublineages exhibited different compositions in each local population. For example, all Kamchatka individuals harbored only R1a, showing no other lineages. All individuals from Primorsky belonging to R1 lineage were typed as the R1a with no R1b or R1c haplotypes. In contrast, more than 40% of individuals from Ural were typed as R1b or R1c haplotypes, whereas no individuals exhibited the R1a haplotype. The Krasnoyarsk population possessed only 1 central haplotype (Hap 1) within the R1a lineage (Fig. 4); therefore, no variation was observed within the population in terms of the R1a lineage, a possible result of the founder effect as discussed below. The R1c sublineage consisted of only 2 haplotypes observed in Ural and Krasnoyarsk, and this sublineage was distantly genetically related to the other R1 haplotypes by at least 4 mutations (Fig. 4). In the R2 lineage, 14 of 20 haplotypes were detected from eastern populations, especially in Primorsky and Khabarovsk, whereas most individuals from the Ural Mountains and Krasnoyarsk showed Hap 10 and its descendants (Hap 40–43), except for 1 individual typed as Hap 35. In addition, the eastern continental Primorsky and Khabarovsk populations exhibited relatively higher nucleotide diversity among the R2 haplotypes (both π = 0.0021; Table 2) compared to the Krasnoyarsk and Ural populations (π = 0.0010 and 0.0012, respectively). The R2 haplotypes possessed by 10

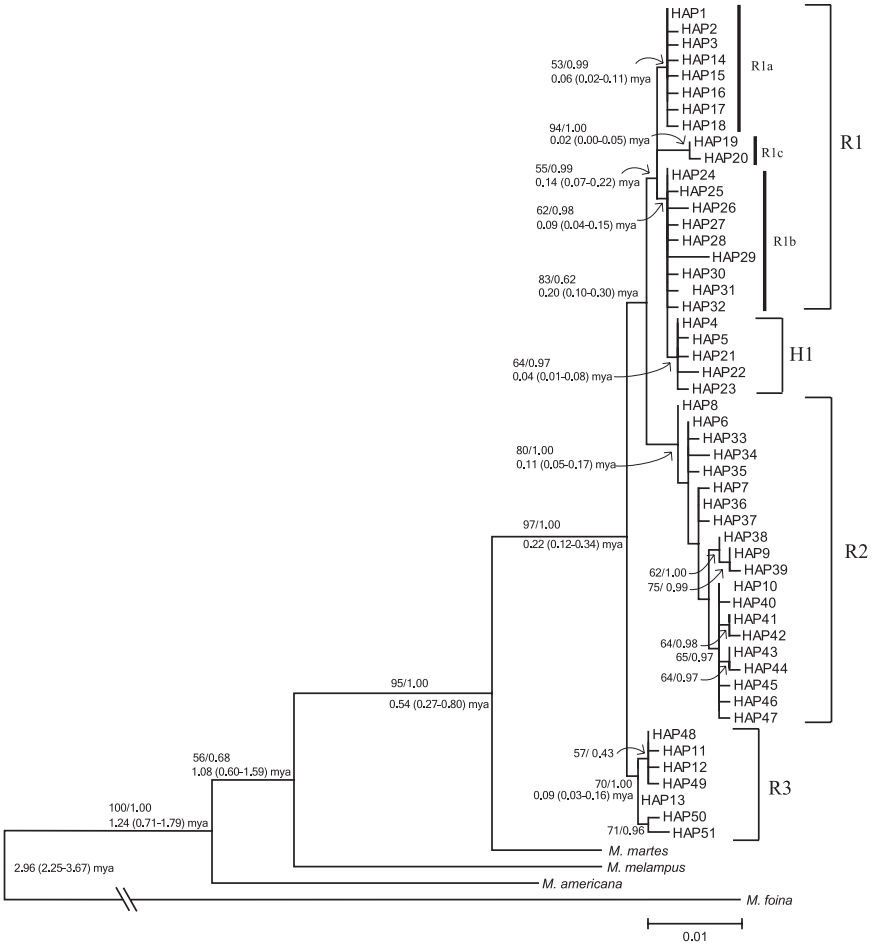

Fig. 2.—The maximum likelihood (ML) phylogenetic tree inferred from the 976 bp nucleotide sequences of the mitochondrial *Nd2* gene for 279 individual sables and other related species in the genus *Martes*. *Martes foina* was used as the outgroup. The Bayesian tree was the same as the ML tree in topology and therefore is not shown. Numbers above branches show bootstrap proportions in the ML analysis (left) and posterior probabilities in the Bayesian inference analysis (right). Numbers below branches represent divergence time estimates (means) with their 95% confidence intervals in parentheses. Only bootstrap values higher than 50% are shown. Lineage names are indicated on the right side of the phylogeny: R1, R1a, R1b, R1c, H1, R2, and R3.

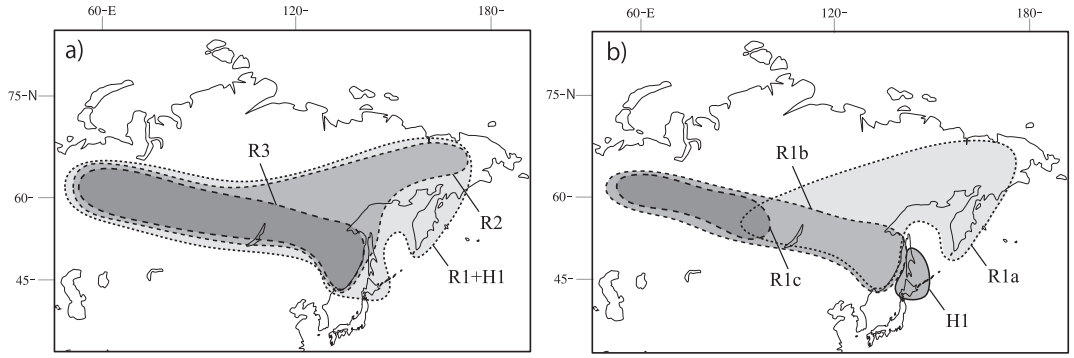

Fig. 3.—Geographic distributions of a) major 3 lineages of the sable, R1 + H1, R2, and R3 and b) sublineages of the R1 + H1 lineage. The R1b + H1 sublineage is shown separately by the R1b and H1 haplotype distributions for to be pragmatic, although R1b cannot be called "lineage" because of its paraphyletic relationships to H1. Range shapes of the distributions for each lineage were depicted according to the existence of the haplotypes in each population shown in Fig. 1.

of 15 Sakhalin individuals (Hap 7, 36, and 37, except 47) were genetically close to one another, and only Hap 7 was shared with one continental individual from Primorsky (Fig. 4). The R3 haplotypes were detected from 4 continental populations but at lower frequencies than the R1 and R2 haplotypes in every population (Table 2).

Genetic diversity of each local population.—Considering the total overall genetic variation across all lineages, the populations

Table 1.—Statistics for demographic analyses. *SSD* = sum of squares deviation.

Lineage	Sample number	Haplotype number	π	Tajima's *D*	Fu's *Fs*	*SSD*	Raggedness index
R1a	86	8	0.0005	−1.5461*	−5.4016*	0.0069	0.1474
R1b	24	9	0.0017	−1.6127*	−3.4299*	0.0044	0.076
R1c	8	2	0.0005	1.1665	0.8664	0.031	0.2921
H1	30	5	0.0008	−1.0883	−1.3575	0.0001	0.0715
R1	118	19	0.0020	−1.7198*	−8.7069*	0.5538*	0.0249
R1b + H1	54	14	0.0017	−1.7514*	−6.6963*	0.0029	0.0531
R1 + H1	148	24	0.0025	−1.659*	−10.9676*	0.0111	0.0329
R2	110	20	0.0024	−1.0849	−8.0033*	0.0123	0.0456
R3	21	7	0.0018	−0.7473	−1.5638	0.0153	0.0663
All	279	51	0.0056	−1.3016	−21.5771*	0.0121	0.0187

*$P < 0.05$.

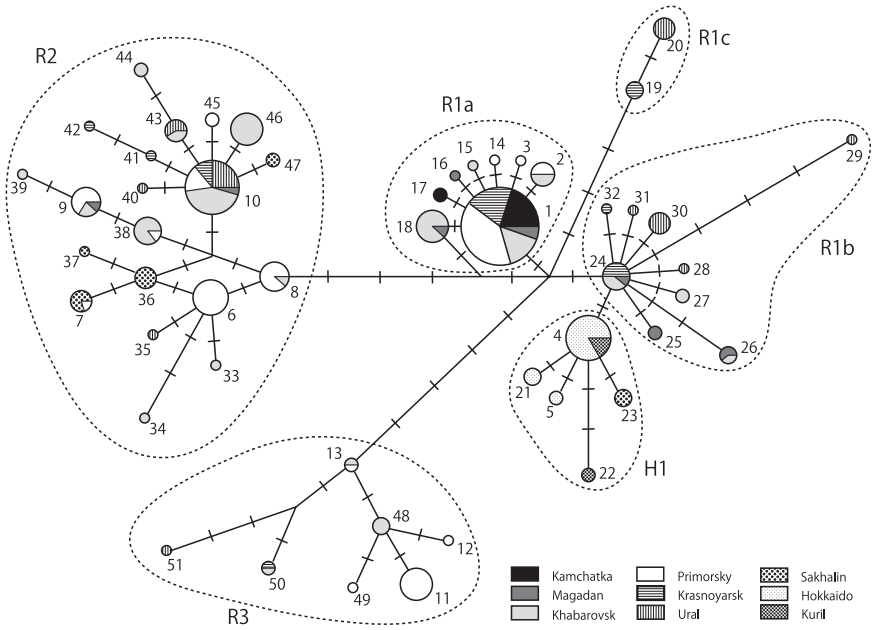

Fig. 4.—A median-joining network reconstructed from the 976 bp nucleotide sequences of the mitochondrial *Nd2* gene for 279 sable individuals. Numbers next to nodes correspond to haplotype numbers in Fig. 2. Node sizes are proportional to haplotype frequencies. Each node indicates the proportion of sampling localities showing the haplotypes. Slashes on branches between nodes indicate mutations. Lineage names are indicated as in Fig. 2.

from the Ural Mountains, Primorsky, and Khabarovsk showed relatively higher genetic diversity, considering both haplotype and nucleotide diversities (h = 0.85, 0.85, and 0.91 and π = 0.0065, 0.0053, and 0.0052, respectively; Table 2). On the other hand, the genetic diversities of the Krasnoyarsk, Magadan, and Sakhalin populations were somewhat lower (h = 0.76, 0.92, and 0.81, respectively, and π = 0.0043, 0.0044, and 0.0043, respectively), whereas values for the Kamchatka, Hokkaido, and Kuril populations were much lower (h = 0.25, 0.39, and 0.60, respectively, and π = 0.0003, 0.0004, and 0.0012, respectively). However, some caution should be used when interpreting the genetic diversity for the Magadan population, which may have been affected by artificial translocations of sables from other regions (Petrovskaya 2007). Powell et al. (2012) summarized that the reintroduction of the 361 sables from the Khabarovsk to Magadan in 1958 was successful. The highest haplotype diversity of the Magadan population (h = 0.92) may reflect such reintroductions. Taking this concern into account, the Ural population in western Russia and the Primorsky and Khabarovsk populations in the Russian Far East clearly possessed higher genetic variation.

Genetic differentiation among local populations of sable.—The SAMOVA analysis revealed genetically distinct groups of sable populations based on intensity of gene flow (Table 3). F_{CT} values were especially high at K = 2 and 3, and slightly decreased as the number of groups increased. When K = 2, two insular populations on Hokkaido and the southern Kuril Islands were together separated from the other populations, and the genetic difference among groups was the highest of all groupings, explaining 33.37% of the total genetic variation. In the analysis of K = 3, the Hokkaido and southern Kuril populations were separated from one another. Increasing the K from 4 to 5 detected new separations for Kamchatka and Sakhalin. Mainland populations of Magadan, Khabarovsk, Primorsky, Krasnoyarsk, and Ural Mountains were grouped as 1 population until K was increased to 6. Populations from Hokkaido

Table 2.—Statistics of sable populations with respect to haplotype compositions. The number "1" represents sample number (number in parentheses are percent frequencies in each population), "2" represents haplotype diversity, "3" nucleotide diversity (π), and "4" haplotype number.

	H1			R1a			R1b			R1c			R1a-c			R2			R3			Total		
Population	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	4
Kamchatka	0			15 (100)	0.25	0.0003	0			0			15 (100)	0.25	0.0003	0			0			15	0.25	0.0003	2
Magadan	0			5 (45.5)	0.70	0.0008	5 (45.5)	0.80	0.0018	0			10 (83.3)	0.89	0.0026	2 (16.7)	1.00	0.0031	0			12	0.92	0.0044	8
Khabarovsk	0			24 (31.2)	0.66	0.0008	6 (7.8)	0.73	0.0012	0			30 (39)	0.78	0.0017	42 (54.5)	0.80	0.0021	5 (6.5)	0.70	0.0014	77	0.91	0.0052	20
Primorsky	0			30 (37.5)	0.30	0.0003	0			0			30 (37.5)	0.30	0.0003	36 (45)	0.79	0.0021	14 (17.5)	0.29	0.0006	80	0.85	0.0053	15
Krasnoyarsk	0			12 (46.2)	0.00	0.0000	5 (19.2)	0.40	0.0004	3 (11.5)	0.00	0.0000	20 (76.9)	0.61	0.0019	5 (19.2)	0.70	0.0010	1 (3.8)	0.00	0.0000	26	0.76	0.0043	8
Ural	0			0			8 (29.6)	0.64	0.0021	5 (18.5)	0.00	0.0000	13 (48.1)	0.74	0.0041	13 (48.1)	0.60	0.0012	1 (3.7)	0.00	0.0000	27	0.85	0.0065	10
Sakhalin	3 (20)	0	0	0			0			0			0			12 (80)	0.74	0.0016	0			15	0.81	0.0043	5
Hokkaido	22 (100)	0.39	0.0004	0			0			0			0			0			0			22	0.39	0.0004	3
Kuril	5 (100)	0.60	0.0012	0			0			0			0			0			0			5	0.60	0.0012	2

and the southern Kuril Islands were typed as the same group at K = 2, 7, and 8. The NJ tree using the Φ_{ST} values among populations also revealed a trend toward a peripheral versus mainland arrangement, where eastern marginal peninsular and insular populations were also placed in a peripheral position in the NJ tree (Fig. 5).

Discussion

We conducted phylogeographic analyses using 279 individual sables from a more comprehensive distribution area than has been previously examined. Three distinct major lineages, R1 + H1, R2, and R3, were among the continental populations (but H1 was not observed in the continent), while 1 insular endemic lineage, H1, was observed on Sakhalin, Hokkaido, and the southern Kuril Islands. The existence of 3 mtDNA lineages on the Eurasian continent is also consistent with the results of previous studies that primarily focused on continental Far Eastern populations (Balmysheva and Solovenchuk 1999a, 1999b; Petrovskaya 2007; Malyarchuk et al. 2010; Sato et al. 2011; Li et al. 2013). In the present study, the large number of newly obtained individuals (n = 209) from more extensive areas of northern Eurasia enabled us to determine that the R1 + H1 lineage contains 3 separate sublineages, R1a, R1b + H1, and R1c. R1, R2, and R3 haplotypes appeared from eastern to western populations on the Eurasian continent, whereas the Kamchatka population was primarily composed of the R1a haplotypes (Figs. 3 and 4). This observation is consistent with the results of Malyarchuk et al. (2010) where the Kamchatka population is almost exclusively composed of one major dominant lineage (A1 in Malyarchuk et al. 2010). Together, our study and these previous studies, which adopted different molecular markers and methodologies, have arrived at a congruent result; however, the present study provides further refined insight into the demographic history of sable populations on the Eurasian continent and the roles of the eastern peripheral peninsula and islands on the genetic diversity of isolated sable populations. Below, we focus on these 2 points and discuss the population history of the sable. Lastly, we compare the knowledge obtained for the sable with other boreal organisms, focusing on their migration histories to eastern marginal islands during the Pleistocene.

Demographic history of the sable on the Eurasian continent.—To determine the origin and process of diversification of sable lineages on the Eurasian continent, several studies have evaluated genetic diversity and demographic indices (Rozhnov et al. 2010; Sato et al. 2011; Li et al. 2013; Rozhnov et al. 2013). Based on the mtDNA variations, they showed higher genetic diversity for the Ural or Russian Far East populations, suggesting that these regions are possible refugia in the glacial periods. The present analyses also clarified that populations in both Ural Mountains and Russian Far East have higher genetic diversity (Table 2). On the other hand, the origin of the lineage expansion was only suggested in the Russian Far East, not in the Ural region. This is because R1a is diverse in the Russian Far East and a founder effect was observed in the more western Krasnoyarsk region; the Ural population has only derived R1b haplotypes (Hap 28–31) and does not contain

Table 3.—Population grouping of sable populations by SAMOVA analysis. SAMOVA = spatial analyses of molecular variance.

Number of groups (*K*)	2	3	4	5	6	7	8
Kamchatka	I	I	I	I	I	I	I
Magadan	I	I	II	II	II	II	II
Khabarovsk	I	I	II	II	III	III	III
Primorsky	I	I	II	II	III	IV	IV
Krasnoyarsk	I	I	II	II	III	II	V
Ural	I	I	II	II	III	V	VI
Sakhalin	I	I	II	III	IV	VI	VII
Hokkaido	II	II	III	IV	V	VII	VIII
Kuril	II	III	IV	V	VI	VII	VIII
F_{SC}[a]	0.1505	0.1571	0.1275	0.1044	0.0989	−0.0200	−0.0457
F_{ST}[a]	0.4340	0.4202	0.3841	0.3534	0.3273	0.2354	0.2336
F_{CT}[a]	0.3337	0.3121	0.2941	0.2780	0.2535	0.2504	0.2671
Among group	33.37	31.21	29.41	27.80	25.35	25.04	26.71
Among populations within group	10.03	10.80	9.00	7.54	7.38	−1.50	−3.35
Within populations	56.60	57.98	61.59	64.66	67.27	76.46	76.64

[a] All fixation indices (F_{SC}, F_{ST}, and F_{CT}) were statistically significant ($P < 0.05$).

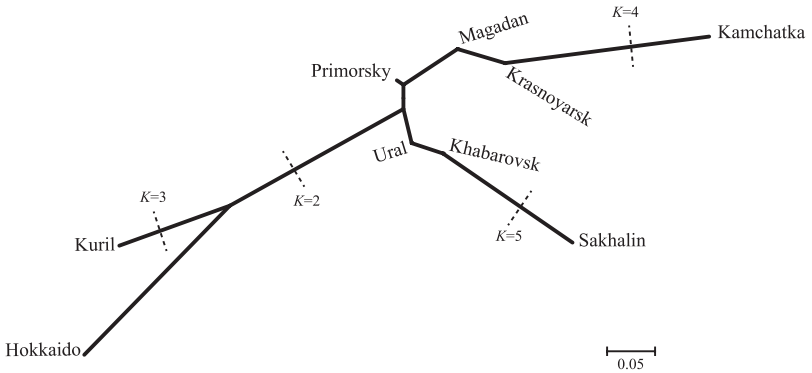

Fig. 5.—Neighbor-joining network based on the pairwise fixation index (Φ_{ST}) values among populations defined in Fig. 1. *K* represents the number of groups set a priori by the authors in the SAMOVA (spatial analyses of molecular variance) analysis, which corresponds to values in Table 3.

the central haplotype (Hap 24) which is shared by more eastern Krasnoyarsk and Russian Far East populations; and the Russian Far East population has higher genetic diversity in the R2 lineage and the Ural and Krasnoyarsk populations only have descendant haplotypes (Hap 40–42) from widely shared Hap 10. These results imply that the Russian Far East would have provided the sable population with important refugia for lineage diversifications. Furthermore, the population expansion was detected for R1a, R1b + H1, and H1 lineages, underpinning that the Russian Far East served as a source area for demographic expansions into eastern peripheral parts such as Kamchatka and Hokkaido. Note, however, that the discussions above do not refute the refugia hypothesis of the southern Ural region (Rozhnov et al. 2013). In fact, we observed higher genetic diversity in the Ural population and determined that the R1c lineage originated in this region. Further studies are needed to validate the western refugia hypothesis.

The effect of the artificial translocations of the sable.—Historically, sables, especially in continental populations, were heavily harvested, and therefore the significant range contraction was induced from 18th to early 20th centuries (Powell et al. 2012). Nearly 20,000 individuals were artificially translocated during 1901 to the 1980s (Powell et al. 2012). Therefore, there is a concern that this artificial translocation disturbs the natural genetic structure and hinders the discussion of their demographic history as described in the last section. However, it is likely that our results were not largely affected by the artificial translocation events. The present analysis revealed that 28 of 33 continental haplotypes that were "tip (terminal haplotype)" in the haplotype network were unique to each population (Fig. 4). Furthermore, most of haplotypes, which occurred in more than 3 populations, were located in the center of star-like clusters of haplotypes (Fig. 4). These phylogeographic structures suggest that genetic diversity was mainly generated by historical demographic events that have occurred gradually over time, rather than recent artificial translocations. We therefore assumed that the effects of augmentations, introductions, and/or reintroductions would be less likely in the present study.

Migration history of the sable on the eastern marginal peninsula and islands.—Our study has revealed the characteristic patterns of genetic variation in peripheral peninsular and insular populations in northeastern Eurasia. The SAMOVA analysis also documented the genetic differentiation of peripheral populations from the other mainland populations (Table 3; Fig. 5). Previous studies have also reported lower genetic variation in the Kamchatka and Hokkaido populations compared to other continental populations (Petrovskaya 2007; Inoue et al. 2010; Malyarchuk et al. 2010; Sato et al. 2011; Rozhnov et al. 2013).

The present findings revealed that the Kamchatka population was composed only of R1a haplotypes, whereas the neighboring population in Magadan harbors R1a, R1b, and R2. On the other hand, insular populations on Hokkaido and the southern Kuril Islands only contain H1, whereas the Sakhalin population harbors both H1 and R2. Populations in the neighboring Russian Far East exhibited higher genetic diversity as described above. Therefore, these results suggest that the eastern marginal peninsular and insular populations possess limited mtDNA lineages, further implying the involvement of founder effects by limited expanded lineages in the formation of the peripheral populations.

As suggested in the demographic analyses, the Kamchatka population appears to have been founded by the expansion event of the R1a sublineage from the southeastern part of the Russian Far East, while most of the insular populations are inferred to have been formed as a result of the expansion of the R1b + H1 sublineage, from which the insular H1 lineage was generated (Figs. 2 and 4). The MRCAs of R1a and R1b + H1 were dated at 0.06 mya (*CI* = 0.02–0.11) and 0.09 mya (*CI* = 0.04–0.15). The colonization of the H1 lineage on the islands presumably occurred within the interval between the MRCAs for the R1b + H1 and H1 lineages (0.04–0.09 mya) in the Late Pleistocene age; this event could have prevented the migration of the sable lineage from Hokkaido to the southern Honshu islands of the Japanese archipelago by the Tsugaru Strait (Ohshima 1990, 1991, 1992; Millien-Parra and Jaeger 1999). In summary, the limited number of lineages in the peripheral regions (Kamchatka and Hokkaido) resulted from demographic expansions that began on continental Eurasia in the Late Pleistocene period.

The most interesting finding of our study is that the R2 haplotypes also occur on Sakhalin, but not on Hokkaido or the southern Kuril islands. Previous studies have suggested that the Hokkaido population has a monophyletic origin and was established by 1 migration event from the continent via Sakhalin (Hosoda et al. 1999; Sato et al. 2011). However, the presence of the R2 lineages on Sakhalin suggests that the migration event to Sakhalin happened at least twice. More frequent colonizations may also have been possible, taking into account the 2 divergent lineages (Hap 47 versus Hap 7, 36, and 37) in the R2 lineage (Fig. 3). The Tatar (Mamiya) Strait located between the Eurasian continent and Sakhalin is narrower and shallower than La Perouse (Soya) Strait between Sakhalin and Hokkaido (Position Information Database 2010), which could have allowed sable migrations to Sakhalin even after the emergence of La Perouse (Soya) Strait. In addition, one of the R2 haplotypes (Hap 7) observed on Sakhalin was shared by 1 Primorsky individual, while the H1 haplotype (Hap 23) observed on Sakhalin diverged from the other H1 haplotypes observed on Hokkaido and the southern Kuril Islands. As a result, we hypothesize that the H1 lineage initially migrated to the eastern marginal islands, followed later by the R2 lineage. The 2nd migration by the R2 lineage was not likely to have reached Hokkaido and the southern Kuril Islands due to the establishment of the La Perouse (Soya) Strait.

Comparative phylogeography of eastern marginal insular populations.—Boreal species exhibit complicated colonization histories on the Far Eastern marginal islands. The fauna of Sakhalin, Hokkaido, and the southern Kuril Islands is similar to those on the continent of the southeastern part of the Russian Far East, as land bridges appeared during most glacial periods, allowing many organisms to migrate onto these islands (Dobson 1994; Millien-Parra and Jaeger 1999; Kawamura 2007). Previous studies have provided insights into the phylogeographic history of Hokkaido mammals, demonstrating species-specific patterns of historical migrations from the continent (e.g., Mckay 2012; Sato 2013). The present study and Sato et al. (2011) suggest that the mtDNA lineage of the sable in Hokkaido was established during the Late Pleistocene. This migration time estimate is consistent with that for the Korean field mouse (Sakka et al. 2010), but not with those for the Eurasian flying squirrel, the gray red-backed vole, and the mountain hare, whose migration times were estimated to occur during the late Middle Pleistocene (Yamada et al. 2002; Oshida et al. 2005; Abramson et al. 2012; Kinoshita et al. 2012). On the other hand, the brown bear *Ursus arctos* and the red fox *Vulpes vulpes* possess several distinctive mtDNA lineages on Hokkaido, suggesting repeated colonizations since the Middle to Late Pleistocene (Matsuhashi et al. 1999, 2001; Inoue et al. 2007; Korsten et al. 2009; Hirata et al. 2013). For Sakhalin, the signature of repeated migrations from the continent has also been suggested for the brown bear and the mountain hare, indicating that the migration to Sakhalin from the continent occurred after the establishment of the Hokkaido lineage (Kinoshita et al. 2012; Hirata et al. 2013). The gray red-backed vole, Korean field mouse, and least shrew may also have exhibited at least 2 migrations onto the island of Sakhalin (Pavlenko 1989; Iwasa et al. 2000; Serizawa et al. 2002; Sakka et al. 2010; Abramson et al. 2012; Ohdachi et al. 2012). The similar pattern of coexistence of old and recent migrants in Sakhalin was also observed for the Siberian salamander (Matsui et al. 2008; Poyarkov and Kuzmin 2008; Malyarchuk et al. 2011, 2013) and the carrion crow (Kryukov et al. 2012). The present study also revealed that the sable experienced at least 2 waves of migration from the continent, during which 2 lineages (H1 and R2) mingled on Sakhalin. Interestingly, nuclear *Mc1r* and *Tcf25* gene analyses have shown that the Hokkaido sable harbored an old endemic nuclear DNA lineage that likely colonized earlier than the modern mtDNA lineages on the island (Ishida et al. 2013). Hence, we conclude that the eastern peripheral insular populations of boreal species were constructed by multiple migration and colonization events.

We assume that not only the repeated appearances of land bridges between islands and the continent, but also the latitudinal climate cline on these peripheral islands have likely played important roles in preserving several lineages that colonized

during different ages. The modern vegetation of Hokkaido Island is classified as a "pan-mixed forest" consisting of a sub-arctic needle-leaved and temperate broad-leaved forest (Tatewaki 1958), whereas the taiga zone forest composed of larch and spruce species is considered to have advanced southward during the last glacial period (Ono 1990; Ohshima 1991; Igarashi and Zharoh 2011; Kito and Ohkuro 2012), in a manner similar to northern continental Asia (Mokhova et al. 2009; Stebich et al. 2009). On the other hand, central Sakhalin is recognized as an important vegetation boundary, known as the Schmidt line (Miyabe and Tatewaki 1937). Phylogeographic analyses using nuclear and cytoplasmic markers for larch, spruce, and fir *Abies* species have revealed that central Sakhalin is a major area of introgression between old island colonists and subsequently migrated lineages (Aizawa et al. 2007; Khatab et al. 2008; Aizawa et al. 2009; Polezhaeva et al. 2010; Semerikova et al. 2011). In the present study, the H1 lineage was observed in a relatively southern area on Sakhalin, whereas the R2 lineage occurred in the north (Fig. 1). Such an observation might reflect the environmental boundary in the central Sakhalin area. We suggest that such a transitional forest zone and its periodic shift have also significantly affected the distribution of boreal mammals on Sakhalin. To clarify the demographic history of the sable on the eastern peripheral islands of Eurasia in more detail, phylogeographic analyses with more comprehensive sampling and multiple genes are required. Such studies could illuminate the past repeated expansion histories of continental boreal species during the Pleistocene, as the signatures of past expansions on the continent might have been erased by more recent expansion events, while eastern peripheral islands would maintain such vestiges of old expansions.

Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Sample information of sables used in this study.

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