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Multiple origins of the Japanese marten *Martes melampus* introduced into Hokkaido Island, Japan, revealed by microsatellite analysis

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Abstract. The Japanese marten *Martes melampus* occurring on Hokkaido Island, Japan, is a domestic alien species, artificially introduced from their native distributional range. To reveal the genetic variation within the Hokkaido marten population and their relationships with native populations, we genotyped 14 individuals from Hokkaido using 10 microsatellite loci, and compared the genotype data with those of native populations reported previously. The Hokkaido population showed the highest number of private alleles and loci with private alleles. Relatively high levels of observed ($H_o = 0.514$) and expected ($H_e = 0.724$) heterozygosities and allelic richness ($R = 5.290$) suggested that the Hokkaido population maintains polymorphisms in microsatellites. These genetic characteristics in the Hokkaido population could have resulted from random mating in fur farms and/or multiple releases from them. Genetic distances among populations showed that the Hokkaido population is closely related to the Chubu and Kitakyushu populations. Bayesian clustering and assignment tests indicated that the Hokkaido population consists of two genetically distinct lineages. These results suggest that the founders were introduced to Hokkaido from multiple locations in the native distributional range in Japan, and that the descendants still maintain genetic polymorphisms.

Key words: Hokkaido, introduced population, Japanese marten, *Martes melampus*, microsatellite.

The Japanese marten *Martes melampus* is a carnivoran mammal endemic to the Japanese islands. It is native in forested regions on Honshu, Kyushu, and Shikoku Islands (Imaizumi 1960; Masuda 2009). Just before World War II, the Japanese marten was introduced to Hokkaido Island due to the fur industry. Founders of the Hokkaido marten population seem to have come from Honshu Island (Kadosaki 2009) and, more specifically, the Tohoku region (Inukai 1975). When feed became unavailable during the war, the animals were released from marten farms into the wild. Currently, the Japanese marten is widely distributed in southwestern Hokkaido, from the Ishikari lowlands to the Oshima Peninsula (Kadosaki 2009; Murakami and Ohtaishi 2000) (Fig. 1). On the other hand, another closely related species, the sable *Martes zibellina*, is natively distributed on Hokkaido (Murakami 2009). In the Ishikari lowlands on Hokkaido, both the sable (Hirakawa 2007; Abe et al. 2011) and the Japanese marten (Hirakawa 2007) are recently recorded.

There have been several genetic studies on the Japa-

nese marten on Hokkaido. Hosoda et al. (1999) examined partial sequences of the mitochondrial DNA (mtDNA) cytochrome *b* gene and restriction fragment length polymorphisms of nuclear ribosomal DNA genes, and reported that the Hokkaido population is genetically similar to several geographic populations in southern Honshu, although the sample size was small. Sato et al. (2009) analyzed the combined sequences of three portions of mtDNA (cytochrome *b*, control region, and NADH dehydrogenase subunit 2) and the nuclear growth hormone receptor gene, and reported that only one individual from Hokkaido was more closely related to two individuals from Okayama Prefecture (western Honshu) than to one from the Tohoku region (northern Honshu). Inoue et al. (2010) examined mtDNA control region sequences, and showed that the genetic diversity in the Hokkaido population was lower than the Honshu and Kyushu populations: three mtDNA haplotypes were found in the Hokkaido population, two of which were restricted to southern areas within habitats. These previ-

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ous studied on genetic characteristics of the Hokkaido population showed that their precise origin(s) is still unclear.

In the present study, we investigated polymorphisms of biparentally inherited microsatellites in the populations of biparentally inherited microsatellites in the populations of introduced Japanese martens in Hokkaido. We then discuss the genetic features and origin of the Hokkaido population, in light of comparable microsatellite data on populations native to Honshu, Kitayushu, and Tsushima, as well as the results of previous studies using mtDNA.

Materials and methods

Sample collection

The tissue samples were obtained from 14 Japanese martens collected in Hokkaido between 1998 and 2001 (Fig. 1). The samples included 13 of those used for mtDNA analysis by Inoue et al. (2010). The samples were stored in 70–100% ethanol at 4°C until use.

DNA extraction, PCR amplification and microsatellite scoring

Ten microsatellite loci (Natali et al. 2010) for each sample were genotyped, as described in Kamada et al. (2012). Analytical methods such as DNA extraction,

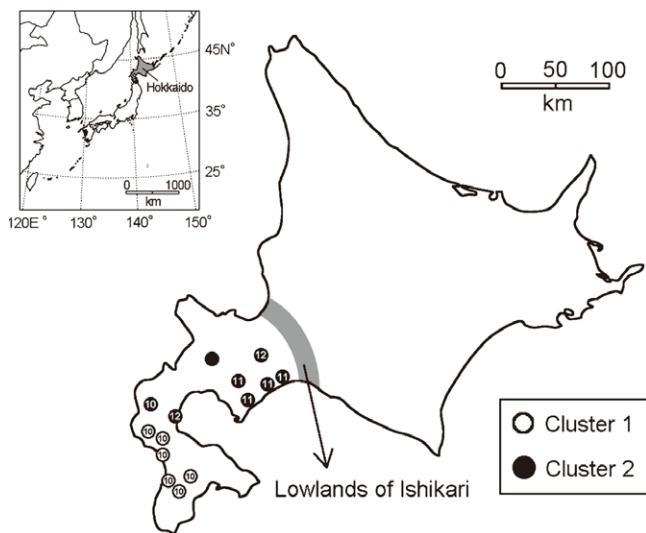


Fig. 1. The upper map including the Japanese islands shows the location of Hokkaido Island. Sampling locations (dots) and the number of specimens of the Japanese marten are shown on Hokkaido Island. Open and closed circles correspond with Clusters 1 and 2, respectively, by the STRUCTURE analysis (Fig. 4). Numbers in circles indicates mtDNA haplotypes for each individual revealed by Inoue et al. (2010). One individual in Cluster 2 has no data of mtDNA haplotype. Animals were collected from southwestern Hokkaido, which almost correspond with the distribution area of introduced Japanese martens.

PCR amplification, and microsatellite scoring were the same as described in Kamada et al. (2012).

Data analysis

Observed (H_o) and expected (H_e) heterozygosities values for the Hokkaido population and pairwise genetic differentiation coefficient (F_{st}) values among five geographic populations (Hokkaido, Chiba, Chubu region, Kitakyushu and Tsushima) were calculated using ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010). Microsatellite genotype data of above four geographic populations (except Hokkaido) were from Kamada et al. (2012). Allelic richness and a within-population inbreeding coefficient (F_{is}) values for the Hokkaido population were obtained using FSTAT 2.9.3.2 (Goudet 2001). Nei's standard genetic distances (D_s ; Nei 1978) were calculated using GENETIX 4.05.2 (Belkhir et al. 2004). The microsatellite data were analyzed in the same way as for the Tsushima and Honshu populations of the Japanese martens (Kamada et al. 2012). The results in the present study were compared with those from three of the geographic populations (Chiba, Chubu region and Kitakyushu) treated in Kamada et al. (2012). The number of private alleles for each locus was counted among five geographic populations. Using F_{st} and D_s values, neighbor-joining networks were constructed with MEGA 4 (Tamura et al. 2007).

Bayesian clustering and assignment tests were implemented in STRUCTURE 2.3 (Pritchard et al. 2000) for four geographic populations, except for the Tsushima population. The STRUCTURE analysis was run with 5 repetitions of 10,000 iterations of Markov chain Monte Carlo, following a burn-in of 10,000 iterations at $K = 1-10$. To estimate the real number of subpopulations (K), the log-likelihood ratio [$\ln P(D)$] was calculated. When individuals had q values (estimated membership in a cluster) > 0.7 , they were assumed to be members of that particular cluster.

GENETIX was used for the four geographic populations (except Tsushima) to visualize patterns of population differentiation by factorial correspondence analysis (FCA) (Benzecri 1973) of individual multilocus genotypes.

Results

Genetic diversity of the Hokkaido population

All microsatellite loci were polymorphic in the Hokkaido population, and eight private alleles among six

Table 1. Frequencies of private alleles found in each geographic population

Microsatellite loci	Number of alleles in all individuals	Numbers of private alleles in each geographic population					Total
		Hokkaido	Chiba*	Chubu*	Kitakyushu*	Tsushima*	
Mar02	11	1	0	2	0	0	3
Mar08	10	0	0	2	0	0	2
Mar15	10	2	0	0	0	0	2
Mar19	10	2	0	0	0	0	2
Mar21	3	0	0	0	0	0	0
Mar36	9	1	0	1	1	0	3
Mar43	15	0	0	0	3	0	3
Mar53	10	1	0	1	0	0	2
Mar56	6	1	0	0	0	0	1
Mar64	8	0	0	0	0	0	0
Total	92	8	0	6	4	0	18

*Data of native marten populations from Kamada et al. (2012).

Table 2. Genetic diversity in each geographic population

Geographic population	Number of samples	Average value of allelic richness	Heterozygosities		<i>Fis</i>
			<i>Ho</i>	<i>He</i>	
Hokkaido	14	5.290	0.514	0.724	0.297
Chiba*	9	2.800	0.457	0.541	0.164
Chubu*	11	5.738	0.747	0.780	0.043
Kitakyushu*	23	5.097	0.587	0.668	0.124
Tsushima*	101	1.675	0.232	0.291	0.204

*Data of native marten populations from Kamada et al. (2012).

loci were observed (Table 1). Table 2 shows average values of *Ho*, *He*, allelic richness and *Fis* for the five geographic populations compared. Among the five populations, the Hokkaido population showed an intermediate value for *Ho* (0.514) and a high value for *He* (0.724), compared with others. The highest values (*Ho*: 0.747, *He*: 0.780) occurred in the Chubu region population, and the lowest values (*Ho*: 0.232, *He*: 0.291) in the Tsushima population. Allelic richness (5.290) in the Hokkaido population was the second to that (5.738) in the Chubu population. The highest *Fis* value was obtained from the Hokkaido population (0.294), and the lowest from the Chubu population (0.043).

Relationships among the Hokkaido population and other geographic populations

Both pairwise *Fst* and *Ds* values (Table 3) were lower between the Hokkaido and Chubu populations (*Fst*: 0.063, *Ds*: 0.181), and between the Hokkaido and Kitakyushu populations (*Fst*: 0.076, *Ds*: 0.200), but highest between the Hokkaido and Chiba populations (*Fst*: 0.179, *Ds*:

Table 3. *Fst* (lower matrix) and *Ds* (upper matrix) between geographic populations

	Hokkaido	Chiba	Chubu	Kitakyushu	Tsushima
Hokkaido		0.391	0.181	0.200	0.739
Chiba	0.179		0.394	0.500	1.130
Chubu	0.063	0.188		0.145	0.555
Kitakyushu	0.076	0.215	0.060		0.710
Tsushima	0.547	0.668	0.525	0.522	

All *Fst* values were statistically significant ($P < 0.05$). Data of populations except the Hokkaido population were from Kamada et al. (2012).

0.391). Neighbor-joining networks based on pairwise *Fst* (Fig. 2a) and *Ds* (Fig. 2b) showed that the Hokkaido population was most closely related to the Chubu and Kitakyushu populations, but distantly to the Chiba population.

Population structure analyses

Bayesian clustering and assignment tests using STRUCTURE calculated the log-likelihood ratio [LnP(D)],

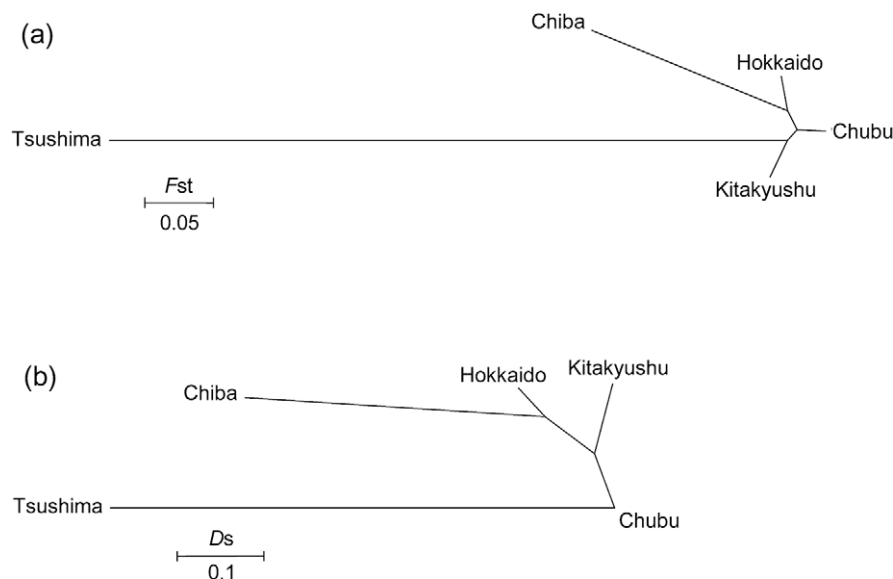


Fig. 2. Neighbor-joining networks among geographic populations, constructed using pairwise F_{st} (a) and D_s (b). The scales show the genetic distance between populations. Microsatellite data of populations except for the Hokkaido population were cited from Kamada et al. (2012).

which was largest at $K = 5$ (Fig. 3). FCA showed the Hokkaido population to be divided into the two groups (Hokkaido 1 and Hokkaido 2; Fig. 4).

For the five clusters estimated by the STRUCTURE analysis, individuals were assumed to be members of the cluster at $q > 0.7$. Table 4 shows the frequencies of individuals in each cluster. Each of Clusters 1, 3 and 5 was composed of members of a single geographic population: Cluster 1 consisted of individuals from Hokkaido; Cluster 3 consisted of those from Chiba, and Cluster 5 consisted of those from Kitakyushu. By contrast, each of Clusters 2 and 4 contained individuals from two geographic populations: Cluster 2 consisted of individuals from Hokkaido and Kitakyushu, and Cluster 4 consisted of those from Chubu region and Kitakyushu.

Discussion

Genetic diversity of the Japanese martens introduced to Hokkaido

All microsatellite loci examined in the present study were polymorphic in the Hokkaido population. Kadosaki (2009) reported that at least four fur farms (located in Sapporo and Iwanai in western Hokkaido, and Yakumo and Mori in southern Hokkaido) released Japanese martens into the wild. Random mating of individuals from different origins in the fur farms and multiple releases of animals from single or multiple farms into the wild could have maintained genetic diversity to some extent,

although precise information on the martens' introduction is not available in literature.

In addition to the present study, as other alien carnivores, the American minks (*Neovison vison*), introduced to Nagano Prefecture, central Japan, showed some genetic variation (average H_o : 0.413, average H_e : 0.482) in 11 microsatellite loci of 126 individuals (Shimatani et al. 2010), suggesting maintenance of genetic polymorphism from their founders. Similarly the masked palm civets (*Paguma larvata*) introduced to Japan had 0.274–0.548 for H_o and 0.307–0.590 for H_e in seven microsatellite loci of 266 individuals from various areas of Honshu and Shikoku, Japan, indicating multiple introductions or independent founding events (Inoue et al. 2012). Thus, in these alien carnivores including the Hokkaido population of the Japanese marten as a domestic alien species, founder effects are not so remarkable, and they still maintain microsatellite polymorphisms.

In contrast, Inoue et al. (2010) reported a low genetic diversity of mtDNA in the Hokkaido population of the Japanese marten. This inconsistency between microsatellite (relatively high) and mtDNA (low) variations suggests that the founders of the Hokkaido population originated from a few maternal lineages with some extent of microsatellite variation in the limited source area. The similar inconsistency between the two kinds of genes was found in the introduced populations of the masked palm civet in Japan (Masuda et al. 2010; Inoue et al. 2012). The lower mtDNA variation in the introduced Japanese

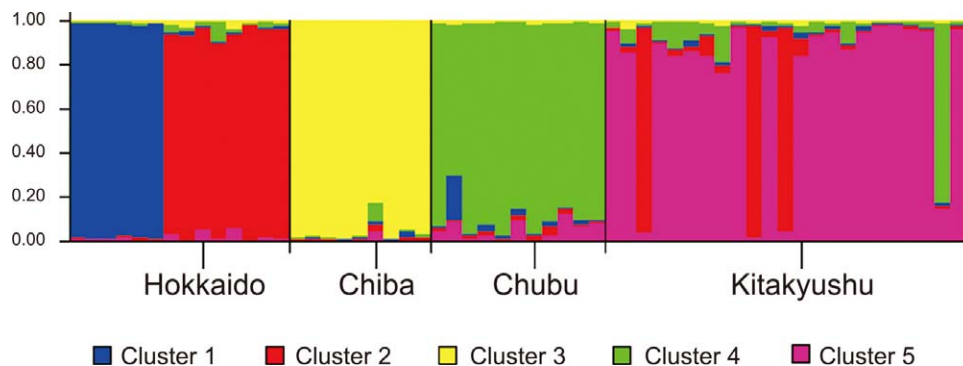


Fig. 3. The structure of the Hokkaido population and the three native populations of the Japanese marten inferred by the STRUCTURE analysis. The vertical axis shows q value, and the horizontal axis indicates the geographic populations. Each individual is represented by one vertical thin line partitioned into the K colored segments, and was arranged according to geographic populations. Log-likelihood ratios [LnP(D)] was largest at $K = 5$.

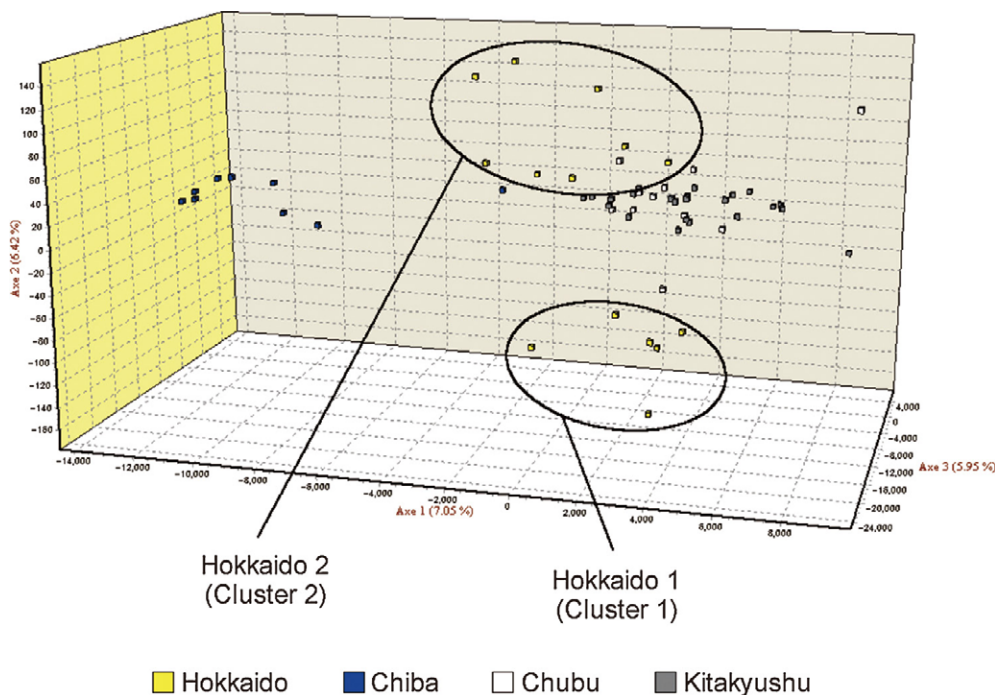


Fig. 4. Factorial Correspondence Analysis (FCA) performed for four geographic populations of the Japanese marten. A cube shows one individual, and the cube colors represent the geographic populations, to which each individual was assigned. The Hokkaido population was separated into two groups (Hokkaido 1 and Hokkaido 2). Hokkaido 1 is located apart from the group of other geographic populations (Chiba, Chubu and Kitakyushu), whereas Hokkaido 2 adjoins them.

Table 4. Frequencies of individuals, which were assigned at $q > 0.7$ to five clusters obtained by the STRUCTURE analysis

Geographic population	Clusters by STRUCTURE analysis					Number not assigned ($q < 0.7$)	Total
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5		
Hokkaido	6	8	0	0	0	0	14
Chiba*	0	0	9	0	0	0	9
Chubu*	0	0	0	10	0	1	11
Kitakyushu*	0	3	0	1	19	0	23
Total	6	11	9	11	19	1	158

*Data of native marten populations from Kamada et al. (2012).

population of the masked palm civet suggests that the founders originated from some restricted areas within Taiwan as the native habitat. Of course, such inconsistency might have partially reflected the difference of the effective population size between nuclear DNA and mtDNA. On the other hand, F_{is} (0.294) observed in the Hokkaido marten population was higher than in the Tsushima Island population (0.204) (Table 2), suggesting a possibility of more inbreeding in the Hokkaido population originating from a small founder size.

Genetic relationships between the Hokkaido population and other geographic populations

The present study revealed that the Hokkaido population to be more closely related to the Chubu- and Kitakyushu-native populations. This suggests that the founders of the Hokkaido population originated from more than one native restricted area. Our results are consistent with previous mtDNA studies (Hosoda et al. 1999; Sato et al. 2009; Inoue et al. 2010), which have similarly suggested that founders of the Hokkaido population originated from various native populations in Honshu. Inoue et al. (2010), for example, found that among three mtDNA haplotypes (MM10, MM11 and MM12) detected in Hokkaido, MM10 was closely related to haplotypes MM6–9 detected in Kyushu, and MM11 was closely related to MM4 detected in Gifu Prefecture, Chubu region. Among the five geographic populations, the largest number of private alleles and loci with private alleles occurred in the Hokkaido population (Table 1), again indicating that the Hokkaido population originated from several native populations, probably including populations we did not examine.

Genetic structure of the Hokkaido population

In the present study, the STRUCTURE analysis revealed the Hokkaido population to comprise two genetic clusters (Fig. 3 and Table 4): one consisting of six individuals from Hokkaido (Cluster 1), and the other consisting of eight individuals from Hokkaido and three from Kitakyushu (Cluster 2). In addition, FCA showed the separation of the Hokkaido population into two groups (Hokkaido 1 and Hokkaido 2: Fig. 4). Hokkaido 1 was well separated from groups containing individuals of other geographic populations (Chiba, Chubu and Kitakyushu), whereas Hokkaido 2 adjoined them. Low values of F_{st} (0.060) and D_s (0.145) suggest that the Kitakyushu population is closely related to the Chubu population (Table 3). These results indicate that the

Hokkaido population is separated into two lineages, one of which is genetically similar to lineages on Honshu and Kyushu.

In a comparison of our results with mtDNA data of Inoue et al. (2010), the six individuals in Cluster 1 (Hokkaido 1) shared one haplotype (MM10), and the eight individuals in Cluster 2 (Hokkaido 2) shared three haplotypes (MM10, MM11 and MM12). Haplotype MM10 was closely related to MM6–9 from Kyushu, and MM11 was closely related to MM4 from Gifu Prefecture, Chubu region. In addition, MM12 was identical to one haplotype from Okayama Prefecture reported by Sato et al. (2009). The maximum-likelihood tree of Sato et al. (2009) also showed one individual from Hokkaido to be most closely related to individuals from Okayama Prefecture. Our results are thus congruent with previous mtDNA studies reporting that Cluster 2 (Hokkaido 2) are genetically similar to populations on Honshu and Kyushu. Although Cluster 1 (Hokkaido 1) identified by microsatellite data comprised only individuals from Hokkaido, their mtDNA haplotypes are closely related to those in the Kyushu population (Inoue et al. 2010). This again supports the conclusion that the founder populations in Hokkaido originated from various native populations, probably including those on Honshu and Kyushu.

As shown in Fig. 1, even within southwestern Hokkaido, the two genetic lineages of alien populations are likely distributed almost allopatrically. It suggests that the alien populations have been expanding from locations of different fur farms (as described by Kadosaki 2009) to the surrounding areas. Only one individual with mtDNA haplotype MM10 as well as Cluster 2 of microsatellites was found near the boundary between the distribution of Cluster 1 and that of Cluster 2 (Fig. 1). This indicates evidence of the alien population's expansion and hybridization between the two genetic lineages within southwestern Hokkaido.

Powell et al. (2012) showed examples of successful introductions and reintroductions of *Martes* species. Their model shows that more founders lead to higher success rates of establishment of feral populations after the introductions. The case of the Japanese marten introduction into Hokkaido seems to support their model hypothesis. Hence, if the Japanese martens cross the Ishikari lowlands, they might make feral populations in eastern Hokkaido. Intensive efforts to eliminate introduced individuals of Japanese martens are necessary to conserve the sable in eastern Hokkaido. Future analysis on temporal changes of their population genetics will

provide more insights to understanding of the migration history and maintenance of the feral populations, and contribute to management of this domestic alien species.

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References

- Abe, G., Hirakawa, H., Masuda, R., Sashika, M., Nakai, M. and Shimada, K. 2011. New records of sables in Nopporo Natural Forest Park, Hokkaido, Japan. *Honyurui Kagaku [Mammalian Science]* 51: 321–325 (in Japanese with English abstract).
- Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. and Bonhomme, F. 2004. GENETIX 4.05, logiciel sous Windows pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5171, Université de Montpellier II, Montpellier, France.
- Benzecri, J. P. 1973. L'analyse des données: T.2, L'analyse des correspondances. Dunoud, Paris.
- Excoffier, L. and Lischer, H. E. L. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10: 564–567.
- Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from <http://www.unil.ch/izea/software/fstat.html>. Updated from Goudet (1995).
- Hirakawa, H. 2007. A record of the Japanese sable, *Martes zibellina* at Hitujigaoka, Sapporo in 1997 and an important meaning of this record. *Hoppingo* 59: 101–104 (in Japanese).
- Hosoda, T., Suzuki, H., Iwasa, M. A., Hayashida, M., Watanabe, S., Tatara, M. and Tsushiya, K. 1999. Genetic relationships within and between the Japanese marten *Martes melampus* and the sable *M. zibellina*, based on variation of mitochondrial DNA and nuclear ribosomal DNA. *Mammal Study* 24: 25–33.
- Imaizumi, Y. 1960. Coloured Illustrations of Mammals of Japan. Hoikusha, Osaka, 196 pp. (in Japanese).
- Inoue, T., Kaneko, Y., Yamazaki, K., Anezaki, T., Yachimori, S., Ochiai, K., Lin, L. K., Pei, K. J. C., Chen, Y. J., Chang, S. W. and Masuda, R. 2012. Genetic population structure of the masked palm civet *Paguma larvata*, (Carnivora: Viverridae) in Japan, revealed from analysis of newly identified compound microsatellites. *Conservation Genetics* 13: 1095–1107.
- Inoue, T., Murakami, T., Alexei, V. and Masuda, R. 2010. Mitochondrial DNA control region variations in the sable *Martes zibellina* of Hokkaido Island and the Eurasian Continent, compared with the Japanese marten *M. melampus*. *Mammal Study* 35: 145–155.
- Inukai, T. 1975. Animals in the Northernmost Japan. Hokuensha, Sapporo, 152 pp. (in Japanese).
- Kadosaki, M. 2009. Illustrated Wildlife Traces. Hokkaido Publication Project Center, Sapporo, 379 pp. (in Japanese).
- Kamada, S., Moteki, S., Baba, M., Ochiai, K. and Masuda, R. 2012. Genetic distinctness and variation in the Tsushima Islands population of the Japanese marten, *Martes melampus* (Carnivora: Mustelidae), revealed by microsatellite analysis. *Zoological Science* 29: 827–833.
- Masuda, R. 2009. *Martes melampus* (Wagner, 1840). In (S. D. Ohdachi, Y. Ishibashi, M. A. Iwasa and T. Saitoh, eds.) *The Wild Mammals of Japan*, pp. 250–251. Shoukadoh Book Sellers, Kyoto.
- Masuda, R., Lin, L. K., Pei, K. J. C., Chen, Y. J., Chang, S. W., Kaneko, Y., Yamazaki, K., Anezaki, T., Yachimori, S. and Oshida, T. 2010. Origins and founder effects on the Japanese masked palm civet *Paguma larvata* (Viverridae, Carnivora), revealed from a comparison with its molecular phylogeography in Taiwan. *Zoological Science* 27: 499–505.
- Murakami, T. 2009. *Martes melampus* (Linnaeus, 1758). In (S. D. Ohdachi, Y. Ishibashi, M. A. Iwasa and T. Saitoh, eds.) *The Wild Mammals of Japan*, pp. 252–253. Shoukadoh Book Sellers, Kyoto.
- Murakami, T. and Ohtaishi, N. 2000. Current distribution of the endemic sable and introduced Japanese marten in Hokkaido. *Mammal Study* 25: 149–152.
- Natali, C., Banchi, E., Ciofi, C., Manzo, E., Bartolommei, P. and Cozzolino, R. 2010. Characterization of 13 polymorphic microsatellite loci in the European pine marten *Martes martes*. *Conservation Genetics Resources* 2: 397–399.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance for small number of individuals. *Genetics* 89: 583–590.
- Powell, R. A., Lewis, J. C., Slugh, B. G., Brainerd, S. M., Jordan, N. R., Abramov, A. V., Monakhov, V., Zollner, P. A. and Murakami, T. 2012. Evaluating translocations of martens, sables, and fishers. In (K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx and S. W. Buskirk, eds.) *Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis*, pp. 93–137. Cornell University Press, New York.
- Pritchard, J. K., Stephens, M. and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945–959.
- Sato, J. J., Yasuda, S. P. and Hosoda, T. 2009. Genetic diversity of the Japanese marten (*Martes melampus*) and its implications for the conservation unit. *Zoological Science* 26: 457–466.
- Shimatani, Y., Fukue, Y., Kishimoto, R. and Masuda, R. 2010. Genetic variation and population structure of the feral American mink (*Neovison vison*) in Nagano, Japan, revealed by microsatellite analysis. *Mammal Study* 35: 1–7.
- Tamura, K., Dudley, J., Nei, M. and Kumar, S. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0. *Molecular Biology and Evolution* 24: 1596–1599.

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