Biogeography of carnivore species occurring extensively in the Northern Hemisphere based on ecomorphological and phylogeographic patterns

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CONTENTS

GENERAL INTRODUCTION

1. Biogeographic studies explain evolutionary history of mammals

Biogeographic study concerned with the investigation of varied environmental determinants that related to the aspects of historical and contemporary distribution of species (Cox & Moore, 2010). Each species has its vestiges of historical adaptation (Wainwright & Reilly, 1994). The historical and contemporary aspects are inseparable, since the various aspects of phylogenetic, morphological and ecological relationships are connected each other, indicative of adaptation traits (Wainwright & Reilly, 1994). Biogeographic studies have been separated heretofore into historical and biological disciplines (Posadas *et al.*, 2006), but most practitioners now realize that both perspectives are necessary to explain geographic patterns (Ricklefs & Schluter, 1993; Wiens & Donoghue, 2004). As a sub-discipline of biogeography, phylogeography play a role of broader temporal context traditional ecogeographic perspectives that emphasize the role of contemporary ecological pressures in forming the spatial distributions of organismal traits (Avise, 2000). Recently, biogeographic studies on mammals are increasing with development of molecular phylogenetic and molecular phylogeographic techniques (e.g., Olalla‑Tárraga *et al.*, 2015; Rodrigues *et al.*, 2015). Since mammals are adapted to variable environments, showing worldwide distribution (e.g., Feldhamer *et al.*, 2007), it could be a model group suitable for exploration of biogeographic pattern.

2. Ecomorphological studies explain evolutionary adaptation of mammals

Morphological characteristics reflect geographic differences of organisms and their adaptations to varying environmental conditions (Freeman, 1981; Avise, 2000). Morphological variation over different geographics often exhibits predictable patterns caused by environmental adaptation (Mayr, 1956). Body size difference is often linked to specific factors, such as climate (James, 1970), food availability (Kolb, 1978; Huston & Wolverton, 2001) and geographic range (Gaston & Lawton, 1988). Skull length has been used as an index to demonstrate ecogeographic variation in body size of homeotherms, as the two measures usually correlate to each other (Ralls & Harvey, 1985). Cline, gradual change across the distributional range along some geographic axis, is occasionally observed from the intraspecific variation (Feldhamer *et al*., 2007). Skull morphological characteristics have multiple functions that might be difficult to interpret organismal performance by an aspect (Slater & Van Valkenburgh, 2009).

Allometry is a change in proportions with increasing or decreasing body size either through ontogeny or phylogeny (Gould, 1966; Wayne, 1986; Feldhamer *et al*., 2007). Morphogeographic patterns show how allometric variation impact variables that may be important for organismal performance, such as those related to feeding and acquiring prey (e.g., Emerson, Greene & Charnov, 1994).

Ecogeographic rule, geographic phenomena that explained by specific ecological determinants, are often observed in mammals (Feldhamer *et al*., 2007). Homeothermic vertebrates tend toward larger body sizes in high-latitude regions with low temperature and humidity and this phenomenon is called Bergmann's rule (Bergmann, 1847; Mayr, 1956; Avise, 2000). Geographic isolation makes morphological features affected by the unique environmental conditions of limited area and biota resources and that is often observed from the insular populations of mammals (Cox & Moore, 2010). Body size evolution in island populations is frequently described as the island rule (Foster's rule), where small species become larger and large species become smaller than mainland populations (Foster, 1964; Van Valen, 1973; Lomolino, 2005). These ecogeographic rules may explain evolutionary adaptation of mammalian species.

3. Carnivores as model organism for testing and exploring questions in biogeography and ecomorphology

Terrestrial carnivore species occurring in wide geographic ranges has remarkable geographic variation in body size. Due to their high mobility and generalist habits, these terrestrial carnivores are the most challenging groups to resolve biogeographic patterns (Gittleman, 1989). Their high adaptability to various environmental conditions influenced on polymorphic characteristics and variety of phylogeographic outcomes (Avise, 2000). Unlike other terrestrial mammal species, probably evolutionary patterns of some carnivore species extensively distributed in the Northern Hemisphere were not primarily affected by the climatic oscillation during glaciations (Vilà *et al.*, 1999; Davison *et al.*, 2011; Rueness *et al.*, 2014).

Grey wolves (*Canis lupus*) used to have broad distribution throughout the Northern Hemisphere (Stroganov, 1962; Mech, 1974; Boitani, 2003), although present occurrences of large and contiguous populations are restricted in northern region of North America, Europe (except for the western part of Europe), and Asia (Wayne, Lehman & Allard, 1992; Mech & Boitani, 2004). Regional scaled studies on the phylogeographic analyses of grey wolves have been conducted to demonstrate genetic relationship with the adjacent populations such as Sweden and Canada (Ellegren, Savolainen & Rosén *et al*., 1996), India (Aggarwal *et al*., 2007), British Columbia of Canada (Muñoz-Fuentes *et al*., 2009), and southern and eastern Europe (Pilot *et al*., 2014). However, there were limitations to demonstrate the evolutionary history of grey wolves in the Northern Hemisphere due to the insufficient of extensive data that cover all distributions. Muñoz-Fuentes *et al*. (2009) reported that the genetic difference could occur in the grey wolf populations that have unique ecosystem: differences of habitat, prey composition, and behavior. This species originated from Palearctic region, and colonized Japanese Islands and North America after the migration during the glacial period (Kutschera *et al*., 2013). Many studies have been debating on the phylogeographic relationships and species status of grey wolves, due to the gene flow, inbreeding, and hybridization in inter- or intra-specific relationships (Sharma *et al*., 2004; Koblmüller *et al*., 2009; vonHoldt *et al*., 2011; Rutledge *et al*., 2012; Pilot *et al*., 2014). The unclear phylogeographic structure and population admixture in grey wolves are explained by its rapid expansion during interglacials (Roy *et al*., 1994; Vilà *et al*., 1999).

Brown bears (*Ursus arctos*), which have wide distribution across the Northern Hemisphere, also have similar biogeographic history to that of grey wolves during glacial period (Davison *et al*., 2011). In European populations of brown bears, phylogeographic (northern and southern Europe: Taberlet & Bouvet, 1994) and skull morphological studies (southern Europe: Loy *et al*., 2008) demonstrated historical evolutionary relationships in restricted region. Over all Holarctic populations were also studied to estimate their demographic history (Miller, Waits & Joyce, 2006; Davison *et al*., 2011), although the limitation of information in Middle East and South Asia was suggested as one of main reasons for the incomplete understanding of brown bear. Previous studies suggested that probably the monophyletic structure of brown bears responses to the less influence on climatic oscillations during ice ages (Valdiosera *et al*., 2007; Calvignac, Hughes & Hänni, 2009; Davison *et al*., 2011). It is difficult to explain their complex demographic histories only by current phylogenetic relationships (Valdiosera *et al*., 2007; Hirata *et al*., 2013).

Mustelidae species have also problematic historical biogeographical patterns. This group also extensively distribute in the Northern Hemisphere. Studies focused on the inter-specific relationships are increasing. However, phylogenetic relationships among the sister taxa within the family Mustelidae (Sato *et al*., 2003) and superfamily Musteloidea (Sato *et al*., 2012) are still under debate. Genetic variations of *Mustela* populations from the Eurasian and North American Continents and a few islands (Taiwan and Japanese Islands) indicate the influence of allopatric speciation and secondary gene flow (Hosoda *et al*., 2000).

Ecogeographic perspectives on the morphological variation could show more simplified and macroscopic view of recent biogeographic patterns in widely distributed carnivore species. Interpretations of multiple influences in various aspects play an important role to evaluate their evolutionary and biogeographic history. Skull morphological variation according to the geographic gradient observed in grey wolves of North America which might be influenced by Bergmann's rule and prey availability (O'keefe *et al*., 2013). Based on the morphological study, omnivorous forms of brown bears were explained by relatively independent of climatic fluctuations in the Pleistocene (Sacco & Van Valkenburgh, 2004). Brown bears also have a various food habit depending on geographic variation (Pasitschniak-Arts, 1993; Barnes *et al*., 2002). Skull morphological variation of brown bears is not only related to their diet and feeding behavior but also has affinities with the phylogenetic relationships (Figueirido *et al*., 2008). Currently, ecomorphological aspects clarified notable body size variation of weasel (*Mustela nivalis*) in terms of the different climatic and landscape conditions that explained by frequent separation of taxa and presence of suitable prey (Abramov & Baryshnikov, 2000). Sato (2013) explained the relationships among seven terrestrial mustelid species in Japanese Islands on the basis of the comparison between phylogeographic relationships and feeding ecological effects.

Of 44 carnivore species, 50% of them show body size variation with geographic gradient (Meiri, Dayan & Simberloff, 2004a and 2004b). This morphological difference varies with distribution pattern within each species (Rosenzweig, 1968; Davis, 1977; Oishi *et al*., 2010). In Asia, Bergmann's rule has been observed in Malayan sun bears

(*Ursus malayanus*: Meijaard, 2004) and tigers (*Panthera tigris*: Mazák, 2010). The island effect has been also observed in carnivore species. Ancient bones of the Cozumel Island fox (*Urocyon* sp.) of Mexico show diminutive body size, compared to those from the mainland (Gompper, Petrites & Lyman, 2006). Island dwarfism has been reported in the small-sized carnivores such as least weasel (Dayan & Simberloff, 1998) and small Indian mongoose (Simberloff *et al*., 2000). Fossil records of Trinil dog (*Mececyon trinilensis*) from Java Island, Indonesia and Sardinian dog (*Cynotherium sardous*) from Sardinia Island, Italy and Corsica Island, France showed insular dwarfism, because of the constraints of food availability in certain ecological conditions (Lyras, van der Geer & Rook, 2010). López-Martín, Ruiz-Olmo & Padró (2006) revealed that pine martens (*Martes martes minoricensis*) of Minolca Island, Spain have larger skulls due to their gigantism imposed by island rule. Certain dental morphotypes of red foxes (*Vulpes vulpes harrimani*) in Kodiak Island, USA are influenced by long isolation from Nearctic populations (Szuma, 2007). Recent examinations, however, debate effects of island rule on carnivore species (Meiri *et al*., 2004a, 2004b, and 2006; Lomolino, 2005; Raia & Meiri, 2011). Meiri, Cooper & Purvis (2008) found that patterns in body size of insular carnivores did not simply explain the island rule, suggesting the complicated effects of biotic and abiotic factors.

What is the most suitable carnivore species to resolve biogeographic and ecomorphological questions? Based on the fundamental dietary types, carnivore species are categorized as three groups: hypercarnivore (diet > 70% vertebrates) such as grey wolf (*Canis lupus*) and spotted hyenas (*Crocuta crocuta*), mesocarnivore (diet is 50–

70% meat, with the balance made up of nonvertebrate foods) such as gray fox (*Urocyon cinereoargenteus*) and Asian palm civets (*Paradoxurus hermaphroditus*), and hypocarnivore (diet > 70% nonvertebrate foods) such as raccoon (*Procyon lotor*) and binturong (*Arctictis binturong*) (Van Valkenburgh, 1988; Van Valkenburgh, 2007). In carnivores, species that have more omnivorous tendency could be more suitable than hypercarnivorous species such as wolves and weasels, due to their higher adaptability to food availability. Brown bear is typical hypocarnivorous species, however, this species has greater locomotive ability and unique hibernation behavior, which may influence on the biogeographic and ecomorphological consequences. Highly polymorphic characteristics on various geographic areas reflect high adaptability in different habitats. Raccoon dog (*Nyctereutes procyonoides*) and red fox (*Vulpes vulpes*) are carnivore species that have opportunistic feeding habits depending on food availability in various geographic areas, which possessed remarkable ability of adaptation. Strong adaptability of these species might be related to their moderate locomotive ability in wide distribution range. Therefore, raccoon dogs and red foxes could be the most ideal model to demonstrate pattern of historical biogeography and ecomorphology influenced by various environmental factors of carnivore species. Raccoon dog is hypocarnivorous species that longitudinally distributed in East Asia. Although raccoon dogs go into a dormant in area with harsh winter, they switch from dormant to active in less cold days of winter (Heptner *et al.*, 1998; Kauhala & Saeki, 2004). Red fox also has omnivorous food habits with mesocarnivorous tendency. Highly polymorphic characteristics of red fox have been reported in their original distribution area, which latitudinally expanded in the Northern Hemisphere.

Ecomorphological study on intraspecific level is challenging work because it is questionable field that rarely studied so far. To estimate biogeographic and ecomorphological patterns of omnivorous species influenced by various environmental factors, I selected raccoon dog and red fox that cover the Northern Hemisphere both longitudinally and latitudinally. To understand the natural history of raccoon dog and red fox at the microevolutionary and macroevolutionary levels, I focused on environmental factors to determine the skull morphological pattern of both species. In order to resolve the factors, I demonstrate relationship between craniometric data and environmental determinants, and then comprehensive discussion was conducted on the evolutionary and biogeographic implications of raccoon dogs and red foxes.

CHAPTER I.

Evolutionary and biogeographical implications on skull morphology of raccoon dogs in East Asia

I-1. Introduction

The raccoon dog, *Nyctereutes procyonoides* (Gray, 1834) is one of most primitive species in the family Canidae (Wayne, Nash & O'Brien, 1986; Bardeleben, Moore & Wayne, 2005). Some studies observed primitive characteristics in this species with external morphological characteristics such as the elongated trunk and rather short limbs (Ellerman and Morrison-scott, 1951; Ward and Wurster-Hill, 1990; Heptner *et al*., 1998). Its highly conserved characteristics could be an important evidence of tracing evolutionary history. Raccoon dog is endemic to East Asia. It is originally distributed from the southern parts of the Russian Far East to China, Korea (South Korea), northern Vietnam, and Japan (Fig. 1). Also, this species is rapidly expanding its range after the introduction to the European country for fur trade and a game animal from 1929 to 1955 (Pitra, Schwarz & Fickel, 2010). Raccoon dogs have a very wide trophic niche breadth and the ability to exploit food resources according to their availability in the various environments (Ward & Wurster-Hill, 1990; Nowak, 2005). Rapid expansion of introduced raccoon dogs in northern and eastern Europe, from Finland to France and Bulgaria (Kauhala & Saeki, 2004) would be typical case to proof high adaptive flexibility. Despite of its opportunistic feeding behaviors and occurrence in various habitats (Kauhala, Helle & Taskinen, 1993; Heptner *et al*., 1998; Nowak, 2005; Choi & Park, 2006a; Saeki, Johnson & Macdonald, 2007), interestingly, original distribution of raccoon dogs is restricted in East Asia.

Currently, wild raccoon dog (IUCN LC 2004) is rarely observed in China (Huang C., personal communication) and Vietnam (Nguyen S. T., personal communication). Current status of Korean raccoon dogs is also not clear, although previous research assumed that the occurrence of raccoon dogs are reducing in their range despite of its illegal hunting and habitat destruction (Won & Smith, 1999). Since they have relatively low genetic diversity (Kim *et al*., 2013) and highly susceptible to various infectious diseases (sylvatic rabies, canine distemper, and sarcoptic mange), demography of raccoon dogs is in regulation (Shibata & Kawamichi, 1999; Kim *et al*., 2006; Eo *et al*., 2008; Han, Kang & Na, 2010; Bengis, Kock & Fischer, 2002). In addition, high mortality in vehicle collisions of Korean and Japanese raccoon dogs was one of the main threats (Saeki & Macdonald, 2004; Choi & Park, 2006b). Therefore, investigation of current status and suggestion of conservation strategies of this species is necessary.

Within the original distribution area, raccoon dogs are currently classified into six subspecies based on morphology and geographic distribution. *Nyctereutes procyonoides ussuriensis* in southeastern Russia and northeastern China has large skull measurements. *Nyctereutes procyonoides koreensis* in Korea has dark cheeks. In addition, this subspecies has brighter ear colors and is larger than *N. p. procyonoides* and *N. p. viverrinus* in body size. Raccoon dogs in southeastern China and northern Vietnam are recognized as *Nyctereutes procyonoides procyonoides*. *Nyctereutes procyonoides orestes* (Thomas, 1923) in southwestern China has smaller skull measurements, compared with *N. p. procyonoides* (Gray, 1834), excepting molar width. *Nyctereutes procyonoides viverrinus* (Temminck, 1838) in Honshu, Shikoku, and Kyushu Islands of

Japan have smaller skull measurements than *N. p. ussuriensis* (Matschie, 1908) and *N. p. koreensis* (Mori, 1922). *Nyctereutes procyonoides albus* is in Hokkaido Island of Japan (Beard, 1904; Hornaday, 1904) (Allen, 1938; Ellerman & Morrison-Scott, 1951). Although skull characters are basic features for distinguishing subspecies, intra-specific taxonomic status and geographic differences are not clearly designated, because of lack of specimens and ecological information of the raccoon dogs especially in China, Korea, and Vietnam.

Morphogeographic patterns are observed in the skull of raccoon dogs of East Asia that could be explained by adaptational responses to different environmental conditions such as cold adaptation and island isolation (Kim *et al*., 2015). This skull morphological variation between populations of continent and island shows analogous patterns to phylogeographic relationships (Kim *et al*., 2013). Previous genealogical studies show that the Japanese populations were derived from a common mainland ancestor, with two subspecies having recently separated from each other (Pitra *et al*., 2010; Kim *et al*., 2013). Kim *et al*. (2013) demonstrate relatively high genetic differences between mainland and Japanese island populations and suggest that they might be the result of restricted gene flow to Japan after geographic isolation. Evidences of chromosomal difference of Japanese raccoon dogs (Ward *et al*., 1987; Wada & Imai, 1991; Wada *et al*., 1991) also support biological and physical isolation after migration. The reduced chromosome number in Japanese raccoon dogs resulted from the Robertsonian translocations that occasionally occur during speciation (Ward *et al*., 1987; Wada & Imai, 1991; Nie *et al*., 2003).

The geographic distribution of raccoon dogs along a longitudinal gradient makes them suitable for study of geographic distribution on craniometric variation. Bergmann's rule is observed in some raccoon dog populations. Haba *et al.* (2008) reported that two subspecies (*N. p. viverrinus* and *N. p. albus*) of Japan have significant craniometric differences according to geographic gradient and isolation by Blakistone's line. Skull sizes of raccoon dogs introduced into Finland are larger than those of Japanese raccoon dogs; it is explained by adaptation to a colder climate and a more carnivorous diet (Kauhala *et al.*, 1998). In Kim *et al.* (2015), craniodental variation among endemic populations demonstrates validity of Bergmann's rule.

The taxonomic status of raccoon dogs is still debated, although six raccoon dog subspecies are designated by geographic distribution. Some external morphological distinctions such as fur color have been compared between Japanese and mainland populations (Korhonen, Mononen & Harri, 1991; Won *et al.*, 2004). Non-metric skeletal characters with high heritability were analyzed for epigenetic variability among raccoon dog populations from several European countries and the Amursk region in Russia (Ansorge *et al.*, 2009). Kauhala *et al.* (1998) found that skull morphological adaptations of Japanese raccoon dogs were different, compared to those in the introduced Finnish population. Chromosomal variation between the raccoon dogs from the continent ($2n = 54 + Bs$) and Japan ($2n = 38 + Bs$) reflects enough evolution during geographic isolation of the Japanese Islands to classify Japanese raccoon dogs as a different species (Wada, Lim & Wurster-Hill, 1991; Nie *et al.*, 2003). Recently, Kim *et al.* (2013) reported the Japanese populations are distantly related to mainland populations based on molecular evidences. Skull morphological implications for interspecific taxonomic status between Japanese Islands and mainland populations were reported and suggested to designate as two different species, *Nyctereutes procyonoides* and *Nyctereutes viverrinus* (Kim *et al*., 2015). In the raccoon dogs, possibility of ecomorphological perspectives of native populations has been reported due to its unique distribution. Diversity in raccoon dogs in East Asia could be explained by specific morphological variations resulting from adaptation to the various environments in their distribution. Their adaptability is identified by the various conditions of habitats along the longitudinal gradient occurring from boreal forest to tropical rain forest (Heptner *et al*., 1998; Kauhala & Saeki, 2004). In the present study, I conducted integrative approach combining molecular, morphological, and ecological data for better understanding of the mechanisms forming species differentiation and the biogeographic pattern (Wainwright & Reilly, 1994; Ledevin & Millen, 2013). To demonstrate what environmental factor determines the morphogeographic pattern of raccoon dogs in East Asia, I tested the following four hypotheses:

1. Craniometric variation might be influenced by phylogenetic patterns, because both previous morphological (Kim *et al*., 2015) and molecular (Nie *et al*., 2003; Kim *et al*., 2013) studies found two significantly different groups, Japanese populations and other mainland populations.

2. Diversity pattern might be influenced by clinal variation due to the geographic gradients such as longitudinal, latitudinal and altitudinal trends with isometric difference. In the raccoon dogs, allometric analysis across their large distributions has

received little attention in the previous craniometric studies. Here, we tested the geographic patterns of skull morphological variation that have multiple functions (Slater & Van Valkenburgh, 2009).

3. Skull morphological variation of raccoon dogs might have specific geographic patterns influenced by specific ecological factors. Raccoon dogs from colder and dryer regions might have larger skull, showing Bergmann's rule. Previous morphological analyses (Kauhala *et al.*, 1998; Haba *et al.*, 2008; Kim *et al.*, 2015) suggested validity of Bergmann's rule among the raccoon dog populations with an indirect comparison by morphogeography. To test this hypothesis, we demonstrated directly correlation between climatic factors such as temperature and precipitation.

4. Influence of environmental factors to the morphological adaptation might be different depending on the land type, mainland and island, according to the island effect. Morphological (Kim *et al.*, 2015) and molecular (Kim *et al.*, 2013) studies demonstrated different evolutionary history of Japanese populations. Here, I will investigate what environmental determinants resulted in distinction of each skull morphological variation of Japanese raccoon dogs.

I-2. Materials and methods

Geographic sampling and measurements

In the present study, I used 338 raccoon dog skull specimens from East Asia (Fig. 1 and Table 1) that have detailed locality information; three mainland populations (Russia, Korea, and Vietnam) and four island populations (Hokkaido, Honshu, Shikoku, and Kyushu of Japan). Conservation Genome Resource Bank for Korean Wildlife (CGRB) provided corpses of Korean raccoon dogs that were donated by Wild Aninal Rescue Centers in Korea. Skeletons are stored at the Department of Anatomy and Cell Biology, Seoul National University, Seoul. Russian specimens are deposited in the Zoological Museum of Moscow State University, Moscow. Japanese specimens are stored in the National Museum of Nature and Science, Tsukuba, the Kanagawa Prefectural Museum of Natural History, Kanagawa, the Osaka Museum of Natural History, Osaka, the NPO Shikoku Institute of Natural History, Kochi, and the Hokkaido University Botanical Gardens, Sapporo. Only adult skull specimens with a completely fused basal suture and a developed sagittal crest were used. This eliminated age-related variation. Specimens with a fully erupted lower third molar (m3) were collected for teeth data. Fifty-seven measurements were selected following the definitions of Von den Driesch (1976) and Kauhala *et al*. (1998). Skull measurements (18 cranium and 7 mandible characters) were obtained using vernier calipers to the nearest 0.01 mm (see Fig. 2 and Table 2).

Selection of ecological factors

To test hypothesis 3, I estimated morphogeographic variation influenced by various ecological factors. Geographic and climatic factors are selected as follows;

longitude, latitude, altitude (m), mean annual minimum temperature (℃), mean annual temperature (℃), mean annual maximum temperature (℃), mean annual minimum of precipitation (mm), mean annual precipitation (mm), mean annual sum of precipitation (mm), and mean annual maximum of precipitation (mm) were selected as possible environmental determinants.

Geographic and climatic data were derived from the 1981-2010 normal database of meteorological institution of each country: Hydrometeorological Centre of Russia, Korea Meteorological Administration, Japan Meteorological Agency, and National Centers for Environmental Information National Oceanic and Atmospheric Administration NOAA of USA.

Statistic analyses

To test my hypotheses, I employed the following statistic methods. All statistical analyses except Mantel test were conducted using R (R Development Core Team, 2013).

1) Mantel test

To test hypothesis 1, I compared skull morphological distance and genetic distance. Mitocohondrial DNA cytochrome *b* (1,140bp) genes of 145 raccoon dog individuals with 35 haplotypes were used for calculation of genetic distance (Kim *et al.*, 2013). All sequence data were deposited in Genbank (accession number: JX099854-099889). Pairwise genetic distance matrix was calculated with the

Kimura-2-parameter method (Kimura, 1980). Mean pairwise morphological differences among populations were quantified as squared Mahalanobis distance matrix. Squared mahalanobis distance was calculated from the pooled within-group covariance matrix based on canonical functions obtained after Canonical Discriminant Function Analysis (DFA) (Marcus, 1990; De Maesschalck, Jouan-Rimbaud & Massart, 2000; Quinn & Keough, 2002). This squared Mahalanobis distances were used in unweighted pair-group method with arithmetic average (UPGMA) cluster analyses to produce dendrograms. To test correlation between morphological and molecular distance matrices, we conducted Mantel test (Mantel, 1967; Quinn & Keough, 2002). Mantel test was performed with PAST v.2.1.7 (Hammer, Harper & Ryan, 2001).

2) Allometric analyses

Allometry was performed by scaling relationships between each skull morphological characteristics and condylobasal length. To compare the allometric relationship depending on the land type and each geographic population, standardized major axis (SMA) regression was used as a line-fitting method (Warton *et al.*, 2006; Warton *et al.*, 2012). The allometric relationship of each variable to the condylobasal length (CBL) was examined with the logarithmic expression of the equation of allometry: $\log y = \alpha \log x + \log b$; where y is any of the measured skull variables, log b is the y-intercept or constant of normalization (b is the constant term of the power growth function), α is the slope of the line or coefficient of allometry, and x is the CBL (Alexander, 1985). Likelihood ratio test was used for a common SMA slope to compare the slopes of mainland and island populations (Warton & Weber, 2002; Warton *et al*., 2006).

3) General linear mixed effect models

To identify the subset of variables that best predicted variation in skull morphological characteristics, we conducted general linear mixed effect models (GLMMs) constructed in the nlme package (Pinheiro *et al*., 2013). Skull measurements were used as the response variable examined against seven environmental factors as fixed effects. 27 groups of raccoon dogs were included as a random effect (Table 1). The seven potential models were compared and most appropriate grouping of six environmental factors; longitude, mean annual minimum temperature (MAMT), mean annual sum of precipitation (MASP), land types (mainland and island), interaction between MAMT and land type, and interaction between MASP and land type were determined by model selection based on Akaike's information criterion (AIC) (Anderson, Burnham & White, 1998). Also, I demonstrated influence of environmental factors on different land types (mainland and island) by including interaction between MAMT and land type, and interaction between MASP and land type as environmental factors for testing hypothesis 4.

The presence of multicollinearity among these environmental factors could lead to misinterpretation of the importance of these environmental variables for size and shape variation of populations. Due to the inadequacy of correlation as a method of detecting collinearity, stepwise variance inflation factor (VIF) selection was employed as follows (Quinn & Keough, 2002);

$$\mathrm{VIF} = \frac{1}{1-r^2}$$

r^2 is coefficient of determination which from regression model of a particular variable as the response variable against the remaining variables as predictors. VIF and tolerance ($1-r^2$) are estimated as an indicator of collinearity. Longitude, altitude, MAMT and MASP are selected as independent variables by multicollinearity test.

I-3. Results

Correlation between skull morphological and phylogenetic patterns

Pairwise genetic distance and morphological distance among 7 populations were calculated (Table 3). Morphological distance demonstrated similar relationship to phylogenetic distance which clearly separated mainland and island populations as two major clades (Fig. 3). In mainland clade, most close relationship between raccoon dogs of China and Korea (7.07 of mahalanobis distance) were showed. Russian raccoon dogs were relatively closely related to Chinese raccoon dogs as compared to other mainland populations, although their genetic distance between populations of Russia and Korea was closer than between populations of Russia and China. Vietnamese population was less related to other continental populations in mainland clade. Relatively close morphological relationship with Japanese populations was observed in Chinese and Vietnamese populations within the mainland raccoon dogs. And raccoon dogs of Russia were most separated from that of Japanese Islands. In the Japanese populations, Hokkaido population was most different both from other Japanese populations (21.92 of average mahalanobis distance) and mainland populations (43.33 of mahalanobis distance). Most closely related population with the Hokkaido raccoon dogs was Honshu raccoon dogs with 18.37 of mahalanobis distance. However, Honshu population showed closer genetic relationship with Hokkaido population than Shikoku population.

I conducted Mantel test among seven geographic populations; Russia, China, Korea, Vietnam, Hokkaido of Japan, Honshu of Japan, and Shikoku of Japan. Average genetic and morphological distance between mainland and island were 2.4% and 25.05, respectively. Morphological distance and phylogenetic pattern were significantly correlated (r = 0.82, p = 0.01).

Allometric variations

I observed complicated allometric patterns between land types (Table 4) and among populations (Table 5) in the raccoon dogs. Allometric patterns were separated as four types, due to the land types. In both mainland and island populations, cranium height (SH), cranium width (ZB), muzzle length (RL and CML), length of buccal cavity (PL), and lower teeth row (LT) were isometric for CBL. And CML and LT had significantly higher allometric slope (α: Table 4) in mainland raccoon dogs. Cranium length (SIZE), nasal length (NPL and NL), muzzle width (RB), breadth of orbital constriction (IC and PB), cranium width (MD), occiput (OCB), and mandible size (MRH, ACP, MH, JT, and MW) were positively allometric in both land types. Among those measurements, MD and MRH were relatively larger in island populations, due to the higher allometric slope (α=2.18 and 1.64, respectively: Table 4). Cranium length (FPL) and mandible length (ML) were positively allometric only in mainland populations. Negatively allometric relationships were observed from cranium length (TL) of island populations. Significant allometric slope differences on land types were found in other measurements: allometric slope of mainland raccoon dogs were larger in cranium length [TL (α=1.00) and FPL (α=1.39)] and mandible length [ML (α=1.34)].

It was observed that more detailed allometric pattern among 8 populations: Russia, China, Korea, Vietnam, Hokkaido, Honshu, Shikoku, and Kyushu populations (Table. 5). Different from the result of allometric scaling between mainland and island raccoon dogs, OCB were isometric in all populations. Skull length (TL and BL) was isometric in most populations, although TL of Honshu population and BL of Hokkaido populations were relatively larger. Skull height also indicated isometric scaling in all populations excluding the raccoon dogs of Russia (negative allometry) and Vietnam (no significant).

Muzzle length (RL) was isometric to all populations. Length of buccal cavity (PL) and mandible length (ML) also showed isometric scaling for all populations except for Korean population. However, upper tooth low (CML) were positively allometric in Korean raccoon dogs and negatively allometric in Kyushu raccoon dogs. In skull width related measurements, ZB showed isometric patterns except for Korean and Honshu populations, however MD were positively allometric in most populations except for Korean, Vietnamese, and Kyushu populations. Nasal length (NPL and NL) was positively allometric for CBL in most populations except for the Vietnam raccoon dogs. In breadth of orbital constriction, POC did not show significant allometric patterns either for each land type or for each population. However, IC and PB were positively allometric either for each land type or for each population excluding Chinese, Vietnamese, and Kyushu populations. Mandible measurements such as MRH, ACP, JT, LT, and MH showed relatively smaller measurements compared to the CBL in the raccoon dogs of China, Vietnam, Shikoku, and Kyushu.

Influence of ecological factors

Most skull measurements indicated larger size in lower minimum temperature with drastic slope changes of island populations, except for the POC and PB of island populations. Breadth of orbital constriction (POC), occiput (OCB), mandible height (MH), and mandible width (MW) of raccoon dogs in East Asia were significantly dependent on MAMT (Fig. 4 and Table 6). The OCB and MH were inversely proportional to MAMT in both mainland and island populations, whereas POC of island populations showed directly proportional relation with MAMT. Also, significantly different slope between mainland and island populations were demonstrated in POC, OCB, and MW (Table 6).

MASP were inversely proportional to IC and POC with significant correlation. Significant interaction between orbital constriction (IC and POC) and land types indicating different influences of MASP (Table 6 and Fig. 5). Mainland population had significantly larger IC and PB than that of island populations while FPL was larger in island populations. The IC and PB were smaller with higher precipitation in both mainland and island populations. It was observed that significantly steeper slope of IC and POC of mainland populations compare to that of island populations. PB of island raccoon dogs was the exception that had larger size with higher precipitation.

Cranium length (FPL, CBL, and SIZE), occiput (OCB), muzzle length (RL), and mandible width (MW) were significantly correlated with longitude. These measurements were larger at higher longitude. On the other hand, FPL of island raccoon dogs showed opposite tendency with larger size at lower longitude.

I demonstrated ecological influences on different sex among raccoon dogs from Russian Far East, Korea, Honshu of Japan, Shikoku of Japan, and Kyushu of Japan. Different ecological determinants influenced on male and female raccoon dogs (Table 6). In male raccoon dogs, most skull measurements: cranium length (FPL, BL, TL, CBL, and SIZE), cranium height (SH), nasal length (NPL and NL), cranium width (ZB, IC, and PB), muzzle length (PL and RL) and mandible size (MRH, ACP, LT, ML, and MW) were significantly influenced by MAMT with inversely proportional relationship (Fig. 6). There was significant interaction between MAMT and land type in cranium length (FPL, BL, TL, CBL, and SIZE), nasal length (NPL), cranium width (ZB and PB), muzzle length (PL and RL), and mandible size (MRH, ACP, LT, ML, and MW) with steeper slope of island populations (Fig. 6). MASP were negatively correlated with cranium length (FPL), cranium width (ZB), breadth of orbital constriction (POC, IC, and PB), and muzzle width (RB) as shown in Fig. 7. Among them, different influences by MASP on land types were observed from IC, which was larger in mainland populations and smaller in island populations with higher precipitation. RB, POC, IC, PB, and MD were significantly influenced on the land types. Nasal length (NPL and NL), muzzle width (RB), and skull width (PB) were inversely proportional to longitude (Fig. 7). Significant correlation with land type demonstrated that mainland raccoon dogs had substantially larger RB and MD and smaller POC and PB.

Female raccoon dogs showed different ecological influence compare to male raccoon dogs. Most ecological factors were not correlated with the craniomandibular morphological variation of female (Table 6). As shown in Fig. 8, CML and RL were inversely proportional to MAMT. The IC and PB were significantly influenced by longitude with inversely proportional relation. There was no significant correlation with land types in morphological variation of female raccoon dogs.

I-4. Discussion

Extraordinary morphological diversity has been exhibited in the order carnivora, both in extant (Ewer, 1973; Goswami & Polly, 2010) and extinct groups (Ewer, 1973). Iterative morphological evolution of skull and tooth has been reported in the carnivorous species that have similar ecotypes mostly characterized by the food habits

(Van Valkenburgh, 2007) and sometimes by the climatic conditions (Meiri *et al.*, 2004a). In the raccoon dogs, I firstly observed significant craniomandibular morphological patterns influenced by various environmental determinants. Present study demonstrated ecological inferences from previous studies on the morphological variations (Kim *et al.*, 2015) and phylogeographic patterns (Kim *et al.*, 2013).

Phylogeographic influence on the skull morphological distances

The present results supported hypothesis 1. Skull morphological variation was influenced by both phylogeographic and ecological influences of raccoon dogs in East Asia. I found that morphological variation of raccoon dogs is closely correlated with their genetic differentiation reported previously (Kim *et al.*, 2013). Both phylogenetic and morphological trees had two major clades separated between mainland and island populations. Among the raccoon dog populations, genetic distances were highly correlated with the morphological distances. Result of cluster analysis of morphological distances showed similar pattern with the phylogenetic relationships among raccoon dog populations. However, there was a disparity between morphological variation and phylogenetic pattern within each land type.

Mainland clade of morphological tree was separated as three subclades that consist of raccoon dogs from Korea and China, Russia, and Vietnam. However, phylogeogenetic tree showed two subclades: one consisting haplotypes of Korea, Russia, and China and the other one consisting haplotypes of Russia, China, and Vietnam. Raccoon dogs of Russia and China shared a haplotype which clustered with raccoon dogs of Vietnam

(Kim *et al*., 2013). Therefore, relatively clear morphological variation among mainland populations might be the result of stronger influence of geographic difference. This result could be supported by the different phylogenetic and morphological pattern of Hokkaido population within the island clade. Hokkaido population was morphologically separated from other Japanese populations but genetically close to the Honshu population. Although three island populations did not share any haplotypes, Honshu haplotypes were clustered not only with the Hokkaido population but also with the Shikoku population due to the expansion of Japanese raccoon dogs from Honshu to other islands after their migration from adjacent continent (e.g., Korea) during Middle Pleistocene (Shikama, 1949; Kawamura, 1991).

Strong morphological difference within the land types may be by the ecogeographic rules (Bergmann's rule and island effect) as reported by Kim *et al.* (2015). Body size-related measurements especially OCB showed strong influence of Bergmann's rule (Kim *et al*., 2015). Vietnam and Russia is the southernmost and northern most distribution range of raccoon dogs, respectively (Ward & Wurster-Hill, 1990; Kauhala & Saeki, 2004).

Allometric patterns in the skull morphological variation

According to the present results, hypothesis 2 was rejected. Diversity pattern of skull morphology was not explained by a simple clinal variation in the raccoon dogs. Their morphological variations, however, were explained by complicated result of allometric scaling. Different allometric patterns among closely related species are often directly reflected by performance requirements which are the ability to carry out certain behaviors (Arnold, 1983; Wainwright & Reilly, 1994). Therefore, the difference in allometric trajectories observed in skull size and shape of raccoon dogs might be related to the functional differences in different environmental conditions.

CBL, which is related to body size, is one of the largest parts among the skull length related measurements selected in this study. This measurement separates raccoon dog populations between mainland and island and within mainland or islands (Kim *et al*., 2015). Possible influence of Bergmann's rule on the skull morphological variation has been suggested in the raccoon dogs of Japan (Haba *et al*., 2008) and East Asia (Kim *et al*., 2015). According to these previous studies, skull length measurements including CBL were one of important characteristics that reflect Bergmann's rule. Interpretation of allometric relationships of skull characteristics with CBL is very important for understanding morphological evolutionary effect. Measurements indicating body size such as skull length, skull height, skull width, and occiput were isometric to CBL especially in mainland populations. Occiput was positively allometric both in mainland and island populations reflecting relative size of OCB is similar in each population, namely OCB follows morphogeographic variation in CBL: relatively larger body size according to the larger skull size is observed from northern population in each mainland and island. Meanwhile, skull length was negatively proportional with higher intercept in island raccoon dogs. Therefore, body size differences between and within mainland and island populations influenced by Bergmann's rule coincide with the Kim *et al*. (2015).

There was similar allometric pattern in the muzzle size related to measurements with larger size of mainland populations. Relatively larger nasal length compared to CBL was observed in northern population of each land type especially in the mainland. Although Japanese populations also showed relatively larger NL, Hokkaido and Kyushu raccoon dogs showed isometric pattern in the NPL, which consists of nasal and premaxillary length. Morphologically, NPL is more closely related to muzzle length than NL. Allometric pattern of NPL was also observed in height of mandible ramus (MRH) and upper tooth low (CML). Other mandible measurements (JT, LT, and ML) showed clear geographic difference between northern and southern raccoon dogs in both of mainland and island. Therefore, smaller mandible size and muzzle size of southern population of each land type could be interpreted as influence of Bergmann's rule.

Morphological affinity among different carnivore species in similar environmental condition was observed (Meloro, Clauss & Raia, 2015). Stayton (2006) suggested three kinds of convergence as follows: a) complete convergence (traditional convergence) implies overlap in the morphospace (here, it is mandibular size and shape as defined by Bookstein, (1989)) by the taxa that are putatively convergent; b) incomplete convergence (most commonly implies) applies when putatively convergent taxa occur in the morphospace that are not overlapped but are closer to each other than their relatives are; c) parallel changes (parallelism) imply convergent taxa (showing parallel phenotypic changes away from their sister groups) do not share common areas of morphospace but share similar pathways of phenotypic transformation.

Morphological affinities of southern populations in mainland and island might be the result of common convergence by adaptive radiation due to the environmental similarities in the relative taxa. Based on the result of allometric scaling, I observed that the muzzle size difference is sometimes interpreted as a result of prey size difference in the carnivore species (Wainwright & Reilly, 1994; Slater & Van Valkenburgh, 2009); in the similar environments, it is known that mainland area has relatively abundant species than those of island (Cox & Moore, 2010). This muzzle size variation between mainland and island populations might be explained by the differences in foraging strategy. Mandible development is important for masticatory behaviors that are generally reflected by dietary differences (Radinsky, 1981a, 1981b, and 1982). Mandible ramus and body provide attachment sites for muscles are related to biting force (Biknevicius & Ruff, 1992). Raccoon dogs have strong omnivorous tendency in diet habit with high dependence on plants in spring, summer, and fall (Heptner *et al*., 1998), although consumption of plants are observed even in winter of some regions where they do not hibernate (Sutor, Kauhala & Ansorge, 2010). Nevertheless, the present results demonstrated the development of mandible in northern region. Mandible measurements showed similar allometric patterns with the muzzle-related measurements. In mainland raccoon dogs, mandible length and lower tooth row were isometric (α=1.34 and 1.06, respectively: Table 4). But isometric in island raccoon dogs with lower allometric slope (α=0.94: Table 4). Positively proportional breadth of mandibular ramus was larger in mainland raccoon dogs than in island raccoon dogs. Both within the mainland and island raccoon dogs, breadth of mandibular ramus was larger in northern populations.

Since the size of attachment site is proportional to muscle development, breadth of mandibular ramus indicates food habits requiring stronger bite force (Raia, 2004).

Among the raccoon dog populations, no significant allometric pattern was observed in POC, but northern population of mainland and island populations had relatively larger IC and PB. The difference in size between PB and POC, the broader attachment site is provided for the temporal muscle for the strong jaw (Haba *et al.*, 2008). Therefore, the skull morphological characteristics of northern raccoon dogs might be adapted to more stronger bite force regarding carnivorous tendency compared to Chinese, Vietnamese, and Kyushu populations.

The skull morphogeographic variations among raccoon dog populations are explained by various allometric patterns. Kim *et al*. (2015) suggested that the smaller skull length (especially frontal to parietal length), skull height, skull width, breadth of mandibular ramus, and mandible length can be recognized as morphological determinants that differentiate Japanese raccoon dogs. Present study suggests relative skull length, muzzle length, and mandible size could be indicator of raccoon dogs assuming environmental difference especially the food habit. No significant allometric pattern was observed from many other skull measurments of Vietnamese and Kyushu populations. More morphological data on southern population is necessary to test convergence.

Morphological adaptation influenced by environmental determinants

Kim *et al*. (2015) explained the taxonomic status of raccoon dogs by comparison between craniodental characteristics with paleontological records (e.g., Shikama, 1949) and genealogical perspectives (e.g., Kim *et al*., 2013), suggesting that Japanese raccoon dogs could be treated as distinct species from mainland raccoon dogs. The relatively smaller skulls (skull length and skull width), mandibles (mandible length, mandible height, mandible ramus size, and mandible width), and carnassial teeth (canines and premolar) were recognized as morphologically diagnostic determinants to identify the Japanese raccoon dogs (*N. p. viverrinus* and *N. p. albus*) as reported by Kim *et al*. (2015). Phylogeographic relationships serve to expand and to balance ecogeographic perspectives (Thorpe *et al*., 1995). Therefore, the present results could be useful to seek the environmental effects on their morphological evolutionary pattern and to understand cause-and-effect relationship.

Hypothesis 3 accords with the present results. Skull morphological variation of raccoon dogs had specific geographic patterns influenced by environmental determinants particularly on the climatic factors. Raccoon dogs in cold condition tend to have larger OCB, which is the surface of skull articulating with the atlas, generally correlates with body size (Martin, 1980). Therefore, morphological evolution of raccoon dogs could be explained by Bergmann's rule as one of various environmental influences. Conformity to Bergmann's rule has been discussed as main effect on the skull morphological variation of raccoon dogs in East Asia (Haba *et al*., 2008; Kim *et al*., 2015). According to the Kim *et al*. (2015), OCB was significantly different among island populations. I observed that the OCB was strongly correlated with MAMT in

Japanese raccoon dogs. This might be interpreted as much more body size variation of island populations. MAMT differences in mainland (-25.43℃ to 11.85℃) were larger than that of islands (-7.3℃ to -0.8℃). Different morphological adaptation in each island of Japan (Hokkaido, Honshu, Shikoku, and Kyushu) might be implied by restricted environmental situation (e.g., isolation), despite of smaller temperature difference. Body size difference of Japanese raccoon dogs might be evolved toward an optimal size determined by their ecological constraints in each Japanese island. Despite of less sexually dimorphic characteristics in skull of this species (Kauhala *et al*., 1998; Haba *et al*., 2008; Kim *et al*., 2012), different environmental influences were observed between male and female. Skull morphological variations of male raccoon dogs of Russia, Korea, Honshu, Shikoku, and Kyushu showed extraordinary negative correlation with MAMT in most craniomandibular traits, while females were not. In male raccoon dogs, morphological pattern of OCB coincided with that result of all raccoon dogs with drastic slope in island populations. Most skull measurements of female raccoon dogs did not show significant correlation with MAMT excluding CML and RL, showing that their muzzle length are larger in cold condition. Both male and female raccoon dogs showed steep morphological difference in island populations, but dissimilar ecological effect was found. Not many ecological studies on the raccoon dogs have been reported in Asia, especially the difference between male and female. Raccoon dogs are basically monogamous and no significant difference has been observed in home range and dispersal distance between sexes, although home range and dispersal distance of male are broader than those of female in some regions (Kauhala *et al*., 1993; Choi & Park, 2006a; Saeki *et al*., 2007; Drygala *et al*., 2010). After they pair with in the mating season, it lasts for several years or more (Heptner *et al*., 1998) and pairs share the home ranges and foraging together (Kauhala *et al*., 1993). Although no sexual dimorphism in body size and body weight was observed (Kauhala, 1993; Asikainen *et al*., 2004), their body weight changes to prepare for the winter: in summer (4-6 kg) is doubled in winter (6-10 kg) (Heptner *et al*., 1998; Saeki, 2009). As summer turned to winter, relatively higher fat reserves are observed in female not only for the cold but also for the pregnant and lactation (Kauhala, 1993). One possible scenario that caused different ecological effect on sexes might be the relatively higher fat reserves before winter in female. Mammals residing in cold regions have wide array of adaptations to cope with food shortages and cold stress (Feldhamer *et al*., 2007). Winter lethargy is one of major features that observed from the raccoon dogs in harsh winter; for example the Finnish raccoon dogs hibernate during winter (Kauhala & Saeki, 2004). Russia and Hokkaido populations have dormant behavior to endure cold conditions by making their metabolism lower, but they occasionally active in less cold days of winter (Heptner *et al*., 1998; Kauhala & Saeki, 2004). Therefore, it is important to accumulate the energy to prepare for winter in northern raccoon dogs (Korhonen, Mononen & Harri, 1991). Higher fat reserves in female raccoon dogs during winter might be a big advantage to bear the cold condition in comparison with males. To reserve the fat, female raccoon dogs might need to consume a lot of food such as fruits and seeds which are most available in fall. Their high fat reserves and food consumption might be the reason for the low morphological correlations with the ambient temperature. Although the result of allometry showed isometric relation between muzzle length and skull length in whole raccoon dog populations, larger muzzle length found only in females might be caused by different food habits such as abundant plant food consumption especially in fall.

Based on the significant correlations between breadth of orbital constriction and MASP, I found that raccoon dogs have larger postorbital process (difference between POC and PB) in relatively humid region of mainland and island. This correlation was more clearly observed in mainland populations with drastic slope change, indicating stronger carnivorous tendency of mainland raccoon dogs in humid condition. In humid condition, difference between POC and PB in male raccoon dogs was larger than that in females, suggesting different influence of precipitation between sexes. Males may tend to have greater morphological variation with high adaptability on different environmental situation. Skull morphological variation of male raccoon dogs might be more susceptible to different environmental conditions, especially on the different temperature and humidity. In this study, ecological influence on the different gender of raccoon dogs from China, Vietnam, and Hokkaido were not observed due to the lack of gender information. Further study on the influence of climate on raccoon dogs of China, Vietnam, and Hokkaido will be necessary to clarify their different environmental adaptation.

I excluded latitude from the fixed effects in the model due to the high multicollinearity of latitude against longitude and ambient temperature. Measurements that have positive correlations with longitudinal differences were larger in northern populations (in each mainland and island population). In male raccoon dogs occurring in northern parts, nasal length was larger, but muzzle width and breadth of orbital constriction were smaller. Female raccoon dogs had smaller breadth of orbital constriction (IC and PB) in northern mainland, and showed less carnivorous tendency in islands. Skull morphological characteristics regarding carnivorous tendency were observed in humid and warm conditions of mainland. However, raccoon dogs excluding Hokkaido population had stronger carnivorous tendency in more humid and more northern area in mainland and island. Highest MASP was observed in the most southern populations (Vietnam and Kyushu Island) of both mainland and island, but lowest MASP was observed in the raccoon dogs of Russian Far East and Hokkaido. Generally, larger prey size and high food availability are influenced by higher precipitation (Yom-tov & Nix, 1986). In isolated island, species richness is increasing in higher precipitation and temperature (Kalmar & Currie, 2006). Although PB did not showed any influence by MASP, island raccoon dogs had larger PB in high MASP and mainland raccoon dogs had larger PB in low MASP. Therefore, the difference between POC and PB were larger in high MASP of island populations but not different in mainland populations. Different from MAMT, island raccoon dogs showed large difference between lowest (932.67 mm in Honshu) and highest (2547.52 mm in Shikoku and 2508.00mm in Kyushu) than that of mainland raccoon dogs (625.00mm to 1656.00 mm). In the previous studies on the craniodental variation among Japanese raccoon dogs, significantly large difference between POC and PB were interpreted as strong bite force by strong carnivorous tendency (Haba *et al*., 2008; Kim *et al*., 2013). During severe winter, it is difficult to find plant food in Hokkaido and raccoon dogs of

Hokkaido do not hibernate over the winter (Kauhala & Saeki, 2004). Therefore, strong carnivorous tendency of Hokkaido raccoon dogs might not be strongly related to precipitation. Precipitation seems to be more strongly related to raccoon dogs of southern islands of Japan (Shikoku and Kyushu) with abundant food availability. According to the MacArthur-Wilson Model theory, small islands have fewer species than large islands, and more distant islands have fewer species than nearer islands from the source area (MacArthur & Wilson, 1967).

This complicated morphological pattern could be interpreted as the influences of various environmental conditions between and within land types. The morphological adaptations of raccoon dogs for mainland and island were demonstrated by the different environmental conditions. Therefore, hypothesis 4 is accepted: skull morphological patterns on climatic conditions were different between land types. Steep morphological variations of island raccoon dogs in different climate conditions indicate greatly changeable ability in island populations. Present study identified previous assumptions on the validity of ecogeographic rules observed from the morphological variation of raccoon dogs. I demonstrated occurrence of Bergmann's rule in larger body size related to skull characteristics in cold conditions of mainland and island. This morphological pattern was stronger in island populations, indicating the influence of island effect not only between land types but also among the Japanese Islands. It was demonstrated that the skull morphological variation among raccoon dog populations is attributed by both phylogenetical and environmental differences. From the morphological viewpoint, raccoon dogs of mainland and island populations could have undergone different evolutionary history.

Table 1. Locality and number of raccoon dog specimens used in this study

Land type	Locality	Groups for ecomorphological analysis	Number of individuals			
			Genetic samples*	Skull specimens**		
				male	female	all individuals
Mainland	Russian Far East	R01-04	11	37	22	70
	China	-	2	-	-	37
	South Korea	K01-04	66	17	10	41
	Vietnam	V01-02	5	-	-	6
Island	Hokkaido, Japan	JA01	10	-	-	42
	Honshu, Japan	JH01-JH11	38	41	30	85
	Shikoku, Japan	JS01-JS03	13	16	18	47
	Kyushu, Japan	JK01-JK02	-	7	3	10
	Total	27	145	118	83	338

* Accession no. JX099854-099889 (Kim *et al*., 2013)
** I used skull specimens reported by Kim *et al*., (2015)

Table 2. Cranium and mandible measurements with abbreviation and definition

	Abbreviation	definition
Cranium	NPL	nasal+premaxillary
	NL	nasal length
	FPL	frontal to parietal length
	SH	height of cranium (meeting point between sagittal crest and interparietal process to the bottom most of tympanic bullar in the right side of skull)
	BL	basal length
	RB	rostrum breadth
	POC	postorbital constriction
	IC	interorbital constriction
	PB	postorbital breadth
	OCB	occipital condyle breadth
	ZB	zygomatic breadth
	TL	total length
	PL	palatal length
	MD	distance between first upper molars
	CBL	condylobasal length
	CML	length of the upper canine to upper molar tooth low
	RL	rostrum length (prosthion to the caudal edge of 2nd upper molar)
	SIZE	cranium length that is independent of rostrum length
Mandible	MRH	height of the mandibular ramus
	ACP	from angular process to coronoid process
	LT	length of the lower tooth row
	JT	jaw thickness (transversal width of the lower jaw beneath the front of first lower molar)
	JH	mandible height in front of first lower molar
	ML	mandible length
	MW	mandible width

Table 3. Pairwise distance matrix of mitochondrial cytochrome *b* gene (above diagonal: Kim *et al*., 2013) and squared Mahalanobis distance of skull measurements (below diagonal) of seven raccoon dog populations.

Population	1	2	3	4	5	6	7
1. Russian Far East		0.004	0.006	0.007	0.025	0.024	0.025
2. Korea	17.79		0.006	0.006	0.024	0.024	0.024
3. China	9.63	7.07		0.007	0.025	0.025	0.026
4. Vietnam	14.80	16.80	13.49		0.023	0.023	0.024
5. Hokkaido of Japan	47.37	39.65	34.66	51.64		0.005	0.008
6. Honshu of Japan	33.24	27.57	22.35	26.96	18.37		0.006
7. Shikoku of Japan	40.41	38.06	33.65	32.91	25.46	5.15	

Table 4. Results of standardized major axis regression of log skull variables (y) and log CBL (x) allometric relationship in raccoon dog populations grouped by land types.

Measurements	Common slope		Mainland			Island		
	between land types	$\alpha \neq 1$	α	β	AR	α	β	AR
TL	*	*	1.00	0.02	I	0.91	0.19	N
BL	NS	NS	0.99	0.00	I	0.97	0.03	N
ZB	NS	NS	1.09	-0.43	I	1.01	-0.26	I
FPL	*	*	1.39	-1.04	P	1.10	-0.44	I
SIZE	NS	*	1.25	-0.82	P	1.20	-0.72	P
NPL	NS	*	1.44	-1.24	P	1.35	-1.02	P
NL	NS	*	1.71	-1.89	P	1.57	-1.57	P
SH	NS	NS	0.94	-0.30	I	0.91	-0.25	I
RB	NS	*	1.22	-1.19	P	-1.07	1.16	P
POC	NS	*	1.93	-2.68	ns	-1.68	4.74	ns
IC	NS	*	1.62	-1.97	P	1.50	-1.69	P
PB	NS	*	1.74	-2.08	P	1.65	-1.82	P
OCB	NS	*	1.18	-1.07	P	1.28	-1.24	P
PL	NS	NS	1.06	-0.42	I	1.08	-0.45	I
MD	*	*	1.74	-2.34	P	2.18	-3.24	P
CML	*	NS	1.06	-0.54	I	0.94	-0.27	I
RL	NS	NS	0.94	-0.17	I	0.96	-0.21	I
MRH	*	*	1.32	-1.06	P	1.64	-1.72	P
ACP	NS	*	1.46	-1.45	P	1.42	-1.37	P
LT	*	*	1.09	-0.54	I	0.89	-0.11	I
JT	NS	*	1.65	-2.59	P	1.49	-2.24	P
MH	NS	*	1.65	-2.32	P	1.81	-2.65	P
ML	*	*	1.34	-0.82	P	0.91	0.06	I
MW	NS	*	1.78	-2.35	P	1.92	-2.64	P

α, indicates slope of the allometric regression line; β, indicates intercept of the allometric regression line; AR, mode of allometric relation; I, indicates isometry; P, indicates positive allometry; N, indicates negative allometry; M, indicates mainland; I, indicates island; NS, no significant difference on slopes between land types or no significant difference of *α* from 1; ns, indicates no significant slope.

Table 5. Results of standardized major axis regression of log skull variables (y) and log CBL (x) allometric relationship in eight raccoon dog populations.

Measurements	Common slope		Russia			China			Korea			Vietnam			Hokkaido			Honshu			Shikoku			Kyushu		
	among populations	$\alpha \neq 1$	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR
TL	NS	NS	1.02	-0.03	I	1.00	0.01	I	0.98	0.05	I	1.13	-0.25	I	0.92	0.17	I	1.09	-0.17	P	0.97	0.09	I	1.00	0.01	I
BL	NS	NS	0.98	0.01	I	1.03	-0.08	I	1.00	-0.02	I	0.98	0.02	I	1.08	-0.19	P	1.00	-0.01	I	1.01	-0.04	I	1.01	-0.04	I
ZB	NS	*	0.98	-0.22	I	1.61	-1.49	I	0.99	-0.22	P	1.17	-0.59	I	1.11	-0.46	I	1.27	-0.80	P	1.19	-0.61	I	0.83	0.10	ns
FPL	*	*	1.51	-1.29	P	1.23	-0.70	I	1.13	-0.51	I	1.96	-2.22	P	1.58	-1.44	P	1.35	-0.96	P	1.15	-0.53	I	0.80	0.16	I
SIZE	NS	*	1.26	-0.84	P	1.19	-0.69	P	1.25	-0.81	P	1.28	-0.87	I	1.23	-0.77	P	1.27	-0.86	P	1.20	-0.71	P	1.46	-1.24	P
NPL	NS	*	1.47	-1.30	P	1.75	-1.87	P	1.46	-1.27	P	0.95	-0.20	ns	1.29	-0.90	I	1.63	-1.58	P	1.75	-1.82	P	1.57	-1.47	I
NL	NS	*	1.47	-1.30	P	1.75	-1.87	P	1.46	-1.27	P	0.95	-0.20	ns	1.29	-0.90	P	1.63	-1.58	P	1.75	-1.82	P	1.57	-1.47	P
SH	NS	NS	0.79	0.01	N	1.08	-0.59	I	0.96	-0.34	I	1.00	-0.43	I	1.04	-0.53	I	1.17	-0.77	I	1.08	-0.58	I	0.74	0.11	ns
RB	NS	*	1.18	-1.10	I	1.35	-1.45	I	1.01	-0.75	I	1.30	-1.35	ns	0.98	-0.69	I	1.45	-1.66	P	1.15	-1.04	I	0.94	-0.61	I
POC	NS	*	1.92	-2.66	ns	-2.40	6.26	ns	-1.82	5.05	ns	0.80	-0.35	ns	-1.84	5.08	ns	-2.45	6.32	ns	1.81	-2.32	ns	-1.77	4.91	ns
IC	NS	*	1.60	-1.95	P	1.67	-2.06	ns	1.35	-1.41	I	1.90	-2.56	ns	1.37	-1.43	P	2.03	-2.77	P	1.74	-2.15	P	1.52	-1.74	ns
PB	NS	*	1.92	-2.47	P	1.64	-1.86	ns	1.41	-1.41	P	0.75	-0.08	ns	1.48	-1.49	P	2.16	-2.87	P	2.00	-2.51	P	1.71	-1.90	ns
OCB	NS	NS	1.18	-1.08	I	1.36	-1.47	I	1.05	-0.80	I	1.00	-0.70	I	1.11	-0.88	I	1.18	-1.05	I	1.00	-0.68	I	1.01	-0.71	I
PL	NS	NS	1.06	-0.42	I	1.24	-0.80	I	1.02	-0.34	P	0.71	0.30	I	1.19	-0.69	I	1.09	-0.47	I	1.00	-0.30	I	0.78	0.17	I
MD	NS	*	1.48	-1.81	P	2.37	-3.64	P	1.56	-1.97	ns	1.96	-2.80	ns	1.84	-2.50	P	1.91	-2.70	P	1.98	-2.80	P	1.59	-2.03	ns
CML	*	*	1.04	-0.50	I	1.33	-1.10	I	1.00	-0.41	P	1.06	-0.53	I	1.05	-0.52	I	1.02	-0.44	I	1.16	-0.71	I	0.72	0.17	N
RL	NS	NS	0.95	-0.21	I	1.04	-0.38	I	0.90	-0.10	I	1.09	-0.49	I	1.05	-0.39	I	0.97	-0.23	I	1.08	-0.45	I	0.71	0.30	I
MRH	*	*	1.25	-0.91	P	1.51	-1.45	P	1.35	-1.11	P	1.87	-2.21	ns	1.24	-0.90	I	2.00	-2.46	P	1.34	-1.10	P	1.20	-0.82	I
ACP	NS	*	1.38	-1.29	P	1.72	-1.99	P	1.32	-1.16	P	1.72	-1.99	ns	1.61	-1.74	P	1.72	-1.97	P	1.39	-1.29	P	1.42	-1.35	ns
LT	NS	*	1.15	-0.66	P	1.09	-0.54	I	1.05	-0.46	I	0.86	-0.05	ns	1.48	-1.34	P	0.98	-0.31	I	0.99	-0.31	I	0.62	0.44	N
JT	NS	*	1.50	-2.28	P	2.14	-3.62	ns	1.67	-2.64	P	0.93	-1.13	ns	1.58	-2.44	P	1.55	-2.38	P	-2.18	5.16	ns	1.50	-2.25	ns
MH	*	*	1.49	-2.01	P	2.42	-3.93	I	1.31	-1.64	P	2.28	-3.63	ns	2.07	-3.18	P	1.83	-2.69	P	1.97	-2.96	P	1.63	-2.28	P
ML	NS	*	1.05	-0.21	I	1.25	-0.65	I	1.08	-0.30	P	1.08	-0.28	I	1.16	-0.46	I	1.15	-0.44	I	1.12	-0.36	I	0.98	-0.09	I
MW	NS	*	1.59	-1.94	P	2.32	-3.46	P	1.52	-1.80	P	2.65	-4.15	ns	1.78	-2.34	P	2.14	-3.11	P	1.49	-1.76	I	1.50	-1.79	I

α, indicates slope of the allometric regression line; β, indicates intercept of the allometric regression line; AR, mode of allometric relation; I, indicates isometry; P, indicates positive allometry; N, indicates negative allometry; M, indicates mainland; I, indicates island; NS, no significant difference on slopes among populations or no significant difference of α from 1; ns, indicates no significant slope.

Table 6. Results from general linear mixed-model analysis of all individuals, male and female raccoon dogs on 25 skull morphological variables in East Asia by ecological factors. Abbreviations of skull morphological measurements are shown in Table 2.

	Ecological factors	NPL			NL			FPL			SH			BL		
		β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*
all	MAMT	0.23	0.37	0.54	0.00	0.00	0.99	-0.01	0.01	0.93	-0.10	0.72	0.40	-0.28	0.85	0.36
	MASP	0.00	0.10	0.76	0.00	0.03	0.87	0.00	0.02	0.90	0.00	0.13	0.72	0.00	0.00	1.00
	Longitude	0.00	0.25	0.62	0.00	0.46	0.50	0.00	4.18	**	0.00	0.09	0.77	0.00	0.74	0.39
	Landtype	8.35	0.93	0.34	2.96	0.14	0.71	9.71	3.47	*	-2.53	0.36	0.56	11.41	1.08	0.31
	MAMT:Landtype	0.26	0.75	0.39	0.06	0.05	0.82	0.04	0.07	0.79	-0.08	0.34	0.56	0.28	0.68	0.41
	MASP:Landtype	0.00	0.56	0.45	0.00	0.01	0.92	0.00	0.06	0.80	0.00	2.09	0.15	0.00	0.03	0.86
male	MAMT	-1.49	4.52	*	-1.33	3.67	*	-1.27	5.98	*	-0.68	4.54	*	-2.89	7.20	**
	MASP	0.00	0.15	0.71	0.00	0.03	0.86	0.00	4.28	*	0.00	1.19	0.30	0.00	0.58	0.46
	Longitude	0.01	6.35	**	0.01	7.45	**	0.00	3.00	0.11	0.00	0.44	0.52	0.00	0.89	0.37
	Landtype	-3.47	0.11	0.75	-9.55	0.82	0.39	12.00	2.34	0.16	-0.35	0.01	0.94	5.46	0.11	0.74
	MAMT:Landtype	1.36	3.44	*	1.15	2.51	0.14	1.42	6.85	**	0.58	3.02	0.11	2.84	6.35	**
	MASP:Landtype	0.01	1.09	0.32	0.01	2.70	0.13	-0.01	1.04	0.33	0.00	0.76	0.40	0.00	0.19	0.67
female	MAMT	-0.73	2.94	0.11	-0.67	3.17	0.10	-0.21	0.33	0.58	-0.39	2.91	0.12	-0.82	2.04	0.18
	MASP	0.00	0.37	0.56	0.00	0.41	0.53	0.00	0.26	0.62	0.00	0.07	0.80	0.00	0.76	0.40
	Longitude	0.00	0.77	0.40	0.00	1.13	0.31	0.00	0.22	0.65	0.00	0.08	0.79	0.00	0.29	0.60
	Landtype	-7.20	0.22	0.65	-14.24	1.11	0.31	19.01	2.13	0.17	0.41	0.00	0.96	7.14	0.12	0.74
	MAMT:Landtype	0.40	0.55	0.47	0.28	0.35	0.57	0.38	0.69	0.43	0.21	0.51	0.49	0.61	0.71	0.42
	MASP:Landtype	0.01	0.54	0.48	0.01	1.86	0.20	-0.01	1.12	0.31	0.00	0.04	0.84	0.00	0.01	0.93

Table 6. Continued

	Ecological factors	RB			POC			IC			PB			OCB		
		β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*
all	MAMT	0.03	0.16	0.69	0.15	4.35	**	-0.04	0.26	0.61	-0.02	0.02	0.89	-0.14	7.15	***
	MASP	0.00	0.74	0.39	0.00	4.52	**	0.00	3.32	*	0.00	0.18	0.67	0.00	1.03	0.31
	Longitude	0.00	1.33	0.25	0.00	1.00	0.32	0.00	0.02	0.90	0.00	1.08	0.30	0.00	3.09	*
	Landtype	-0.98	0.16	0.69	-4.15	2.54	0.12	-7.05	5.96	**	-16.94	9.98	***	3.23	3.00	*
	MAMT:Landtype	-0.07	0.79	0.38	-0.21	7.11	***	-0.09	0.91	0.34	-0.29	3.12	*	0.19	10.93	***
	MASP:Landtype	0.00	3.64	*	0.00	0.68	0.41	0.01	10.34	***	0.01	8.81	**	0.00	2.17	0.14
male	MAMT	-0.22	1.89	0.20	0.08	0.06	0.82	-0.55	5.18	*	-0.35	0.61	0.45	-0.35	3.98	*
	MASP	0.00	3.53	*	0.00	7.36	**	0.00	8.50	**	0.00	5.91	**	0.00	0.00	0.95
	Longitude	0.00	0.88	0.37	0.00	0.10	0.76	0.00	0.11	0.75	0.00	3.40	*	0.00	0.35	0.57
	Landtype	-1.40	0.32	0.58	-10.23	4.34	*	-9.31	6.52	**	-15.64	5.27	**	2.79	1.09	0.32
	MAMT:Landtype	0.20	1.33	0.28	-0.22	0.42	0.53	0.40	2.56	0.14	0.18	0.15	0.71	0.37	4.03	*
	MASP:Landtype	0.00	3.28	0.10	0.00	2.21	0.17	0.01	8.10	**	0.01	2.51	0.14	0.00	0.76	0.40
female	MAMT	0.04	0.14	0.71	-0.09	0.17	0.69	-0.35	3.02	0.11	-0.13	0.15	0.71	0.05	0.16	0.70
	MASP	0.00	0.17	0.69	0.00	0.14	0.72	0.00	0.13	0.72	0.00	0.00	0.99	0.00	0.09	0.76
	Longitude	0.00	0.29	0.60	0.00	0.30	0.59	0.00	5.37	**	0.00	6.52	0.03	0.00	1.52	0.24
	Landtype	0.46	0.01	0.91	8.93	1.35	0.27	0.82	0.01	0.91	0.75	0.00	0.95	1.02	0.05	0.84
	MAMT:Landtype	-0.07	0.25	0.63	0.28	1.10	0.32	0.39	2.35	0.15	0.18	0.19	0.67	-0.04	0.07	0.80
	MASP:Landtype	0.00	0.49	0.50	-0.01	1.72	0.22	0.00	0.00	0.95	0.00	0.26	0.62	0.00	0.00	1.00

Table 6. Continued

	Ecological factors	ZB			TL			PL			MD			CBL		
		β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*
all	MAMT	-0.13	0.86	0.35	-0.25	0.69	0.41	-0.23	1.91	0.17	-0.04	0.25	0.62	-0.31	1.07	0.30
	MASP	0.00	0.97	0.33	0.00	0.02	0.88	0.00	0.01	0.91	0.00	0.02	0.90	0.00	0.00	0.97
	Longitude	0.00	0.03	0.87	0.00	1.25	0.26	0.00	0.48	0.49	0.00	2.57	0.11	0.00	3.28	*
	Landtype	-4.55	0.77	0.39	10.71	0.96	0.34	5.39	0.82	0.37	2.82	0.72	0.40	16.94	2.49	0.13
	MAMT:Landtype	-0.07	0.18	0.67	0.25	0.55	0.46	0.22	1.40	0.24	0.08	0.57	0.45	0.44	1.78	0.18
	MASP:Landtype	0.01	3.70	*	0.00	0.00	0.97	0.00	0.10	0.75	0.00	0.06	0.81	0.00	0.16	0.69
male	MAMT	-1.20	8.50	**	-3.08	12.02	***	-1.36	7.37	**	-0.29	1.89	0.20	-3.14	8.59	**
	MASP	0.00	7.56	**	0.00	1.65	0.23	0.00	0.16	0.70	0.00	0.15	0.71	0.00	0.95	0.35
	Longitude	0.00	0.49	0.50	0.00	0.67	0.43	0.00	0.32	0.58	0.00	1.11	0.32	0.00	0.99	0.34
	Landtype	-5.52	0.79	0.40	9.22	0.47	0.51	0.38	0.00	0.96	8.90	8.00	**	13.96	0.74	0.41
	MAMT:Landtype	1.06	6.06	**	3.15	11.47	***	1.25	5.67	**	0.47	4.58	*	3.30	8.64	**
	MASP:Landtype	0.01	2.00	0.19	0.00	0.04	0.85	0.00	0.26	0.62	0.00	2.61	0.14	0.00	0.00	0.99
female	MAMT	-0.36	1.32	0.28	-0.92	2.03	0.18	-0.66	3.21	0.10	-0.18	1.98	0.19	-0.73	1.96	0.19
	MASP	0.00	0.27	0.61	0.00	0.69	0.43	0.00	0.30	0.59	0.00	1.79	0.21	0.00	0.84	0.38
	Longitude	0.00	1.07	0.32	0.00	0.15	0.71	0.00	0.01	0.91	0.00	0.09	0.77	0.00	1.15	0.31
	Landtype	-2.07	0.03	0.86	9.36	0.16	0.70	7.54	0.33	0.58	0.45	0.01	0.92	16.44	0.77	0.40
	MAMT:Landtype	0.15	0.15	0.71	0.77	0.88	0.37	0.66	2.03	0.18	0.11	0.53	0.48	0.80	1.48	0.25
	MASP:Landtype	0.00	0.10	0.75	0.00	0.00	1.00	0.00	0.09	0.77	0.00	0.24	0.63	0.00	0.01	0.91

Table 6. Continued

	Ecological factors	CML			RL			SIZE			MRH			ACP		
		β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*
all	MAMT	-0.04	0.20	0.65	-0.18	1.96	0.16	-0.12	0.43	0.51	-0.06	0.10	0.75	-0.04	0.10	0.76
	MASP	0.00	0.58	0.45	0.00	0.00	0.95	0.00	0.00	0.98	0.00	0.00	0.99	0.00	0.10	0.76
	Longitude	0.00	2.43	0.12	0.00	2.78	*	0.00	3.31	**	0.00	2.09	0.15	0.00	0.70	0.40
	Landtype	5.46	2.61	0.12	6.89	2.18	0.15	10.49	2.53	0.12	0.92	0.01	0.91	1.41	0.07	0.79
	MAMT:Landtype	0.12	1.30	0.26	0.25	3.07	*	0.20	0.96	0.33	-0.04	0.03	0.86	-0.04	0.08	0.78
	MASP:Landtype	0.00	0.63	0.43	0.00	0.34	0.56	0.00	0.08	0.78	0.00	0.55	0.46	0.00	0.25	0.62
male	MAMT	-0.75	1.83	0.21	-1.09	3.41	*	-2.05	13.56	***	-2.18	9.85	**	-1.35	7.26	**
	MASP	0.00	0.36	0.56	0.00	0.34	0.57	0.00	1.58	0.24	0.00	0.61	0.45	0.00	0.86	0.38
	Longitude	0.00	0.78	0.40	0.00	0.92	0.36	0.00	0.80	0.39	0.00	0.19	0.67	0.00	0.01	0.92
	Landtype	0.60	0.01	0.94	0.96	0.01	0.92	12.97	2.37	0.15	3.47	0.11	0.75	-3.80	0.25	0.63
	MAMT:Landtype	0.73	1.59	0.24	1.06	2.98	0.12	2.23	14.63	***	2.16	8.83	**	1.18	5.06	**
	MASP:Landtype	0.00	0.19	0.67	0.00	0.23	0.64	0.00	0.23	0.64	0.00	0.12	0.73	0.00	1.01	0.34
female	MAMT	-0.37	3.69	*	-0.45	4.01	*	-0.27	0.62	0.45	-0.87	6.04	**	-0.22	0.57	0.47
	MASP	0.00	0.51	0.49	0.00	1.83	0.20	0.00	0.23	0.64	0.00	0.24	0.64	0.00	0.29	0.60
	Longitude	0.00	1.72	0.22	0.00	3.09	0.11	0.00	0.21	0.66	0.00	0.00	0.98	0.00	0.22	0.65
	Landtype	4.86	0.50	0.49	3.09	0.14	0.71	13.35	1.12	0.31	3.27	0.07	0.80	1.78	0.03	0.87
	MAMT:Landtype	0.37	2.41	0.15	0.39	1.82	0.20	0.41	0.88	0.37	0.72	2.61	0.13	0.14	0.14	0.72
	MASP:Landtype	0.00	0.07	0.80	0.00	0.06	0.82	0.00	0.11	0.75	0.00	0.02	0.89	0.00	0.01	0.94

Table 6. Continued

	Ecological factors	LT			JT			MH			ML			MW		
		β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*	β	*F*	*P*
all	MAMT	-0.02	0.03	0.87	0.04	2.48	0.12	-0.09	4.05	**	-0.13	0.24	0.62	-0.22	11.51	***
	MASP	0.00	0.08	0.78	0.00	0.70	0.40	0.00	0.48	0.49	0.00	0.07	0.79	0.00	0.08	0.77
	Longitude	0.00	1.52	0.22	0.00	0.15	0.70	0.00	0.37	0.54	0.00	1.30	0.26	0.00	2.80	*
	Landtype	6.89	2.09	0.16	-0.48	0.24	0.63	-0.05	0.00	0.98	7.37	0.53	0.47	0.81	0.11	0.74
	MAMT:Landtype	0.09	0.37	0.54	-0.06	4.19	**	0.06	1.38	0.24	-0.07	0.05	0.82	0.16	5.20	**
	MASP:Landtype	0.00	0.54	0.46	0.00	0.57	0.45	0.00	0.98	0.32	0.00	0.45	0.50	0.00	4.34	**
male	MAMT	-1.08	4.94	*	0.01	0.06	0.81	-0.27	3.08	0.11	-2.59	7.64	**	-0.73	8.72	**
	MASP	0.00	0.14	0.72	0.00	2.48	0.15	0.00	1.03	0.34	0.00	0.16	0.70	0.00	0.17	0.69
	Longitude	0.00	2.48	0.15	0.00	0.50	0.50	0.00	0.33	0.58	0.00	0.32	0.58	0.00	0.43	0.53
	Landtype	2.24	0.09	0.77	-1.64	3.07	0.11	-0.81	0.12	0.73	8.37	0.35	0.57	-1.50	0.16	0.70
	MAMT:Landtype	1.09	4.54	*	-0.05	0.70	0.42	0.25	2.38	0.15	2.42	6.10	**	0.62	5.75	**
	MASP:Landtype	0.00	0.32	0.58	0.00	3.55	*	0.00	1.38	0.27	0.00	0.00	0.98	0.00	3.05	0.11
female	MAMT	-0.47	2.91	0.12	0.02	0.08	0.78	-0.13	2.32	0.16	-0.01	0.00	0.99	-0.15	1.33	0.28
	MASP	0.00	0.68	0.43	0.00	0.99	0.34	0.00	0.38	0.55	0.00	0.03	0.87	0.00	0.49	0.50
	Longitude	0.00	0.75	0.41	0.00	0.01	0.93	0.00	0.55	0.47	0.00	0.90	0.36	0.00	0.55	0.48
	Landtype	-0.20	0.00	0.98	-1.28	0.30	0.60	-0.59	0.03	0.86	13.08	0.31	0.59	-1.23	0.11	0.74
	MAMT:Landtype	0.32	0.87	0.37	-0.06	0.63	0.45	0.06	0.29	0.60	-0.15	0.03	0.86	0.05	0.10	0.76
	MASP:Landtype	0.00	0.10	0.75	0.00	0.37	0.55	0.00	0.17	0.68	-0.01	0.43	0.53	0.00	1.61	0.24

β, indicates estimated coefficient; MAMT, indicates mean annual minimum temperature; MASP, indicates mean annual sum of precipitation; MAMT:Landtype, indicates interaction between MAMT and land type; MASP:Landtype, indicates interaction between MASP and land type.

*$P < 0.1$, **$P < 0.05$, ***$P < 0.01$

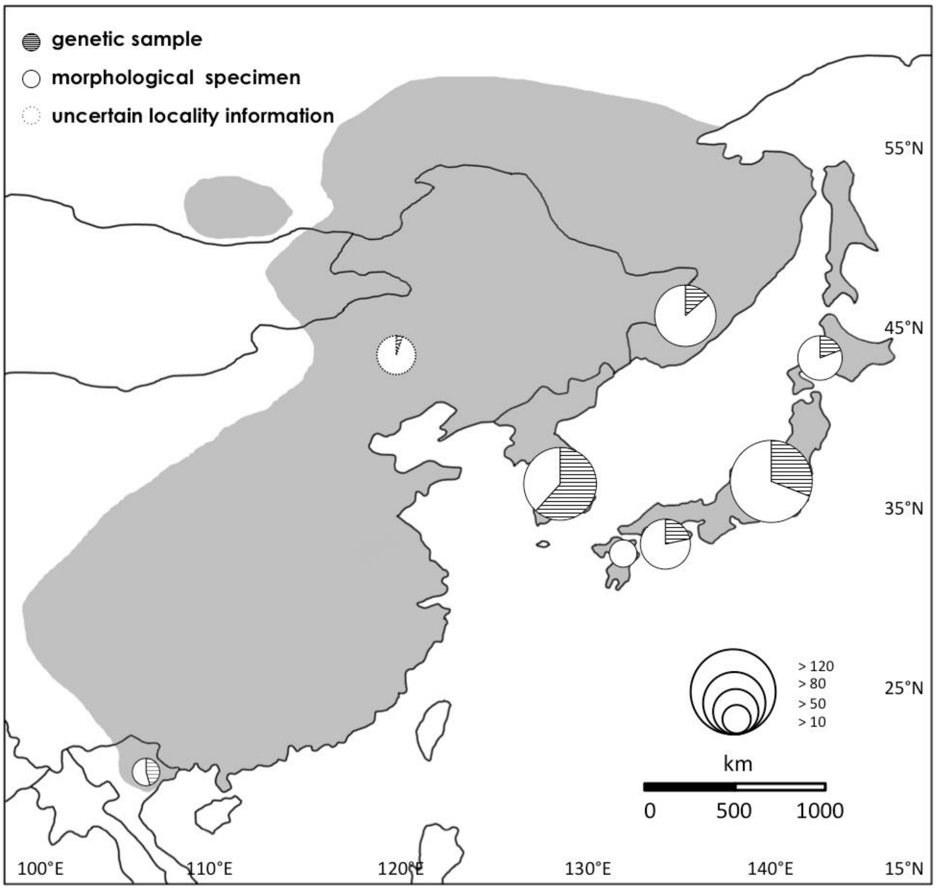


Fig. 1. Current distribution of raccoon dogs (*Nyctereutes procyonoides*) in East Asia (grey shading). Collection localities of individuals used for genetic (diagonal) and morphological (white) analyses are designated with circle. Distribution modified from Kauhala & Saeki (2004).

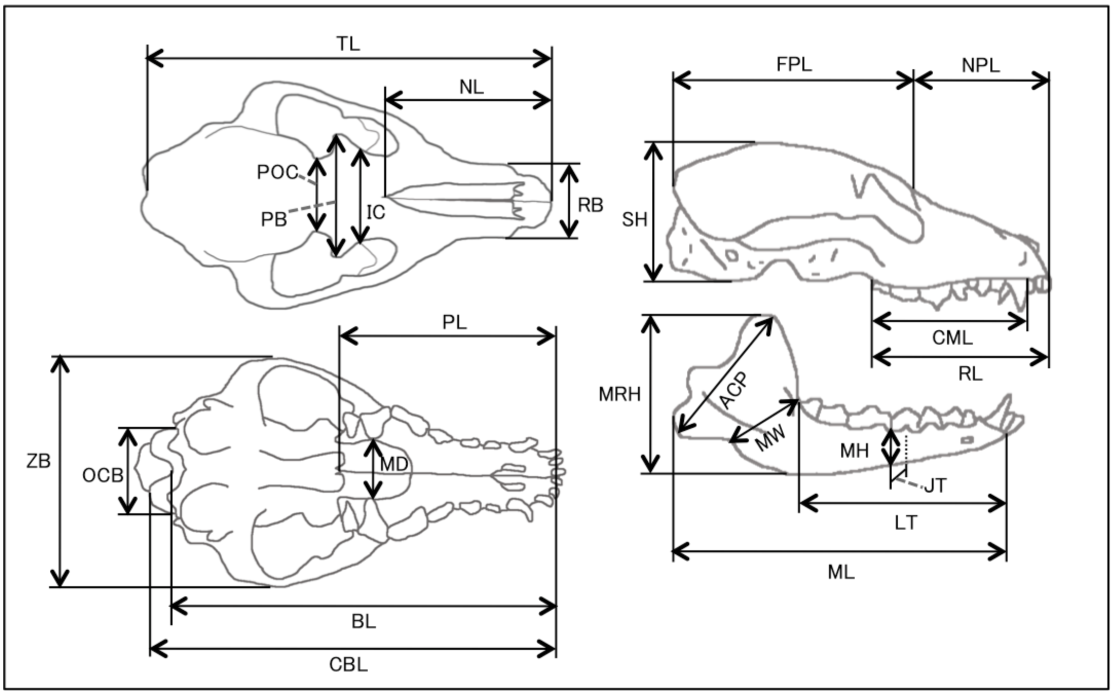


Fig. 2. Cranium and mandible measurements of the raccoon dogs used in this study. Abbreviations are defined in Table 2.

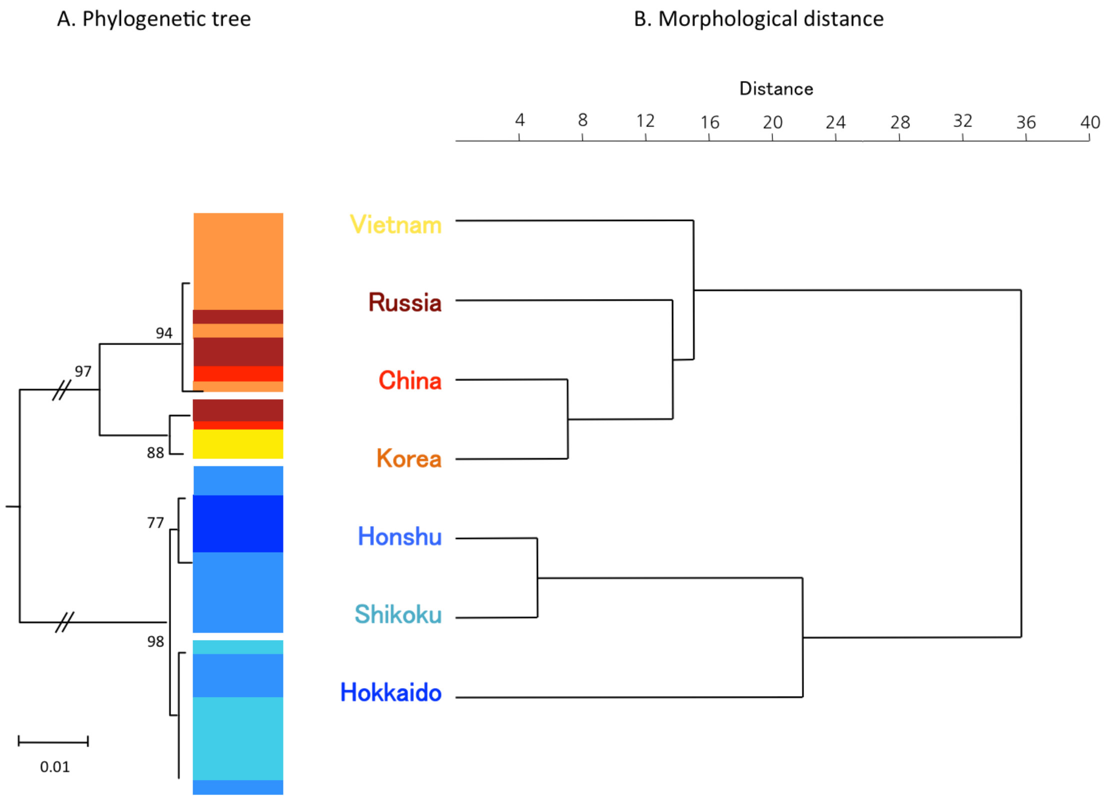


Fig. 3. Comparison between A. phylogenetic tree constructed by neighbour joining method using cytochrome *b* nucleotide sequences (the numbers at the branches indicate bootstrap values (%) derived from 10,000 replications) and B. UPGMA dendrogram of 25 skull morphological characteristics derived from squared Mahalanobis distance of seven raccoon dog populations.

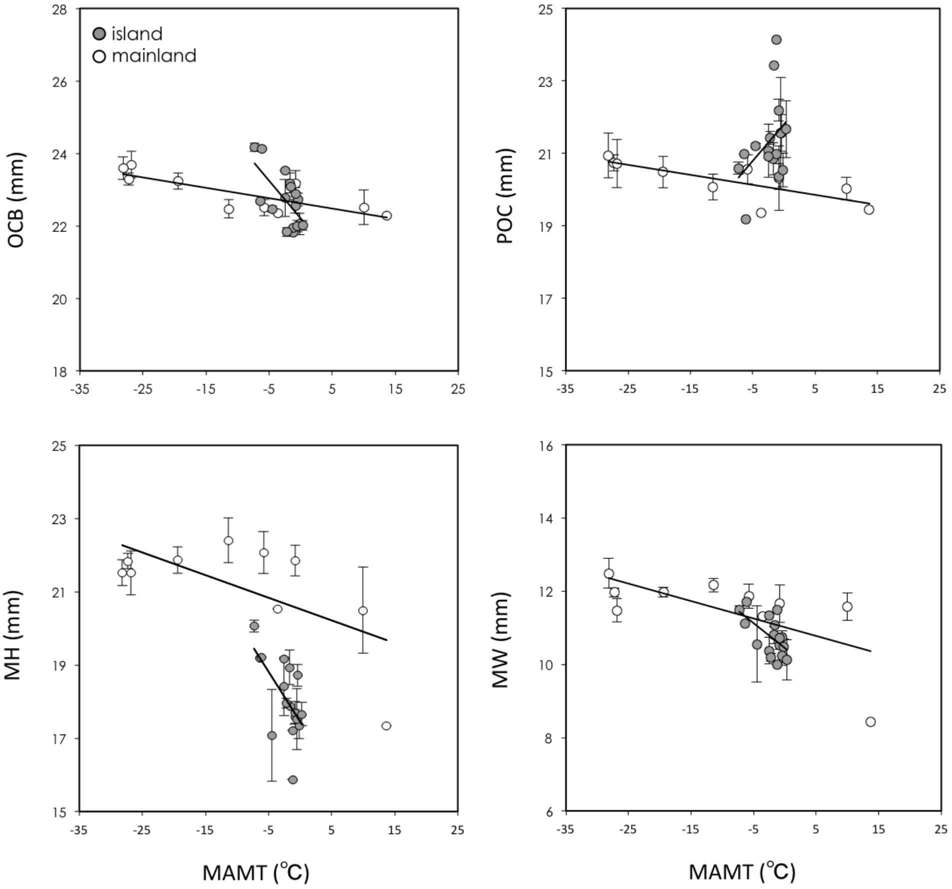


Fig. 4. Size variation of the four skull measurements (mm) with MAMT (x-axis) of each island and mainland population. Regression lines showed with significant influence of interaction with the land type.

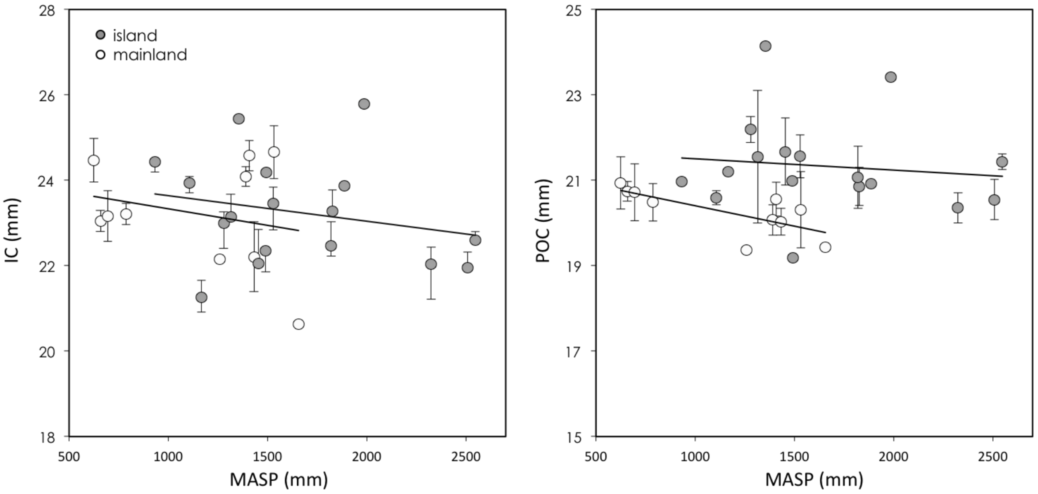


Fig. 5. Size variation of IC and POC with MASP (x-axis) of each mainland (white circle) and island (grey circle) population. Regression lines showed with significant influence of interaction with the land type.

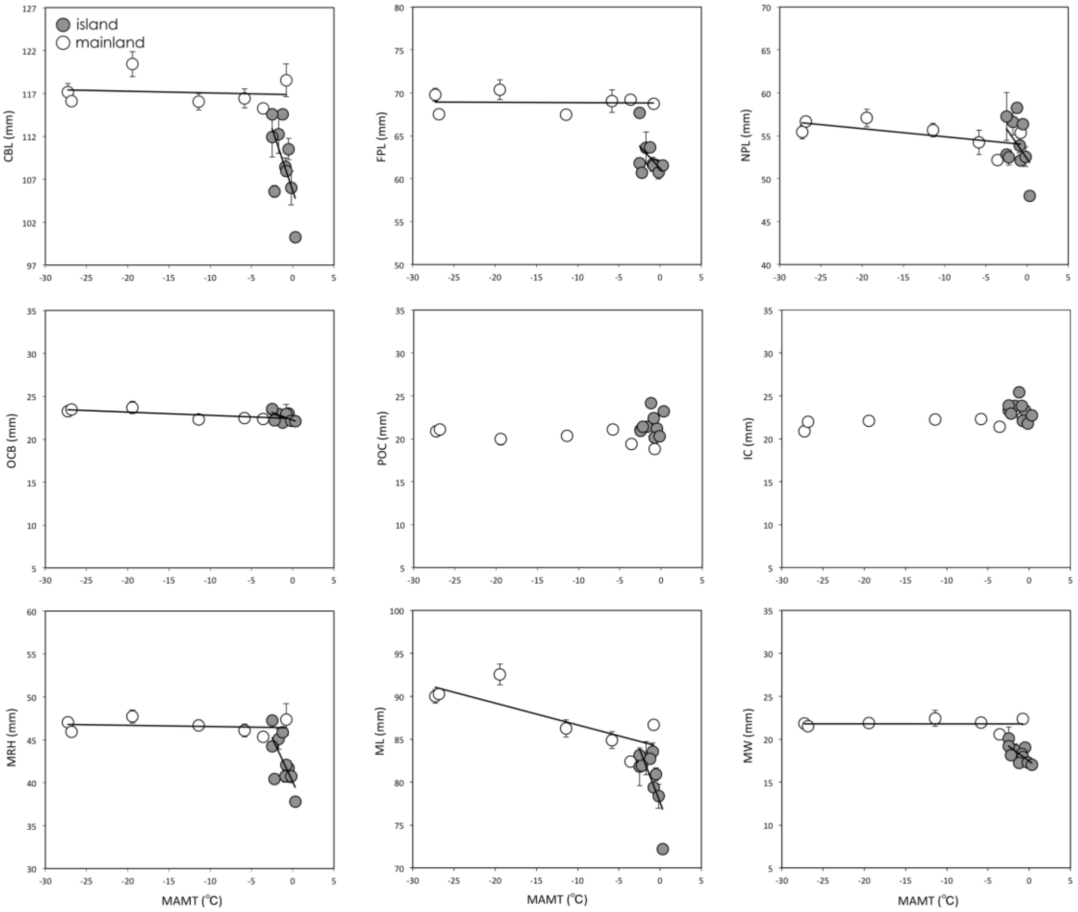


Fig. 6. Size variation of nine skull measurements with MAMT (x-axis) of each mainland (white circle) and island (grey circle) population in male raccoon dogs. Regression lines showed with significant influence of interaction with the land type.

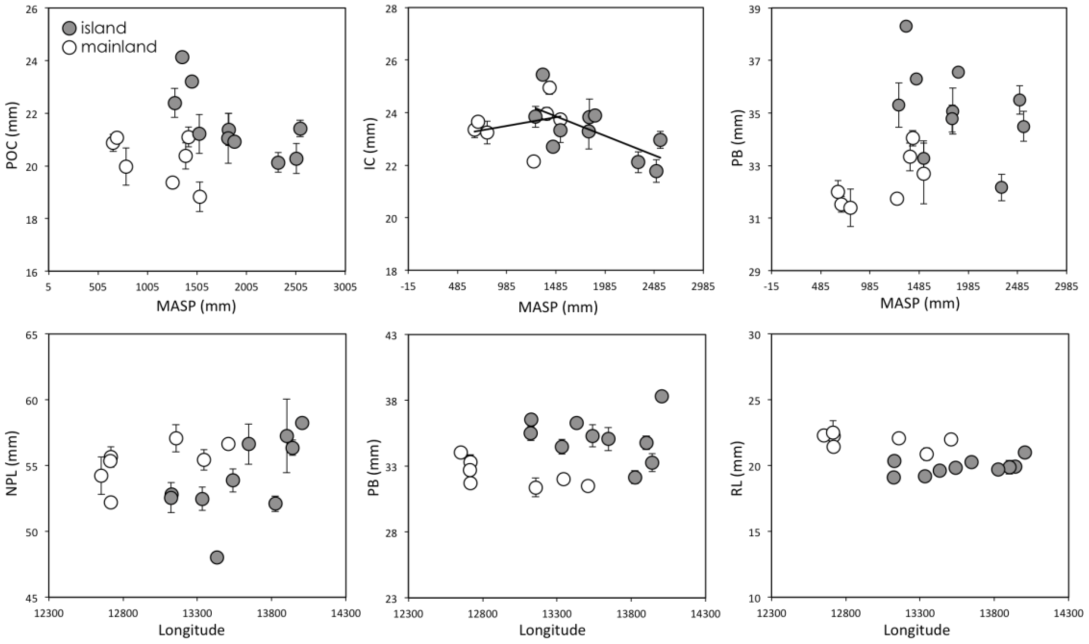


Fig. 7. Size variation of six skull measurements with MASP (upper) and longitude (lower) as x-axis of each mainland (white circle) and island (grey circle) population in male raccoon dogs. Regression lines showed with significant influence of interaction with the land type.

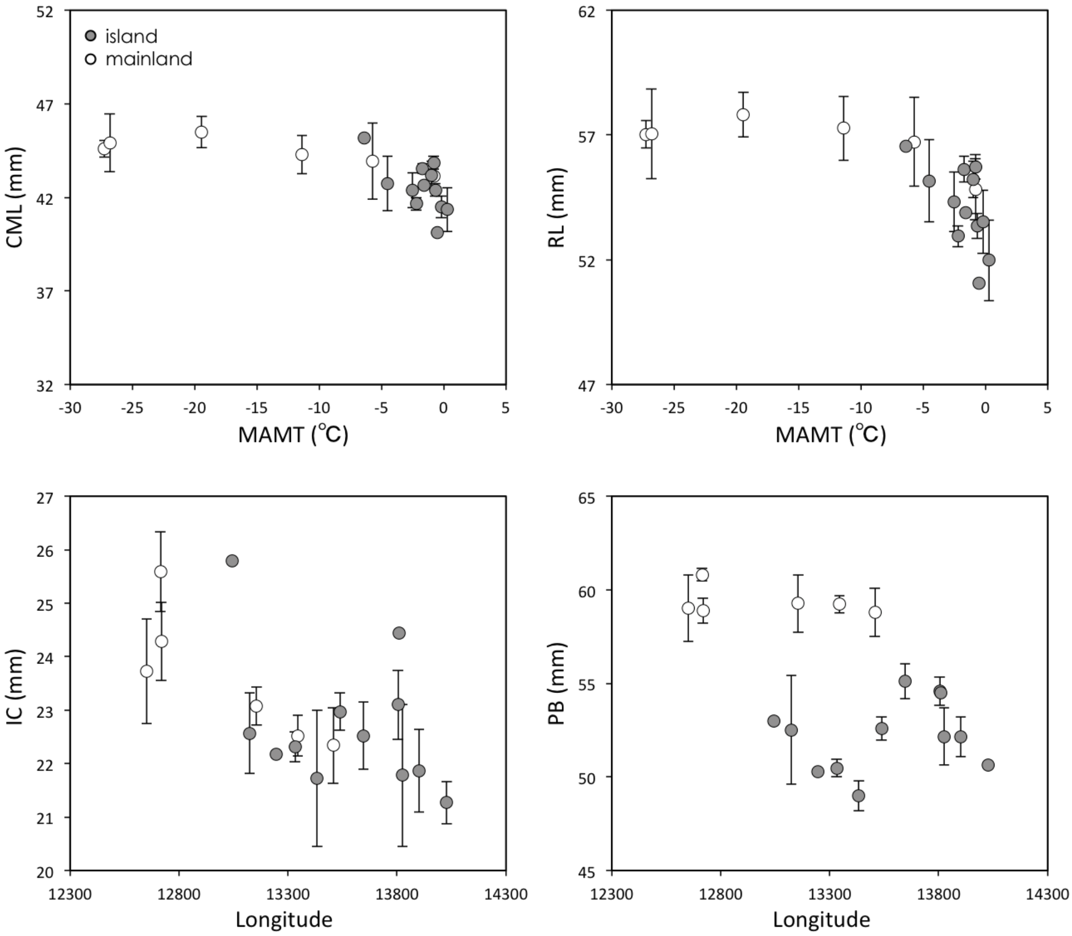


Fig. 8. Size variation of four skull measurements with MAMT (upper) and longitude (lower) as x-axis of each mainland (white circle) and island (grey circle) population in female raccoon dogs.

CHAPTER II.

Evolutionary and biogeographical implications on skull morphology of red foxes in the Northern Hemisphere

II-1. Introduction

Red fox, *Vulpes vulpes* (Linnaeus, 1758) is one of most widely distributed carnivore species in the Northern Hemisphere except for the extreme desert, high latitude of tundra, and the greater part of arctic (Voigt, 1987; Larivière & Pasitschniak-Arts, 1996). Also the successful expansion of introduced red foxes has been observed in Australia in 1800s (Kinnear, Sumner & Onus, 2002). This species is ecological generalist with great dispersal capacity and a high adaptability (Nowak, 2005) such as other Holarctic carnivores (e.g., grey wolf and brown bear). Habitats of the red foxes are highly variable ranging from semi-arid desert to southern tundra and they are observed from lowland to the line of perennial snow according to the food availability (Stroganov, 1962).

Red foxes have heavily polymorphic characteristics. Based on regional morphological characteristics, this species is classified into 43-45 subspecies with poor ecological difference (Larivière & Pasitschniak-Arts, 1996; Heptner *et al*., 1998). Phylogeographic relationship of this species is not completely solved; especially populations of Middle East and East Asia are most problematic. However, historical distribution of red foxes on a continental scale has been deeply discussed heretofore. Red fox is derived from the Old World (Kurtén & Anderson, 1980; Ginsberg, 1999) and its geographic origin is estimated as Middle East (southwest Anatolia of Turkey: Szuma, 2008), North Africa (de Bonis *et al*., 2007; Szuma, 2008) or China (Kurtén, 1968) based on the fossil records of early Pleistocene stage. In North America, fossil evidence of earliest putative red fox in Alaska of the Illinoian glacial age (~300-130kya; Pèwè & Hopkins, 1967) and confirmed specimens of Sangamonian interglacial age (~130-75kya; Kurtén & Anderson, 1980) was found. In Europe, the Iberian and Italian Peninsulas are regarded as possible glacial refugia for red foxes (Sommer & Benecke, 2005). Like grey wolves (Vilà *et al*., 1999; Pilot *et al*., 2014) and brown bears (Valdiosera *et al*., 2007; Davison *et al*., 2011), red foxes of North America and Japan are derived from the Eurasian populations, which had been originally diversified since the Pleistocene (Kutschera *et al*., 2013). Red foxes of Alaska show close relationship with original Eurasian populations on the basis of mitochondrial phylogeographic studies (Aubry *et al*., 2009; Kutschera *et al*., 2013). Phylogeographic pattern of red foxes in East Asia has not been clearly revealed and origin of Japanese populations is still ambiguous (Inoue *et al*., 2007). However, Statham *et al*. (2014) demonstrated obvious genetic differences between the Eurasian and North American Continents described red fox as a model of peripatric speciation by using the microsatellite DNA markers: 11 autosomal loci (corresponding to anonymous canine BAC ends: Sacks & Louie, 2008) and two linked Y-chromosome loci (corresponding to 1-4300 bp of Y-chromosome: Natanaelsson *et al*., 2006). Present study suggested that extant red fox of North America is the daughter species between red foxes from Eurasia and Southern part of North America (Statham *et al*., 2014).

Morphometric studies of this species have been carried out on a regional scale. External morphological differences such as fur color variations and body size variations were described among red fox subspecies from Russian Siberia (Stroganov, 1962).

Heptner *et al*. (1998) described the strong geographic variation related to the geographic races and the amplitude of morphogeographic variation in Russian red fox populations. Geographic variation on the morphological characteristics was reported in some populations of United Kingdom and Ireland (Huson & Page, 1979; Fairley & Bruton, 1984). Among red fox populations of United Kingdom, Italy, Norway, and United States of America (north central and north eastern parts), Cavallini (1995) showed the significant body size disparity with the latitudinal relations at the continental level. The biogeographic patterns throughout the Northern Hemisphere, however, blur with their high dispersal ability and adaptability, especially in Asia.

Red fox is known as dominant species with highly variable density regarding its regional distribution in northern areas (Lloyd, 1980; Stroganov, 1962; Larivière & Pasitschniak-Arts, 1996). Cavallini (1995) referred possible influence of population density on the morphological variation in central Italy and Scotland. They are monogamous, but occasionally polygynyous. Their mating unit consists of single male and two to five females and depends on the population density or sex ratio (Ables, 1969; Macdonald, 1983; Gittleman, 1989). Sexual dimorphism has been observed in the body size (Cavallini, 1995; Macdonald & Reynolds, 2004) and skull morphology (Huson & Page, 1979; Fairley & Bruton, 1984; Lynch. 1996).

Regarding the apparent environmental influences on the red foxes of North America, it was observed that the climate warming after the Last Glaciation (Wisconsinan glaciation) promoted the distribution range as it shrank toward the north (Kurtén & Anderson, 1980). Bartoń & Zalewski (2007) suggested that the further climate warming in Eurasia could increase the expansion of red fox toward the north. Morphotype patterns in teeth of this species are explained by not only the phylogeographical evolutionary trends and historical distribution but also by the environmental factors: longitude, latitude, temperature, and precipitation (Szuma, 2007). Dental polymorphism separated between Eurasian and North American red foxes, except for some populations of Alaska which showed more similar teeth shape to Eurasian populations.

Among canid species, the body size differences are recognized, resulting from different feeding habits such as solitary or social predator (Macdonald & Moehlman, 1982). Red fox is basically omnivorous and preferred food resources biased to small animals especially the small rodents (Larivière & Pasitschniak-Arts, 1996). Red foxes are well suited for preying on small rodents due to its physically adapted morphology of relatively longer hind legs and physiologically developed great sense of precision to find the prey (Macdonald & Reynolds, 2004). Their various food habits on varied habitats may appear as morphological variation. Red foxes of the Iberian Peninsular showed latitudinal and altitudinal diet patterns depending on the seasons (Díaz-Ruiz *et al.*, 2013). Generally, various range of prey size is reflected by environmental factors, and the various diet habit of red fox is not the exception (Gittleman, 1989).

Some red fox populations have been threatened by human effect such as indiscriminating hunting for fur trade and habitat destruction (Won & Smith, 1999; Heydon & Reynolds, 2000). In South Korea, red fox was recognized as extinct species and designated as "endangered species I" (Ministry of the Environment of Korea, 2005).

Although the fox hunting was prohibited in 1965, indiscriminate hunting for the fur and heavy use of rodenticide (potassium cyanide: KCN) for the pest control were the main reasons for the extinction of Korean red fox (Won & Smith, 1999; An, 2009). In addition to Korean red fox, other many carnivore species such as Siberian tiger (*Panthera tigris altaica*), leopard (*Panthera pardus orientalis*), lynx (*Lynx lynx*), brown bear (*Ursus arctos lasiotus*), Asiatic black bear (*Ursus thibetanus ussuriensis*), dhole (*Cuon alpinus*), and gray wolf (*Canis lupus chanco*) become extinct in South Korea due to the over-exploitation since the early 1900's (Won & Smith, 1999). It is difficult to understand the ecological status before the extermination of those extinct species as well as Korean red fox.

Ecological characteristics of distribution ranges are important factors that influence morphological adaptation. Significant skull morphological variation is found not only in general dimensions but also in proportions (Heptner *et al*., 1998). Phylogenetic studies demonstrated previous dispersal of the red fox since the Quaternary era (e.g., Kutschera *et al*., 2013) and explain the process of formation of current broad distribution of this species in the Northern Hemisphere. This high natal habitat-biased dispersal might result in the clinal morphological pattern in the red fox. Therefore, it could be important to understand morphological evolutionary patterns, which are affected by environmental determinants in the red foxes.

What evolutionary factors influenced skull morphological variation of red foxes across the Northern Hemisphere? In order to demonstrate environmental influences on morphogeographic patterns within continent (Eurasia or North America), between continents (Eurasia and North America), and between the continent and adjacent islands, I examined four environmental determinants based on the following hypotheses;

1. Morphogeographic pattern of red fox in Northern Hemisphere might be reflected by the effect of phylogenetic constraints. Phylogenetic effect is crucial for understanding patterns of morphological evolution to the adaptive significance (Wainwright & Reilly, 1994). Possible influence of genetic differentiation on the morphological difference is discussed in the red fox (Cavallini, 1995; Szuma, 2007). Geographic origin of red fox is thought to be North Africa or China based on the fossil records (e.g., Kurtén, 1968). As first step to understand morphological adaptation, evolutionary correlation is demonstrated by comparing morphological characteristics of red fox populations with their phylogenetic relationships. Especially, I compared morphologeographic variation with phylogeographic pattern between the Eurasian and North American Continents.

2. Morphogeographic differences in the skull characteristics might be explained by the clinal variation. Clinal patterns reflect environmental gradients as adaptational responses by ecological pressures (Endler, 1977; Avise, 2000). Gradual differences of red foxes might be observed especially in a large geographic scale due to the gradual selection pressures during their expansion. To test cline's rule in the cranial variation, allometric analysis is conducted and geographic gradients are compared with the morphological characteristics of the red foxes in the Northern Hemisphere.

3. Skull morphological variation of red fox may show specific geographic pattern influenced by climatic differences due to their various habitats across the Northern

Hemisphere. Climatic differences lead indirectly to an effect on the morphological patterns (Caumul & Polly, 2005). According to the Szuma (2007), dental polymorphism explained different geographic patterns between two continents, Eurasia and North America, due to the different climatic influences. Previous studies showed that the red foxes occurring in restricted regions conform to Bergmann's rule in the body size (Rosenzweig, 1968; Davis, 1981; Cavallini, 1995; Frafjord & Stevy, 1998) and skull morphology (Dayan *et al.*, 1989). Therefore, I tested Bergmann's rule, which is most closely related ecogeographic rule with the climatic factors, temperature and humidity.

4. Various habitat types with the extensive vegetational differences might affect the skull morphological variation pattern. Food size of red fox might be closely affected by vegetational difference as other omnivorous carnivore species such as Malagasay civet (*Fossa fossa*) (Albignac, 1972), African lion (*Panthera leo*) (Guggisburg, 1975), black-backed jackal (*Canis mesomelas*) and side-striped jackal (*Canis adustus*) (Moehlman, 1983), and strictly carnivorous carnivore species such as leopard (*Panthera pardus),* jaguar (*Panthera onca*), tiger (*Panthera tigris*), and mountain lion (*Felis concolor*) (Gittleman, 1984). Strong seasonal biases in their varied diets also indicate that the skull morphological characteristics of red fox must be impacted by the vegetational differences. However, specific ecomorphological patterns related to diets in a large scale have not yet been intensively focused. By demonstrating influence of vegetational difference on the craniometric variation, more precise understanding on the morphological adaptation related to food availability could be expected.

Throughout this study, I will demonstrate whether the morphological characteristics adapted to particular environmental conditions accompany the evolutionary pathway of red foxes. This challenging study will contribute to resolve its historic and ecological biogeography.

II-2. Materials and methods

Geographic sampling and measurements

A total of 800 skull specimens of adult red foxes from the natural ranges of the Northern Hemisphere were used for this study (Fig. 1 and Table 1). All specimens are deposited in Institute of Zoology, Chinese Academy of Science, Beijing, China; Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary; Hokkaido Institute of Public Health, Sapporo, Japan; Laboratory of Mammalogy, Zoological Institute Russian Academy of Sciences, Saint-Petersburg, Russia; National Museum of Nature and Science, Tokyo, Japan; Smithsonian Institution National Museum of Natural History, Washington D.C., United States of America (USA); Spanish National Research Council, Madrid, Spain; Swedish Museum of Natural History, Stockholm, Sweden. Adult specimens that have no age information were determined by full eruption of dentition and completely closed basal suture. I referred to the definitions of Von den Driesch (1976) to select 17 cranium and six mandible measurements (Fig. 2 and Table 2). Craniomandibular characteristics were obtained using vernier calipers (NTD12-15PMX 573-621, Mitutoyo; E-LSM 20B, KANON) to the nearest 0.01 mm.

Selection of ecological factors

To assess the correlation between morphogeographic patterns and ecological factors for testing the hypotheses 2 and 3, factors in respect of geographic gradients that showed possible influence on morphological variation in the previous researches were sorted. I selected latitude based on a) the studies on the body and skull size reduction from north to south (Rosenzweig, 1968; Dayan *et al.*, 1989; Cavallini, 1995; Heptner *et al.*, 1998); b) the expected dispersal direction from the original population in North America is from south to north (Kurtén, 1968; de Bonis *et al.*, 2007; Statham *et al.*, 2014). Also, longitude was chosen as another geographic factor according to the previous observation on the correlation with the teeth morphology (Szuma, 2007). As the other geographic factors, I included altitude (m) that showed relationships with the body size (Cavallini, 1995) and skull size (Yom-tov, Yom-tov & Zachos, 2013).

Climatic factors were selected to test their effect on craniometric variation as explained in hypothesis 3. Environmental temperature and humidity are often related to body size with in the homeothermic animals (e.g., Bergmann, 1847). To identify what characteristics of temperature influenced on morphological variation, mean annual minimum temperature (℃), mean annual temperature (℃), and mean annual maximum temperature (℃) are included as climatic factors. Mean annual sum of precipitation (mm), reflecting environmental humidity, is also selected to test this hypothesis.

Land type and interaction between latitude and land type are included as ecological factors to demonstrate influence of environmental factors on different land types: continent (Eurasia and North America) and island. Geographic and climatic data were derived from the 1981-2010 normal databases of meteorological institution of Russia (Hydrometeorological Centre of Russia), Japan (Japan Meteorological Agency and National centers for Environmental Information National Oceanic), and USA (Atmospheric Administration NOAA of USA).

Continental ecosystems are classified as biomes, specific type of plant community determined by climate, and soil characteristics (Feldhamer *et al.*, 2007). Vegetation difference occasionally indicates the niche difference in some regions (Meng & McKenna, 1998; Andrews & O'Brien, 2000). Skull morphological shape in some mammal species presumed to have been directly effected by the vegetation types (Caumul & Polly, 2005). Major vegetation of the Northern Hemisphere are categorized as five types: A) tropical, B) arid desert or steppe, C) temperate, D) boreal or taiga, and E) arctic tundra (Peel, Finlayson & McMahon, 2007). Of them, B, C, and D were selected as vegetation types that mainly occur throughout the distribution of red fox and used as vegetation factor to test hypothesis 4.

Statistic analyses

1) Skull morphogeographic variation

Morphological variation analyses were conducted based on 13 geographic populations that have gender information (Table 1). Two-way analysis of variance

(ANOVA) was conducted to evaluate the correlation between morphogeographic variation and sexual size dimorphism in the red foxes used in this study. Substantial effect of interaction between sex and population was not observed from the red foxes. Bonferroni correction for multiple comparisons was carried out on the 13 populations. Further analyses were conducted on each data set: total, female, and male red foxes due to the absence of significant interaction effect between sex and population.

Two multivariate analyses were used to determine the skull morphological characteristics that correlated with geographic differences. Principal component analysis (PCA) was conducted based on a variance–covariance matrix to describe multivariate variation among populations (Quinn & Keough, 2002). Stepwise canonical discriminant function analysis (DFA) determined craniometric variation and variables, which contribute to effective discrimination among populations. Both ANOVA and DFA were assessed with PASW Statistics v.18 (IBM Acquires SPSS Inc.). The PCA was applied with PAST v.2.17 (Hammer, Harper & Ryan, 2001).

2) Mantel test

To verify the relation between the morphological variation and phylogenetic variation on geographic difference, mantel test was carried out (Mantel, 1967; Quinn & Keough, 2002). A total of 190 haplotypes of partial mitochondrial DNA cytochrome *b* genes (250 bp) from 10 geographic regions in the Northern Hemisphere (Honshu and Kyushu of Japan, Hokkaido of Japan, East Central Europe, Southwestern Europe, Middle East, Alaska, Western Canada, Eastern Canada and northeastern USA, and

Western USA) were used as genetic data. All sequence data were deposited in Genbank (Table 3). Pairwise genetic distance matrix was calculated with the Kimura-2-parameter method (Kimura, 1980). Mean pairwise morphological differences among populations were quantified as squared Mahalanobis distance matrix. Squared mahalanobis distance was calculated from the pooled within-group covariance matrix based on canonical functions obtained after Canonical Discriminant Function Analysis (DFA) (Marcus, 1990; De Maesschalck, Jouan-Rimbaud & Massart, 2000; Quinn & Keough, 2002). This squared Mahalanobis distances were used in unweighted pair-group method with arithmetic average (UPGMA) cluster analyses to produce dendrograms. To test correlation between morphological and molecular distance matrices, we conducted Mantel test (Mantel, 1967; Quinn & Keough, 2002). Mantel test was performed with PAST v.2.1.7 (Hammer, Harper & Ryan, 2001).

3) Allometric analyses

Allometry was performed by scaling relationships between each skull measurement and condylobasal length (CBL). To compare the allometric relationships among the three land types and the 13 geographic populations, standardized major axis (SMA) regression was used as a line-fitting method (Warton *et al*., 2006). The allometric relationship of each variable to the condylobasal length (CBL) was examined with the logarithmic expression of the equation of allometry: $\log y = \alpha \log x + \log b$; where y is any of the measured skull variables, log b is the y-intercept or constant of normalization and (b is the constant term of the power growth function), α is the slope of the line or coefficient of allometry, and x is the CBL (Alexander, 1985). Likelihood ratio test was used for a common SMA slope to compare the slopes of mainland and island populations (Warton & Weber, 2002; Warton *et al*., 2006). Allometric analysis was conducted using R (R Development Core Team, 2013).

4) General linear mixed effect models

The presence of multicollinearity among these environmental factors could lead to misinterpretation of the importance of these environmental variables for size and shape variation of populations. Due to the inadequate correlation for detecting collinearity, stepwise variance inflation factor (VIF) selection was employed as follows (Quinn & Keough, 2002);

$$\mathrm{VIF} = \frac{1}{1-r^2}$$

r^2 is coefficient of determination which from regression model of a particular variable as the response variable against the remaining variables as predictors. VIF and tolerance ($1-r^2$) are estimated as an indicator of collinearity. Latitude, longitude, altitude, mean annual minimum temperature (MAMT), and mean annual sum of precipitation (MASP) are selected as independent variables by multicollinearity test. To identify the subset of variables that best predicted variation in skull morphological characteristics, we conducted general linear mixed effect models (GLMMs) constructed in the nlme package (Pinheiro *et al*., 2013). Skull measurements were used as the response variable examined against eight ecological factors as fixed effects. The 16 potential models including categorical variables were compared and most appropriate grouping of seven environmental factors; latitude, longitude, altitude, MAMT, MASP, land types (Palearctic, Nearctic, or Island), sexes (female or male), interactions between latitude and land type, interactions between longitude and land type, and vegetation (B, C, or D) were determined by model selection based on Akaike's information criterion (AIC) (Anderson *et al.*, 1998). Totally 180 geographic zones (Fig. 1) depending on the longitude and latitude are included as a random effect. Morphological data of skull specimens with exact locality information are used for GLMMs. Here, I used R (R Development Core Team, 2013) for GLMMs.

II-3. Results

Morphogeographic variation

1) Two-way ANOVA

Two-way ANOVA showed a significant effect of sex and population in most of skull morphological characteristics: skull length (TL, BL, CBL, and FPL), nasal length (NPL and NL), skull width (ZB), skull height (SH), breadth of orbital constriction (IC), muzzle length (CML and RL), muzzle width (RB), length of buccal cavity (PL), and mandible size (LT, JT, MH, ML, and MW) (Table 4). As noted above, interaction between sex and population was not found. Therefore, morphogeographic variations among 13 populations and sexual size dimorphism were separately considered in this study. According to the post hoc multiple comparisons, specific morphogeographic patterns showed larger skull measurements (all measurements that showed significant difference among 13 populations) in northern populations of either the Eurasian and North American Continents. Among the continental populations, red foxes from western part of China (CW), western Europe (EW), and Middle East (ME) were significantly smaller in skull length (TL, BL, and CBL), nasal length (NPL and NL), skull width (ZB), muzzle length (CML and RL), and mandible length (LT) compared to northern populations from Russia (RE and RW), central east Asia, East Central Europe (ECE), Alaska (NA), and western Canada (NW). In other measurements on skull length (BL and CBL), nasal length (NPL), breadth of orbital constriction (IC), muzzle width (RB), length of buccal cavity (PL), and mandible size (JT, MH, ML, and MW), similar pattern was observed only in European and North American populations except for the East Asian populations. Only in European populations, geographic difference between northern and southern red foxes were showed in FPL. In North America, marked morphogeographic variation between northern [Alaskan (NA) and western Canada (NW)] and southern [eastern Canada and northeastern USA (NE); western and southern USA (NS)] populations was observed from most of characteristics excluding skull height (SH), breadth of orbital constriction (POC and PB), occiput (OCB), skull width (MD), and mandible size (ACP). Among the skull characteristics, IC and JT described relatively weak pattern in North American populations due to the ambiguous difference of western Canadian population. Only the skull height (SH) explained significant difference between Eurasian and North American Continents in this analysis. However, this morphological pattern did not accord with that of Island populations. I found the relatively larger skull measurements (especially in the skull width (ZB and MD), muzzle size (RB), length of buccal cavity (PL), and mandible size (ML and MW) in Honshu and Kyushu populations (JH) than in Hokkaido one (JA). Significant morphological variation was observed, especially in the PL and MH in the result of multiple comparisons, indicating relatively smaller skull measurements in Hokkaido red foxes compared with other Japanese populations.

Sexual size dimorphism was observed from all cranial and mandible measurements except for the POC. Most populations showed larger values in male red foxes, but East Asian populations (western China in PB; Eastern part of Russia in OCB; Central East Asia in MD) and North American populations (Alaskan population in SH and PL; western and southern USA population in IC; eastern Canadian and northeastern USA population in JT) were larger in female red foxes. However, distant sexual dimorphism pattern did not affect to the morphogeographic difference among 13 populations of all individuals.

2) Principal component analysis

PCA is conducted on 13populations of total (aPCA), females (fPCA), and males (mPCA) data sets. The results of PCA1 yielded two possible axes of principal components (PCs). The aPC1 strongly accounted for 84.25% of total variation (Table 5) in most measurements except for skull height (SH) and breadth of orbital constriction (POC). Skull length (TL, BL, and CBL), nasal length (NPL), muzzle (CML and RL), length of buccal cavity (PL), and mandible (LT and ML) had large and positive coefficients, showing strong correlation with aPC1. Although aPC1 did not clearly separate red fox populations, tendency of slight distinctions between several northern (RE, RW, ECE, NA, and NW) and southern populations (WE, ME, NE, and NS) were recognized (Fig. 3(a)). Japanese populations, JA and JH tend to have close relationships with the southern populations by the aPC1. The aPC2 (4.15% of variation) was dominated by breadth of orbital constriction (PB) with positive variables. There was no clear geographic difference except for the Japanese populations, showing one-sided scatter plot by aPC2. Similar to aPC1, aPC2 tended to separate northern populations and southern populations.

Result of fPCA showed analogous morphogeographic patterns to that of aPCA. Relatively clear geographic difference was observed from fPCA (Fig. 3(b) and (c)). The fPC1 (83.46%) separated continental red foxes into northern and southern populations by the skull length (TL, BL, and CBL), nasal length (NPL), muzzle (CML and RL), length of buccal cavity (PL), and mandible (LT and ML) (Table 5). The island red foxes (Japanese populations) were separated from continental populations by breadth of orbital constriction (POC and PB) in fPC2 (4.66%) (Fig. 3(b)).

By contrast, scattered individuals and unclear geographic patterns were observed in the result of mPCA (Fig. 3(c)). The mPC1 (81.88%) slightly explained separation of continental red foxes between northern and southern populations, especially from the skull length (TL, BL, and CBL), muzzle length (CML, and RL), length of buccal cavity

(PL), and mandible length (ML). No clear geographic pattern was observed from the mPC2 (4.75%).

3) Stepwise canonical discriminant function analysis

Results of DFA using skull morphometric data of 13 red fox populations are shown in Fig. 4. Also, I carried out DFA for three data sets: total (aDFA), females (fDFA), and males (mDFA). In the result of aDFA, 16 skull measurements: skull length (TL), skull width (ZB and MD), nasal length (NL and NPL), skull height (SH), muzzle size (RB, CML, and RL), length of buccal cavity (PL), breadth of orbital constriction (IC and POC), occiput (OCB), and mandible (LT, JT, and MH) demonstrated clear geographic separation, especially between Palearctic and Nearctic populations (Table 6). First discriminant function, aDF1 (eigenvalue = 2.82, total variance = 52.4%) against second discriminant function, aDF2 (eigenvalue = 0.98, total variance = 18.3%) and canonical discriminant function of aDFA among 13 red fox populations explained difference among Eurasian, Japanese, and North American populations (Fig. 4(a)). Most important variables separated the Palearctic and Nearctic populations with large standard canonical discriminant coefficient were SH, TL, and RL for aDF1. Japanese populations were segregated from other Eurasian red foxes with ZB, NPL, NL, CML, and RL that have relatively large coefficients for aDF2. Although it is not clear, RB for aDF3 (eigenvalue = 0.51, total variance = 9.4%) and RL for aDF4 (eigenvalue = 0.37, total variance = 6.9%) slightly separated populations into three land types: Eurasia, Japanese Islands, and North America.

Results of fDFA and mDFA yielded similar geographic separation to aDFA, but morphological variation was observed in different characteristics (Fig. 4(b) and (c); Table 6). In fDFA, Palearctic Nearctic and Japanese populations of females were separated with high explanation of fDF1 (eigenvalue = 2.94, total variance = 76.2%) that strongly affected by SH and TL. The fDF2 (eigenvalue = 0.68, total variance = 17.5%) segregated Japanese females from Eurasian females with TL, NL, and PB that have large coefficient values (Fig. 4(b)).

Although male red foxes between Palearctic and Nearctic populations indicated less morphological differences than those females showed, 10 skull traits: skull width (ZB), nasal length (NPL and NL), skull height (SH), muzzle (RB, CML, and RL), occiput (OCB), and mandible (LT and JT) supported mDFA (Table 6). In mDFA (Fig. 4(c)), the mDF1 (eigenvalue = 2.68, total variance = 53.8%) that separated Palearctic and Nearctic males were strongly explained by SH and NPL with larger coefficients. Compared with the female red foxes, in male red foxes I found that Japanese populations were more clearly separated from Eurasian populations with strong coefficients of ZB, NPL, NL, CML, and RL for mDF2 (eigenvalue = 0.96, total variance = 19.3 %). RB for mDF3 (eigenvalue = 0.51, total variance = 10.3 %) displayed a difference between ECE and EW weakly.

Phylogenetic relationship of red fox in Northern Hemisphere

Phylogenetic tree was obtained using 190 haplotypes of partial mitochondrial DNA cytochrome *b* genes (250 bp). Phylogenetic pattern of red foxes used in this study showed paraphyletic relationship with not high bootstrap values (Fig. 5) as previously described (Teacher, Thomas & Barns, 2011; Kutschera *et al*., 2013). Although red foxes did not show clear separation by geographic differences, three clades are recognized: *clade i*, *ii*, and *iii* (Fig. 5). *Clade i* consists of Holarctic populations except for the eastern Canadian and northeastern USA population. Some haplotypes from Middle East, Asia, Honshu and Kyushu of Japan, and Europe showed close relationships with Nearctic haplotypes. Those haplotypes did not form the monophyletic groups according to the geographic regions, and were scattered across the *clade i*. Nearctic red foxes excluding western Canadian population are placed in *clade ii.* Possible ancestor group was located in basal clade (*clade iii*) of phylogenetic tree and included Middle East, Europe, and Hokkaido populations. Basal haplotypes of Middle East populations were from southwestern Anatolian part (which called as Asia Minor) and northern part of Turkey. It was essentially consistent with the result of previous studies (e.g., Szuma, 2008; İbiş, Tez & Özcan, 2014). The other haplotypes from Turkey were located in *clade i* with other Holarctic haplotypes. These separations among Holarctic, Nearctic, and basal clades coincided with the previous studies (Aubry *et al*., 2009; Statham *et al*., 2014).

Genetic distances among 10 geographic populations were calculated to compare with the morphological distance (Table 7). Following this genetic distance, phylogenetic tree was reconstructed by cluster analysis (Fig. 6A). Ten populations were divided into two clades; the Nearctic red foxes excluding Alaskan population and the Palearctic red foxes and Alaskan population. Genetic distance between these two clades was 2.35%. In Nearctic clade, eastern Canadian and northeastern USA population and western USA population had relatively closer genetic distance (0.80%) than western Canadian population with 1.90% of mean genetic distance. Palearctic clade includes other 7 populations, which were divided into three groups: Middle East, Hokkaido, and the other populations. Populations of Asia and East Central Europe were most closely related to each other with 0.6% of genetic distance. Largest genetic distance (2.71%) between populations of western Canada and Hokkaido and second largest genetic distance (2.67%) between populations of western Canada and Middle East were observed.

Environmental influences on the morphogeographic variation

1) Phylogenetic influences

Significant correlation between phylogenetic pattern and skull morphological variation was found in the result of Mantel test (r = 0.50, *P* = 0.00). Both pairwise genetic and morphological distances among 10 populations were shown in Table 7. Mahalanobis distance on skull morphological data strongly reflected both phylogenetic and geographic differences. It was observed between Nearctic and Palearctic populations with 25.16 of average squared Mahalanobis distance (Table 7 and Fig. 6B). Nearctic clade separated as two subclades, northwestern and southeastern populations. Most close morphological distance was observed between eastern Canada and northeastern USA population and western and southern USA population with 1.96 of squared Mahalanobis distance. Palearctic clade also showed morphological separation between two subclades: Honshu and Kyushu population and other Palearctic populations (13.32 of average squared Mahalanobis distance). Population of Honshu and Kyushu was morphologically different both from other Palearctic populations and Nearctic populations except for Hokkaido population. In Palearctic populations, red foxes of Eurasian Continent (Asia, western Europe, East Central Europe, and Middle East) showed close morphological relation each other. Comparatively close morphological distance was observed between East Central European red foxes and western European red foxes among the Palearctic populations. Population of western Europe also had close morphological relationship with that of Middle East. Hokkaido red foxes had similar morphological distance with other red fox populations of Palearctic except for the Middle East population that was closely related (7.79 of squared Mahalanobis distance) to Hokkaido population. In the Palearctic populations, red foxes of Asia and Middle East had relatively close morphological relationship with Nearctic populations especially with the eastern Canada and northeastern USA population. In addition, Asian population was morphologically close to Alaskan population within the Nearctic populations.

Although population of Alaska did not genetically clustered to other Nearctic populations, reconstricted phylogenetic tree showed two major clades consisting of Nearctic and Palearctic populations, respectively (1.56% of average genetic distance; Fig. 6). While genetic distance between North American (excluding Alaska) and Eurasian populations was relatively larger (2.41%), Alaskan population was genetically closer to the Eurasian populations with 1.43% of genetic distance and most closely related to Asian population with 1.13% of genetic distance. Genetic distance between Alaskan and other North American populations were 2.00%. Close genetic and morphological relationship was observed between eastern Canada and northeastern USA population and western and southern USA population. Different from the morphological tree, reconstructed phylogenetic tree showed that the Middle East and Hokkaido populations clustered separately within the Palearctic clade. In Eurasian populations, Asian population was most closely related to East Central Europe population with 0.64% of genetic distance. Similar to the phylogeographic tree (Fig. 5), the demdrogram of phylogenetic tree demonstrated paraphyletic relationships of Holarctic red foxes with weak phylogeographic structure (Fig. 6A).

2) Allometric scaling of skull morphology in red fox populations

Allometric patterns were demonstrated among and within 13 red fox populations (Table 8). Different allometric relationships were observed on the basis of skull characteristics with various specific patterns. Among all populations, allometric slope of each population was estimated as equal in all skull measurements except for NPL, NL, and RL. In BL, FPL, OCB, and UT, common slope regarding all individuals was isometric to CBL. In the skull length measurements, FPL was isometric to CBL in all populations and TL and BL were positively allometric to CBL in ECE and NE populations, respectively. Only SH showed negative allometric relation in all red fox populations except for two Eurasian populations (ME and CW). Muzzle length (CML and RL) had similar isometric pattern among populations except for JH population that showed negative allometry. The RE and CEA populations were positively allometric only in CML. However, muzzle width (RB) was positively allometric in 6 populations [Russian (RW), Middle East (ME), European (ECE and WE), North American (NE), and Japanese (JA)] and was isometric in other populations. Length of buccal cavity (PL) was isometric except for ECE, WE, JA, and NE populations, which were positively allometric. Positive allometric relation in majority populations was estimated in the nasal length (NPL and NL), although JH and NW populations showed isometric relation. Breadth of orbital constriction (IC and PB) also indicated positive allometry, but POC had no significant allometric relationship in each population except for CW (positive allometric) populations. In skull width, MD was positively allometric in most of populations excluding CW, NW, NA, and JH, while ZB was mostly isometry except for RE, ECE, EW, and NA with positive allometric patterns. Mandible measurements (ACP, JT, MH, ML, and MW) showed identical pattern of positive allometric in ECE, EW, NE, NS, and JA populations. Otherwise, LT was isometric in all populations except for EW with negatively allometric patterns.

3) Influences of factors on geographic gradients

Skull morphological variation of red fox populations was significantly dependent on various environmental determinants. One of most strongly affected environmental factors was geographic gradient. Although longitude did not show significant correlation with the skull measurements except for the nasal length, latitude and altitude showed specific geographic patterns among the red foxes. Morphological patterns influenced by latitude on land types were observed in skull width (ZB and MD), muzzle width (RB), breadth of orbital constriction (POC), occiput (OCB), length of buccal cavity (PL), and mandible (JT, MH, and MW). These characteristics excluding RB and JT showed significantly different influence of latitude on land types. Positive tendency concerning latitude and continental populations (Eurasia and North America) was found in ZB, OCB, IC, and MD. POC also showed different influences of latitude between continents and islands, although slight negative relation was observed from North American populations. Opposite tendency to continental populations was observed from the island populations with negative relation in most skull measurements (Fig. 7). This tendency was stronger in males than in females. Occiput (OCB) and length of buccal cavity (PL) showed different relationship with the latitude between continental and island male red foxes (Fig. 7). In skull length (BL and CBL), muzzle width (RB), skull width (MD), muzzle length (RL), and mandible size (MH, ML, and MW), significant interaction between latitude and land type was observed only between males of North America and islands. Most of skull measurements of males (except for FPL, IC, and MD) and females (except for BL, FPL, SH, IC, PB, OCB, MD, CML, and MH) were significantly different on land types. Longitudinal difference was not related to male red fox but female red fox. Skull length, nasal length, length of buccal cavity, muzzle length, and mandible length showed longitudinal difference in the female with no interaction with the land types. Only jaw thickness (JT) was significantly influenced by the interactions between land types and latitude or land types and longitude in female. Although there were no clear differences in slope among land types on latitude, the larger JT was found in the lower longitude in North American populations and the smaller JT was detected in the higher longitude in Eurasian and island populations. Skull height (SH) and occiput (OCB) were larger at higher altitude (Fig. 8). This positive correlation with the altitude was observed from the SH of females. No significant influence of altitude was found in male red foxes.

4) Influences of climatic factors

Climatic factors also influenced on morphological patterns (Figs. 9 and 10). Negative correlation with MAMT in most skull measurements (excluding BL, NPL, MD, ACP, JT, ML, and MW) of continental populations explains that the skull size of red foxes across the Northern Hemisphere is generally larger in lower MAMT (Fig. 9). However, MAMT was positively related to the red fox of Japanese Islands. This result coincides with the different influence of latitude on two land types, continents and islands. Positively influenced MASP was observed on skull width (MD), but skull height (SH) was negatively influenced by MASP (Fig. 10). Although female red foxes did not show the significant correlation with the climatic factors, male red foxes showed significant relation to the MAMT and MASP. ZB, RB, and PL were negatively influenced by MAMT. SH and MD were influenced by MASP with negative and positive relations, respectively.

4) Influences of vegetation differences

Skull measurements also showed significant patterns explained by vegetation difference. Red foxes of vegetation C (temperate forests) had different morphological characteristics from that of B and D in skull length (BL) and mandible size (ML) (Fig. 11). FPL was different only between B and C, while other skull length (TL and CBL), breadth of orbital constriction (IC), length of buccal cavity (PL), and muzzle length (CML and RL) were different only between C and D. Individuals from vegetation D (boreal or taiga) were significantly larger in nasal length (NPL and NL).

Morphological difference was related to the land type from most of skull characteristics excluding skull length (FPL and TL), breadth of orbital constriction (IC and PB), skull width (MD), muzzle length (CML), and mandible (LT). However, no clear tendency among land types were observed except for the POC and JT, which were significantly larger in North American red foxes than in island one.

Female red foxes strongly correlated with the vegetation condition in most characteristics except for PB, MH, and MW. Skull length (TL and CBL), nasal length (NPL and NL), muzzle size (RB, CML, and RL), length of buccal cavity (PL), and mandible size (ACP and ML) of individuals from vegetation D were significantly different compared to vegetation B and C. Morphological distinction between the red foxes from vegetation B and D were found in the skull length (FPL), occiput (OCB), skull width (ZB and MD), and mandible size (LT and JT). Male red foxes have relatively lower correlations with the vegetation difference. NL, FPL, PL, and ML were significantly related to the vegetation but only PL and ML showed specific patterns which differ between vegetation B and C.

II-4. Discussion

Phylogeographic influence on the skull morphological distances

In the present study, skull morphological variation of Holarctic red foxes was strongly influenced by geographic differences. The skull morphogeographic patterns were essentially similar to dental polymorphism (Szuma, 2007) and body size differences (Cavallini, 1995), which were detected previously at large geographic scale. Skull height could be important indicator to distinguish Palearctic red foxes from Nearctic red foxes. The SH of Nearctic red foxes was larger than that of Palearctic red foxes. The results of DFA showed similar tendency for the SH, TL and RL, which divided red foxes into two continental populations with smaller SH, larger TL, and larger RL of Palearctic populations. Also, the SH separated Hokkaido population from other continental populations with smallest value.

The results of Mantel test on the skull morphological variation showed coincide patterns with the genetic relationship except for some populations. Although only 190 haplotypes of cyt *b* were used in this analysis, reconstructed phylogenetic tree was concurred with previous mtDNA phylogeographic studies (e.g., Kutschera *et al*., 2013). Among ten red fox populations, reconstructed phylogenetic tree showed paraphyletic relationship, but two major clades were observed by cluster analysis using phylogenetic distance (Fig. 6A): one with the North American populations excluding Alaskan population and the other with the Palearctic and Alaskan populations. Alaskan population was genetically close to other Eurasian red foxes. Morphological distance separated red fox populations as two major clades: Nearctic and Palearctic populations (Fig. 6B). This result indicates phylogenetic influence of skull morphological pattern on red fox populations except for the Alaskan population. Morphological separation of Alaskan population from Palearctic populations could be interpreted as strong influence of geographic difference.

This compositive effect of phylogenetic and geographic difference on the morphological distance was also observed within each major clade. In Nearctic clade, morphological separation between northwestern and southeastern populations reflected geographic difference. Populations in the Palearctic clade also showed different patterns between genetic and morphological distance. Interestingly, genetic distance fell the Middle East and Hokkaido populations into each different subclade and other Eurasian populations were clustered with Alaskan populations. In the Palearctic clade, phylogenetic tree demonstrated less related Middle East and Hokkaido populations to other Palearctic populations especially Western European and Honshu and Kyushu populations. Although Hokkaido and Middle East populations were clustered with other Eurasian populations in the morphological relationship, relatively less close relationship with other Eurasian populations in the Palearctic clade was coincide with the phylogenetic pattern. Different from the phylogenetic pattern, Honshu and Kyushu population was clustered as one subclade and separated from other Palearctic populations. Reconstructed phylogenetic tree demonstrated genetically intimate relationships among Asian, western European, and East Central European populations, which showed close genetic relationships one another in one major clade (Fig. 6A). This pattern was strongly reflected in the Morphological tree. Although Honshu and Kyushu population was not showed close morphological relation to other Eurasian populations, relatively close to Asian population both genetically and morphologically. Likewise, Alaskan population was separated morphologically from Palearctic populations but was relatively close to Asian population. Judging from these results, it is difficult to interpret the relationship within the Palearctic red foxes between genetic and morphological distances. Paraphyletic relationship of red foxes in phylogenetic analyses might be one of the reasons for the different pattern of Palearctic red foxes with the morphological distance, which showed complex effect of genetic and geographic difference. Intermingled Nearctic and Palearctic lineages with unique haplotypes to either continent are interpreted as the consequences of recent biogeographic events such as repeated migration and gene flow between and within the continents (Teacher *et al*., 2011; Kutschera *et al*., 2013). Close morphological relationship between Asia and Japanese Islands or Alaska could be explained by the geographic proximity and multiple migrations during glacial periods. Between phylogenetic and morphological distances, the similar pattern with the significant interrelationship was observed despite of different relationship among some populations. This indicate the morphological and phylogenetic difference of inter-clades is more powerful than that of intra-clades.

In the present study, close morphological relation among populations was not explained by only the adjacent geographic regions, but by the similar environmental condition between geographically separated regions. Intimate relationship between Middle East and western European populations were not observed in the phylogenetic pattern, but the morphological pattern. This result might be the convergent evolution of skull morphology due to the similar environmental condition between Middle East and western Europe. Morphological affinity among different carnivore species in similar environmental condition was observed (Meloro, Clauss & Raia, 2015). The Middle East population was morphologically closer to western European population than East Central European population. Similar climatic condition of Middle East to western Europe rather than East Central Europe is expected due to the analogous geographic gradient (latitude) and vegetation type (B, arid desert or steppe: Peel *et al.*, 2007). Therefore, this assumption is reasonable to explain morphological affinity of those two populations.

Similar to the population structure based on nuclear markers (Statham *et al.*, 2014), clear geographic difference in red fox populations was found in the skull morphological distances. Statham *et al.* (2014) suggested that current phylogenetic pattern of Holarctic red foxes are reciprocally monophyly, according to the central to the genealogical species concept, which means two groups come from different species if they form each distinct monophyletic group (De Quieroz, 2007; Hudson & Coyne, 2002). Middle East red foxes are recognized as the original population, since this population has Palearctic basal mtDNA haplotypes (Statham *et al.*, 2014). Although reciprocally monophyletic clade with strong bootstrap support was not found in this study, three major clades were observed: *i*) Holarctic clade including haplotypes from all 10 populations except for the eastern Canadian and northeastern USA population; *ii*) North America clade excluding western Canada; *iii*) Palearctic basal clade including Middle East, Hokkaido, and Europe

(Fig. 5). Two major clades of morphological distance, Nearctic and Palearctic populations might be comparable to *clade ii* and combined *clade i* and *iii* of phylogenetic tree (Fig. 5), respectively. Skull length, skull height, skull width, and occiput are generally recognized as measurements related to body size. Correlation between those skull measurements and brain size has been demonstrated from ancestral (Finarelli & Flynn, 2006.) and extant (Finarelli, 2006) carnivore species. In the red fox, however, skull height showed unique morphogeographic difference compared to skull length, skull width, and occiput. The skull height seems to be closely related to the geographic and genetic insulation among three land types. This could be explained by the significant difference of SH between northern and southern population within each continent.

There are two red fox subspecies on Japan, *V. v. japonica* (Gray, 1868) of southern islands (Honshu and Kyushu) and *V. v. schrencki* (e.g., Imaizumi, 1960) of northern island (Hokkaido) which have independent migration history (Inoue *et al.*, 2007; Kutschera *et al.*, 2013). According to the phylogeographic events, Honshu and Kyushu red foxes colonized from southern part of Asian continent after Late Pleistocene (LP) or Last Glacial Maximum (LGM), while Hokkaido red foxes colonized twice from northern part of Asian continent during the end of LP to LGM and LGM to Holocene (Kutschera *et al.*, 2013). In the present study, reconstructed phylogenetic tree showed distant relationship between two Japanese populations. However, the genetic relationships were different from the morphological relationships. Honshu and Kyushu populations were morphologically close to western Canadian and western and southern

USA, but genetically close to Asian and Alaskan populations. Hokkaido population was closely related to the population of eastern Canada and northeastern USA morphologically, but genetically close to Asian and European populations. Previous reports on morphological differences between southern and northern island populations of Japan demonstrated smaller skull size (Takeuchi, 1995; Oishi *et al*., 2010) and larger body size (Imaizumi, 1960; Uraguchi, 2009) on the Hokkaido red foxes. Disparity of phylogenetic and morphological status of Hokkaido red foxes supports the previous phylogeographic interpretation of basal position by the consequences of random homoplasy according to the independent evolution (İbiş *et al*., 2014).

Result of present study indicates different morphological pattern of Japanese populations, compared with the continental populations closely related to the different environmental effect of islands. In comparison with the morphogeographic variation, the results of Mantel test could be interpreted as the different influence on each skull characteristics. Therefore, present study accepts hypothesis 1: morphogeographic pattern of red foxes on the Northern Hemisphere reflected by the effect of phylogenetic constraints. However, morphological variation of Holarctic red foxes might be the outcome of environmental adjustments.

Morphogeographic pattern explained by allometric relation and influence of geographic gradients

Clinal variation is the result of 1) secondary contact between populations that diverged in isolation, 2) primary contact with a gradient of selection pressures among populations along a transect, and 3) selection against hybrid individuals from partially isolated populations, or 4) mixing of individuals from two currently isolated populations (Feldhamer *et al*., 2007). However, discriminating distinct patterns of clinal variation is extremely difficult as described in the previous studies (Owen & Baker, 2001). In red fox, close genetic relationship between Eurasian population and Alaskan and western Canadian populations with apparent morphometric cline across northern part of North America (Alaska through the south eastern Canada) has been argued by isolation with distance within a single lineage (Churcher, 1959) and secondary contact and incomplete mixing of two distinct lineages (Aubry *et al*., 2009).

The present study partly accepts hypothesis 2: morphogeographic differences in the skull characteristics related to body size explained by the clinal variation. However, other skull components reflect ecological effects and evolutionary status. Allometric analyses were not explained by clinal variation in the Holarctic red foxes. Most characteristics indicated equivalent slope among all 13 populations. Skull length, occipital condyle breadth, and length of tooth low were isometric to CBL. Although common slope did not show the isometric pattern, skull width was also mostly isometric within each population. Skull length, skull width, and occipital condyle breadth are recognized as measurements related to the body size (Creighton, 1980; Martin, 1980; Yom-Tov, 2007). In the result of GLMM, skull width and occipital condyle breadth were larger on continental populations, but smaller on island populations at higher latitude. In the Holarctic region, especially red foxes occurring in northern area of Nearctic region have larger cranium and mandible. Latitudinal gradient is sometimes found in species diversity that is on the decrease from the equator toward the poles (Feldhamer *et al*., 2007). In the higher latitude, colder and drier climate is observed. It has been reported that body size or body mass of red foxes follow the Bergmann's rule (Rosenzweig, 1968; Cavallini, 1995). Latitude is one of the main impacts that explain Bergmann's rule as Mayr (1956) pointed out. According to the present results, latitudinal influence on body size of red foxes occurring in the Eurasian and North American Continents explain the conformity to Bergmann's rule.

The different scaling exponents on each measurement of skull explained by functional division of each component of cranium. (Van der Klaauw, 1946). Although Szuma (2007) reported the different dental morphotype frequency on the geographic gradients between two continental populations, it was not observed in the present study. Unlike the skull length, the length of tooth low and muzzle length were relatively small in western Europe and southern islands of Japan. Nasal length was longer when the skull length was longer except southern islands of Japan. Nasal length and muzzle length are directly proportional to each other in the carnivore species (Wroe & Milne, 2007). Different food availability might affect relatively short muzzle length of red fox in warmer condition. Various environmental conditions such as latitudinal difference affect dietary composition and diversity (Hill & Dunbar, 2002). According to the Rosenzweig (1995), diverse feeding habits have been observed at lower latitudes where the potential prey richness is greater. This tendency was observed in the medium-sized carnivores that have the variations in the distribution of potential prey species across biogeographical region (Eurasian otter (*Lutra lurra*): Clavero *et al*., 2003; wildcat (*Felis sylvestris Schreber*): Lozano, Moleón & Virgós, 2006).

Similar pattern was observed in the northern populations of continents (Russia, Alaska, and central east Asia) with larger skull size and southern island populations of Japan had relatively short mandible length, jaw thickness, and mandible ramus. The relatively short muzzle and mandible length of red fox might be influenced by strong bite force (Radinsky, 1981a, 1981b & 1982). Although the opposite result was observed from the narrower mandible ramus, which indicates narrower attachment site of masseter muscle (for mastication) and temporal muscle (for biting force), this might be the consequence of relatively small mandible size.

In the present study, I did not find proper reason for the different geographic influences on gender, but relatively strong influence of latitude on male red fox might be related to the different home range size. Previous studies on the red fox showed that the average home range size and dispersal distance were smaller in female compared to those of male in USA (Storm, 1965) and in UK (Kolb, 1986). Relatively broader expansion and territory might be related to strong adaptation to climate difference in the male. Unlike the continental populations, island populations had larger skull characteristics in southern locality, which is the opposite influence on the latitude. Japanese red foxes showed coincident allometric pattern with continental red foxes in the characteristics related to body size. However, of Japanese populations, the significantly different skull characteristics from adjacent continental populations (RF, CEA, and CW) were observed only in the JA, Hokkaido population. Hokkaido population was significantly smaller in most characteristics except for the TL, NPL, PC, PB, OCB, MD, ACP, and MH. The present study suggests that the island dwarfism is expected in the Hokkaido red foxes. Body size difference in carnivores occurring in islands has been demonstrated at the species level such as least weasel (Dayan & Simberloff, 1998), small Indian mongoose (Simberloff *et al.*, 2000), raccoon dog (Kim *et al.*, 2015), and brown bear (Matsubayashi *et al.*, 2016). Also, this has been shown at the family level of carnivores (Lomolino, 2005; Lyras, van der Geer & Rook, 2010), and are explained by island rule. Major determinants of body size on island are resource limitation, interspecific competition, and insular predation (Lomolino, 1985). Previous studies on food habit of red fox revealed carnivorous tendency of Hokkaido populations compared to other populations of southern islands. During severe winter, Hokkaido red foxes mainly forage animal resources, particularly small mammals and fish (Abe, 1975). Tsukada (1997) reported higher fibrous contents in the feces of red foxes from southern islands compared to those of the red foxes from northern island. This carnivorous tendency of Hokkaido population did not appear in the current research on the craniodental variation (Oishi *et al.*, 2010). Present study also observed proportionally shorter upper and lower tooth low in the red foxes of southern islands and longer nasal length in the red foxes of Hokkaido, which is characteristic contrary to carnivorous tendency of Hokkaido red foxes. However, proportionally longer postorbital process (difference between POC and PB) could be interpreted by positive allometry of PB and this result support carnivorous tendency of Hokkaido red foxes. One of the possible reasons for island dwarfism of Hokkaido red fox may be the competition for the limited prey resources with the other middle sized carnivorous species such as raccoon dog, least weasel, stoat, and sable in the island environment. In the cold season, the food niche of the omnivorous mammals such as the raccoon dog and red fox, which used to have a broader habitat niche (Baltrūnaitė, 2006), narrowed due to the limited food items. Possible strong carnivorous tendency of Hokkaido population was observed from the craniodental variation in the raccoon dogs (Kim *et al*., 2015). Previous studies discussed on the competition between red foxes and raccoon dogs or mustelids due to the food niche overlap (Storch, Lindström & de Jounge, 1990; Baltrūnaitė, 2006). Although, the mustelids occasionally are killed (Weber *et al*., 2002) or eaten by red fox (Latham, 1952; Drew, 1995; Ohdachi *et al*., 2009) and raccoon dog avoids competition with red fox due to its dormancy during winter, the direct and indirect competition between red fox and other middle-sized carnivores have been suggested by ecologists (Serafini & Lovari, 1993; Macdonald & Reynolds, 2004).

Skull height showed apparently different allometric pattern from other characteristics. Apart from the Middle East and Western China, most red fox populations showed negative relationship with CBL in skull height. In skull dimensional measurements, skull height is one of characteristics related to brain size and also has correlation with the body size (Radinsky, 1967; Jerison, 1970; Lande, 1979). Therefore, significantly different skull height could be interpreted as different brain size proportionally to the skull size. As mentioned above, Middle East and Western China are recognized as basal populations of red foxes. Their skull height (brain size) did not show negative allometry to skull length (body size) and this could be one of evidences for original population. Isometric responses to CBL and larger value of northward population in the skull measurements related to body size might reflect clinal variation in skull length, width, and OCB. However, negative allometry between body weight and brain weight has been extensively reported on interspecific scaling of brain size (Jerison, 1973; Gould, 1975; Bauchot, 1978). Radinsky (1981a) observed negative allometric scaling in the neurocranial components, bulla volume and orbit area related to skull length and body weight, although non-neurocranial components scaled isometrically or positive allometry. Therefore, allometric scaling of skull height on CBL might indicate the relationship of neurocranial component to body size of red fox. Comparative brain size within the order Carnivora revealed increased brain size with more complex foraging strategy involved in selection for rapid prey detection and consumption in interspecific level (Gittleman, 1986). However, there is limitation to apply hypotheses invoking ecological characteristics when intraspecific scaling is considered (Martin & Harvey, 1985). Further study on the neurocranial components related to body size and body weight of taxonomic group size of individual species will be necessary to understand the taxonomic level in the red fox.

Longitudinal influence was observed in nasal length with significantly different influence on the Japanese red foxes with drastically negative effects. However, this geographic pattern seems to be explained by indirect influence of latitudinal effect because Japanese Islands locate diagonally from northeastern island (Hokkaido) to southwestern island (Kyushu). Female red foxes showed slightly positive slope with longitude. This means that female red foxes of Hokkaido have slightly larger skull length, nasal length, muzzle length, jaw thickness, and mandible length.

Altitudinal gradient was observed in the measurements of skull height and occipital condyle breadth with slightly positive correlations but the slope showed gradual ascent toward higher altitude (Fig. 8). This positive tendency of body size might be explained by the Bergmann's rule in the continental red foxes. Similar pattern between altitude and measurements related to body size was also observed in the Japanese populations. However, this result cannot be interpreted as the conformity to Bergmann's rule of island populations, because latitude was negatively influenced on the Japanese red foxes. Previous studies reported on the critical assumptions behind Bergmann's rule that simple latitude-temperature correlation is confused in the low latitude ranges of high mountains (Gittleman, 1989). In Japanese populations, positive influence of altitude may be explained by relatively lower average altitude (421.3 m) of Hokkaido population with regard to the average altitude (893 m) of Honshu and Kyushu populations. In the red foxes, expansion to the north due to the climate change was reported in the North America (Kurtén & Anderson, 1980). Red foxes of southern Japanese Islands might prefer the high mountain region to avoid the hot weather. To demonstrate detailed altitudinal variation, it is necessary to compare with the data from more altitudinal ranges within the similar latitudinal ranges that cover the southern Japanese Islands.

Morphological adaptation influenced by climatic variation

In the present study, hypothesis 3, ‘skull morphological variation of red fox may show specific geographic pattern influenced by climatic differences’ is accepted, demonstrating strong influence of Bergmann’s rule and Island effect. Climate had definitely an influence on the skull characteristics. Especially the skull size (skull length and skull width), skull height, muzzle length, mandible height, and orbital constriction were larger in cold condition. This result is another evidence to support influence of Bergmann’s rule in the red fox as previously reported in the restricted populations: Scotland (Kolb, 1978), Saharo-Arabian region (Dayan *et al*., 1989), UK, Ireland, Norway, Italy, USA, and Australia (Cavallini, 1995), Norway (Frafjord & Stevy, 1998), and Saudi Arabia (Macdonald *et al*., 1999). Temperature and food habit do not seem to be closely related to each other, due to the similar morphological patterns observed in the skull components related bite force and muzzle size. Both male and female body size were larger in low temperature, but this tendency was more clearly observed in the other skull components (skull height, nasal length, and muzzle length) of male red fox.

The other possible reason of dwarfism on Hokkaido red foxes might be less effect of climate. Although the present study did not observe the interaction between MAMT and land types, only island populations of Japan were positively related to MAMT because of larger skull characteristics of southern islands populations. This result indicates stronger influence of other island specific environmental conditions such as food availability on Japanese red foxes than that of Bergmann’s rule.

In humid environmental condition, small skull height and wide buccal cavity were observed in the red fox. Morphological difference of skull height might be closely related to another phenomenon according to Bergmann's rule, although other measurements related to body size did not show specific pattern on the MASP. Generally, cold air is extremely dry due to the capacity of air to hold moisture decreases with decreasing temperature. Bartholomew & Dawson (1953) found that when the body size and weight increase, the respiratory water loss decreases in the avian species occurring in desert. Therefore, larger sized birds would be at an advantage in arid areas (Hamilton, 1958). It is suggested as aridity effect, modified Bergmann's rule (Hamilton, 1961). This aridity effect might be applied to the red foxes. In comparison with the mesic foxes, desert foxes have smaller body size with lower total evaporate water loss, which was roughly explained by resource limitation hypothesis (natural selection favors smaller individuals in a resource-limited environment, especially during periods of severe food shortage) (Williams *et al*., 2004). According to the Yom-tov & Nix (1986), precipitation often has a close correlation with body size than temperature, when prey size variation and food availability are influenced. Higher MASP (above 1,500 mm) was mostly observed in the southern islands of Japan (Honshu and Kyushu), western Europe, and Middle East populations. Therefore, red foxes from those humid zones might be strongly affected by high precipitation, which results in high plant primary production and food availability to animals (Yom-Tov & Geffen, 2006).

Morphological adaptation influenced by different vegetation

Morphological variation on vegetation difference was observed especially between vegetations C (temperate forest) and D (boreal or taiga) in skull length, nasal length, muzzle length, and mandible length. Red fox of vegetations B (arid desert or steppe) and C showed different morphological patterns from the vegetation D. Significantly smaller nasal length, muzzle width, and mandible length were estimated from the populations of vegetation B compared to those of populations of vegetation D. Although it is the lowest humidity of vegetation B, the relatively warmer climate of B than D seems to be closely related to the morphological variation on vegetation difference. However, variation of BL, FPL, and ML between B and C does not seem to be reflected by temperature differences, but by the humidity. Boreal forests (or taiga) are distributed throughout the high northern latitudes of the Northern Hemisphere. Since the boreal forests have cold and arid environmental condition, relatively larger skull of vegetation D implies the influence of Bergmann’s rule in the red fox. Although interpretation on the result of morphological influence by different vegetation was quite different from expected prey size difference, strong influence of Bergmann’s rule might be the inevitable consequence because the distribution of vegetation is controlled by climatic factors (Krebs, 2009). Therefore, the present results accept hypothesis 4, extensive vegetation differences affected the skull morphological variation pattern, although the specific pattern reflecting prey size or food availability on vegetation difference was not shown.

Smallest values of skull measurements were observed in the red foxes of vegetation C (Fig. 11). Here, I suggest three presumable reasons for the smaller morphological characteristics of red fox in temperate forests. Firstly, rodents play an important role in the temperate forests as one of most abundant prey (Jedrzejewska &

Jedrzejewski, 1998). Red fox may be adapted to small sized prey in the temperate forests. Secondly, it might be the result of interspecific competition caused by high carnivore species richness in temperate forests. Studies on the trophic status of carnivores observed that abundant potential food resources such as fruits and arthropods in tropical forest did not affect the carnivore species richness (Ray & Sunquist, 2001). Therefore, correlation with other species that have similar ecological niches than prey-pradator relationships might be more affected to the vegetational difference. Thirdly, intraspecific competition might occur due to the high population density in the temperate forest. In terrestrial carnivores, larger home range area is one of the factors to affect larger body size, probably due to the higher home range productivity (Lindstedt, Miller & Buskirk, 1986). Species in higher latitudes occupy a broader range of habitat due to the higher tolerance of climatic variability and this phenomenon is called Rapoport's rule (Krebs, 2009). Red fox of vegetation C probably occupies narrower territory than vegetation D. Also, the preference of diverse vegetation and avoidance of large homogeneous tracts were reported in the red fox despite of its various habitat range (Ables, 1975). Based on this, red fox might prefer vegetation C to B or D. Smaller skull size could be reflected by the intensive intraspecific competition in vegetation C with high population density. Lastly, highest humidity among three vegetation types might be related to the smaller size of red fox in temperate forest. The presumption is related to Bergmann's rule that explains the smaller body size in high temperature and high humidity. Relation between vegetation type and the morphological variation of middle-sized carnivore species have been poorly studied. This present study might offer a clue to interpret morphological convergence in sympatric species affected by similar ecological pressure.

The present study firstly demonstrated the skull morphogeographic pattern adapted to each different peripheral environment. The various morphological patterns indicated different adaptation responses on its environmental influences: vegetation difference, climatic difference, geographic gradient, and geographic difference. This study could contribute toward understanding ecomorphological adaptations and its historical biogeography of terrestrial carnivorous species.

Table 1. Locality and number of red fox skull specimens used in this study.

Ecozone	Land types	Country	Locality	Population ID (abbreviation)	Female	Male	All
Palearctic	Eurasian Continent	China	Western part	Western part of China (CW)	5	11	45
			Northeastern part	Central east Asia (CEA)	15	26	47
		Mongolia					
		Russia	Southern half of Far East				
			Northern part of Far East	Eastern part of Russia (RE)	5	23	58
			Central Siberia				
			Ural	Western part of Russia (RW)	15	25	78
			European Russia				
			Kalmykya	Middle East (ME)	14	21	47
			Caucasus				
		Turkmenistan					
		Tadjikistan					
		Uzbekistan					
		Kyrgyzstan					
		Iran					
		Pakistan					
		Yemen					
		Hungary		East Central Europe (ECE)	59	64	132
		Germany					
		Poland					
		Romania					
		Serbia					
		Slovakia					
		Belarus					
		Ukraine					
		Spain		Western Europe (EW)	44	65	144
	Japanese Islands	Japan	Hokkaido	Hokkaido of Japan (JA)	40	43	83
			Honshu	Honshu and Kyushu of Japan (JH)	4	6	15
			Kyushu				
Nearctic	North America	Canada	Western Canada	Western Canada (NW)	4	3	28
			Eastern Canada	Eastern Canada and northeastern USA (NE)	12	22	52
		United States of America (USA)	Northeastern USA				
			Western and southern USA	Western and southern USA (NS)	21	17	47
			Alaska	Alaska (NA)	3	5	24
		Total			241	331	800

Table 2. Cranium and mandible measurements with abbreviation and definition.

	Abbreviation	Definition
Cranium	NPL	nasal+premaxillary
	NL	nasal length
	FPL	frontal to parietal length
	SH	height of cranium (meeting point between sagittal crest and interparietal process to the bottom most of tympanic bullar in the right side of skull)
	BL	basal length
	RB	rostrum breadth
	POC	postorbital constriction
	IC	interorbital constriction
	PB	postorbital breadth
	OCB	occipital condyle breadth
	ZB	zygomatic breadth
	TL	total length
	PL	palatal length
	MD	distance between first upper molars
	CBL	condylobasal length
	CML	length of the upper canine to upper molar tooth low
	RL	rostrum length (prosthion to the caudal edge of 2nd upper molar)
Mandible	ACP	from angular process to coronoid process
	LT	length of the lower tooth row
	JT	jaw thickness (transversal width of the lower jaw beneath the front of first lower molar)
	JH	mandible height in front of first lower molar
	ML	mandible length
	MW	mandible width

Table 3. Sequence information for all individuals analyzed in this study. Geographic areas, the number of haplotypes of cytochrome *b* (250 bp), GenBank accession numbers and the corresponding references are provided.

Population	Number of haplotypes	Accession number	Reference
Asia (East Asia and eastern Siberia)	30	JX013646-JX013648; JN652603-JN652618, JN711443; KF387633; FJ830765-FJ830767, FJ830770, FJ830773; AB292752, AB292754	Yu *et al*. (2012); Aubry *et al*. (2009); Inoue *et al*. (2007)
Honshu and Kyushu of Japan	6	AB292756-AB292760,	Inoue *et al*. (2007)
Hokkaido of Japan	17	AB292741-AB292751, AB292753, AB292755, AB292761-AB292765	
Middle East	10	KM068792-KM068801	İbiş, Tez & Özcan, (2014)
Western Europe	48	KM225298-KM225303; AJ441335; Z80957-Z80975-Z80983, Z80985-Z80987, Z80994; AY586403-AY586406l; AF028158; EF689058-EF689062,	Palomares *et al*. (2002); Frati *et al*. (1998); Wayne *et al*. (1997); Fernandes *et al*. (2008)
East Central Europe	62	Z80984-Z80993; KM657039-KM657043; EF064207-EF064220; FJ830768, FJ830769; JN232446, JN232448, JN232449, JN232451-JN232472, JN232474-JN232479	Frati *et al*. (1998); Volkmann *et al*. (2015); Perrine *et al*. (2007); Aubry *et al*. (2009); Teacher, Thomas & Barnes (2011)
Alaska	6	FJ830761, FJ830762, FJ830771, FJ830774-FJ830776	Aubry *et al*. (2009)
Western Canada	2	FJ830756, FJ830772	Aubry *et al*. (2009)
Eastern Canada and northeastern USA	3	FJ830759, FJ8307560; HM590011	Aubry *et al*. (2009); Statham *et al*. (2012)
Western and southern USA	6	KM657038; GU004541; FJ830757, FJ830758, FJ830763, FJ830764	Volkmann *et al*. (2015); Sacks *et al*. (2010); Aubry *et al*. (2009)
Total	190		

Table 4. Results of two-way ANOVA on 13 red fox populations for testing effect of sex and population.

Source		Mean Square	*F*	*P*
TL	sex	2268.88	53.69	*
	population	586.08	13.87	*
	sex × population	38.38	0.91	ns
BL	sex	1758.13	50.61	*
	population	465.64	13.40	*
	sex × population	37.13	1.07	ns
CBL	sex	1913.33	53.08	*
	population	457.40	12.69	*
	sex × population	38.87	1.08	ns
ZB	sex	589.94	42.02	*
	population	247.44	17.63	*
	sex × population	19.55	1.39	ns
FPL	sex	571.46	41.81	*
	population	139.74	10.22	*
	sex × population	13.37	0.98	ns
NPL	sex	661.77	38.80	*
	population	227.66	13.35	*
	sex × population	12.38	0.73	ns
NL	sex	468.53	32.43	*
	population	155.44	10.76	*
	sex × population	7.87	0.54	ns
SH	sex	66.51	23.21	*
	population	156.33	54.55	*
	sex × population	3.32	1.16	ns
RB	sex	71.59	38.12	*
	population	37.19	19.80	*
	sex × population	1.53	0.81	ns
POC	sex	4.36	1.84	NS
	population	21.52	9.06	*
	sex × population	3.07	1.29	ns
IC	sex	86.76	25.79	*
	population	63.06	18.75	*
	sex × population	4.78	1.42	ns
PB	sex	156.58	18.20	*
	population	102.40	11.90	*
	sex × population	6.41	0.74	ns
OCB	sex	25.35	20.86	*
	population	17.85	14.69	*
	sex × population	1.46	1.20	ns
PL	sex	458.58	34.08	*
	population	211.78	15.74	*
	sex × population	13.35	0.99	ns
MD	sex	25.52	14.36	*
	population	20.21	11.37	*
	sex × population	1.76	0.99	ns
CML	sex	299.99	35.51	*
	population	72.09	8.53	*
	sex × population	10.88	1.29	ns
RL	sex	436.00	40.85	*
	population	130.73	12.25	*
	sex × population	11.24	1.05	ns
ACP	sex	196.44	41.77	*
	population	44.87	9.54	*
	sex × population	5.85	1.24	ns
LT	sex	467.96	43.12	*
	population	99.69	9.19	*
	sex × population	11.65	1.07	ns
JT	sex	3.69	15.87	*
	population	2.92	12.54	*
	sex × population	0.21	0.90	ns
MH	sex	32.23	26.36	*
	population	6.04	4.94	*
	sex × population	1.63	1.33	ns
ML	sex	1365.12	51.86	*
	population	299.38	11.37	*
	sex × population	26.76	1.02	ns
MW	sex	21.87	19.60	*
	population	14.82	13.28	*
	sex × population	0.72	0.64	ns

* *P*<0.001; Sex × population, indicates the interaction between these two independent variables; NS, indicates no significant variation; ns, indicates no significant interaction between two variables

Table 5. Factor loadings of PCA for comparing cranial and mandibular measurements from total red fox populations (aPCA), female red fox populations (fPCA), and male red fox populations (mPCA). Variables with high loading are marked with bold type.

	aPCA		fPCA		mPCA	
Variable	aPC1	aPC2	fPC1	fPC2	mPC1	mPC2
TL	**0.99**	-0.01	**0.99**	-0.04	**0.99**	0.00
BL	**0.99**	-0.03	**0.99**	-0.05	**0.99**	-0.01
CBL	**0.99**	-0.04	**0.99**	-0.07	**0.99**	-0.02
ZB	0.81	0.46	0.79	0.51	0.79	0.45
FPL	0.84	0.28	**0.80**	0.08	0.82	0.39
NPL	**0.90**	-0.27	**0.91**	-0.11	0.88	-0.37
NL	0.83	-0.34	**0.82**	-0.17	0.80	-0.43
SH	0.47	0.22	0.42	0.38	0.45	0.13
RB	0.77	0.28	0.75	0.32	0.74	0.24
POC	-0.08	0.31	-0.06	**0.61**	-0.11	0.08
IC	0.75	0.38	0.72	0.47	0.73	0.29
PB	0.59	**0.55**	0.51	**0.75**	0.58	0.42
OCB	0.70	0.05	0.65	0.07	0.68	0.07
PL	**0.95**	-0.04	**0.96**	-0.04	**0.94**	-0.03
MD	0.59	0.34	0.53	0.40	0.60	0.30
CML	**0.93**	-0.11	**0.94**	-0.10	**0.92**	-0.09
RL	**0.96**	-0.10	**0.97**	-0.08	**0.95**	-0.10
ACP	0.83	0.08	**0.83**	0.01	0.79	0.10
LT	**0.92**	-0.10	**0.92**	-0.05	**0.90**	-0.12
JT	0.59	0.28	0.58	0.25	0.55	0.29
MH	0.75	0.16	0.76	0.18	0.70	0.17
ML	**0.96**	-0.01	**0.98**	-0.03	**0.95**	-0.01
MW	0.73	0.24	0.71	0.25	0.71	0.23
Eigenvalue	319.41	15.73	273.04	15.25	286.37	16.61
Proportion	84.25	4.15	83.46	4.66	81.88	4.75
Cumulative	84.25	88.40	83.46	88.13	81.88	86.63

Table 6. Results of stepwise discriminant function analysis among total red fox populations (aDFA), female red fox populations (fDFA), and male red fox populations (mDFA). At each step the variable that minimizes the overall Wilks' Lambda is entered. Maximum number of steps is 16, 4, and 10, respectively.

aDFA				fDFA				mDFA			
Entered variables	Wilks' Lambda	*F*	*P*	Entered variables	Wilks' Lambda	*F*	*P*	Entered variables	Wilks' Lambda	*F*	*P*
TL	0.49	49.27	*	SH	0.39	29.30	*	SH	0.50	26.54	*
ZB	0.24	48.11	*	TL	0.19	24.43	*	TL	0.25	26.03	*
NPL	0.19	34.04	*	NL	0.15	16.61	*	NL	0.20	18.95	*
NL	0.16	27.27	*	PB	0.12	13.20	*	RB	0.16	15.65	*
SH	0.13	23.17	*					JT	0.12	13.82	*
RB	0.11	20.68	*					NPL	0.10	12.45	*
POC	0.09	19.12	*					ZB	0.08	11.52	*
IC	0.08	17.59	*					LT	0.07	10.82	*
OCB	0.07	16.38	*					UT	0.06	10.20	*
PL	0.06	15.40	*					TL removed	0.06	11.22	*
MD	0.05	14.70	*					RL	0.05	10.63	*
CML	0.05	13.93	*					OCB	0.04	10.02	*
RL	0.04	13.23	*								
LT	0.04	12.62	*								
JT	0.04	12.09	*								
MH	0.03	11.60	*								

* $P<0.05$

Table 7. Pairwise distance matrix of mitochondrial cytochrome *b* gene sequences obtained from Genbank (250 bp; above diagonal) and squared Mahalanobis distance of skull measurements (below diagonal) of ten red fox populations.

Population	1	2	3	4	5	6	7	8	9	10
1. Asia		0.009	0.008	0.006	0.011	0.016	0.017	0.021	0.024	0.022
2. Western Europe	4.37		0.015	0.008	0.016	0.018	0.020	0.025	0.026	0.025
3. Honshu and Kyushu of Japan	12.98	14.30		0.013	0.013	0.021	0.021	0.023	0.025	0.024
4. East Central Europe	3.88	3.02	12.11		0.013	0.016	0.018	0.022	0.024	0.022
5. Alaska	15.67	22.37	35.66	18.76		0.020	0.020	0.020	0.020	0.019
6. Hokkaido of Japan	8.43	8.52	8.51	8.58	33.15		0.023	0.027	0.024	0.025
7. Middle East	6.84	4.02	18.69	5.63	21.42	7.79		0.027	0.025	0.025
8. Western Canada	17.28	25.26	39.77	21.09	2.73	36.88	23.45		0.019	0.019
9. Eastern Canada and northeastern USA	15.64	20.66	33.88	18.90	7.05	27.42	16.40	4.51		0.008
10. Western and southern USA	19.11	23.49	42.24	23.41	6.90	33.61	18.25	4.22	1.96	

Table 8. Results of standardized major axis regression of log skull variables (y) and log CBL (x) allometric relationship in the 13geographic populations of red fox.

	Common slope		RE			RW			ME			ECE			EW			CW		
	among populations	$\alpha \neq 1$	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR	α	β	AR
TL	NS	*	1.01	-0.01	I	1.04	-0.06	I	1.04	-0.07	I	1.08	-0.15	P	1.02	-0.03	I	1.06	-0.12	I
BL	NS	NS	1.04	-0.10	I	1.01	-0.03	I	1.03	-0.08	I	1.01	-0.03	I	1.01	-0.04	I	1.02	-0.05	I
ZB	NS	*	1.27	-0.84	P	1.26	-0.82	I	0.97	-0.20	I	1.16	-0.61	P	1.26	-0.81	P	1.26	-0.82	I
FPL	NS	NS	0.97	-0.18	I	1.18	-0.63	I	0.98	-0.20	I	1.05	-0.35	I	1.00	-0.23	I	1.11	-0.47	I
NPL	*	*	1.57	-1.53	P	1.38	-1.12	P	1.55	-1.49	P	1.48	-1.34	P	1.25	-0.84	P	1.17	-0.69	P
NL	*	*	1.97	-2.49	P	1.83	-2.19	P	1.70	-1.91	P	1.59	-1.67	P	1.57	-1.64	P	1.46	-1.40	P
SH	NS	*	0.68	0.24	N	0.72	0.14	N	0.65	0.30	ns	0.84	-0.11	N	0.69	0.21	N	0.92	-0.27	I
RB	NS	*	1.35	-1.51	I	1.39	-1.62	P	1.41	-1.65	P	1.38	-1.58	P	1.21	-1.23	P	1.19	-1.16	I
POC	NS	*	-1.58	4.77	ns	-2.22	6.15	ns	-1.29	4.10	ns	1.38	-1.62	P	-1.40	4.36	ns	-2.03	5.69	P
IC	NS	*	1.32	-1.35	I	1.23	-1.15	I	1.54	-1.82	I	1.32	-1.34	P	1.26	-1.22	P	1.28	-1.27	I
PB	NS	*	1.57	-1.82	P	2.13	-3.01	ns	2.02	-2.77	ns	2.19	-3.15	P	1.64	-1.97	P	1.90	-2.52	ns
OCB	NS	NS	0.84	-0.38	I	0.82	-0.33	I	1.18	-1.11	I	0.86	-0.43	N	0.89	-0.49	I	0.93	-0.58	I
PL	NS	*	1.05	-0.37	I	1.09	-0.46	I	1.01	-0.28	I	1.16	-0.62	P	1.12	-0.52	P	1.07	-0.43	I
MD	NS	*	1.69	-2.38	P	1.66	-2.30	P	1.93	-2.90	P	1.62	-2.22	P	1.44	-1.82	P	2.12	-3.30	ns
CML	NS	NS	1.23	-0.82	P	1.03	-0.40	I	0.98	-0.29	I	0.99	-0.33	I	0.99	-0.31	I	0.95	-0.23	I
RL	*	*	1.04	-0.33	I	0.98	-0.22	I	0.95	-0.15	I	0.94	-0.13	I	0.94	-0.13	N	0.86	0.03	I
ACP	NS	*	1.24	-1.09	I	1.25	-1.11	I	1.33	-1.28	P	1.40	-1.43	P	1.32	-1.24	P	1.43	-1.48	P
LT	NS	NS	1.08	-0.43	I	0.90	-0.05	I	0.95	-0.16	I	0.97	-0.20	I	0.92	-0.10	N	1.03	-0.34	I
JT	NS	*	1.07	-1.46	ns	1.61	-2.64	P	1.76	-2.95	P	1.68	-2.77	P	1.26	-1.87	P	1.43	-2.21	I
MH	NS	*	2.42	-4.05	P	1.71	-2.55	P	1.44	-1.94	P	1.87	-2.89	P	1.62	-2.33	P	1.82	-2.74	P
ML	NS	*	1.09	-0.30	I	0.96	-0.03	I	1.09	-0.30	I	1.06	-0.24	P	1.05	-0.22	P	1.15	-0.43	P
MW	NS	*	1.45	-1.94	P	1.49	-2.02	P	1.68	-2.41	P	1.74	-2.55	P	1.35	-1.71	P	1.48	-1.98	I

Table 8. Continued.

	CEA			JH			JA			NW			NE			NS			NA		
	α	*β*	AR	*α*	*β*	AR	*α*	*β*	AR	*α*	*β*	AR	*α*	*β*	AR	*α*	*β*	AR	*α*	*β*	AR
TL	1.01	-0.01	I	1.04	-0.07	I	1.01	-0.01	I	0.91	0.20	I	1.03	-0.05	I	1.04	-0.07	I	1.15	-0.30	I
BL	1.00	-0.01	I	0.93	0.13	I	0.98	0.02	I	0.95	0.10	I	1.04	-0.09	P	1.01	-0.04	I	1.10	-0.22	I
ZB	0.99	-0.24	I	1.00	-0.27	I	1.04	-0.36	I	1.18	-0.66	I	1.05	-0.37	I	1.27	-0.83	I	1.52	-1.37	P
FPL	1.11	-0.47	I	1.12	-0.51	I	1.02	-0.28	I	0.80	0.18	I	0.92	-0.06	I	1.07	-0.39	I	0.93	-0.10	I
NPL	1.22	-0.77	P	1.08	-0.48	I	1.32	-0.99	P	1.34	-1.01	I	1.17	-0.68	P	1.38	-1.12	P	1.52	-1.40	P
NL	1.45	-1.37	P	1.09	-0.58	I	1.42	-1.29	P	1.36	-1.15	I	1.33	-1.12	P	1.59	-1.65	P	1.57	-1.60	P
SH	0.74	0.11	N	0.65	0.29	N	0.81	-0.05	N	0.66	0.31	N	0.63	0.38	N	0.59	0.47	N	0.55	0.56	N
RB	1.20	-1.20	I	1.54	-1.93	I	1.29	-1.39	P	1.37	-1.56	I	1.38	-1.58	P	1.22	-1.25	I	1.37	-1.54	I
POC	-1.38	4.33	ns	-1.18	3.89	ns	-1.33	4.18	ns	-0.84	3.18	I	-0.86	3.20	ns	-1.51	4.59	ns	-1.25	4.08	ns
IC	1.16	-1.00	I	1.50	-1.73	I	1.51	-1.77	P	0.86	-0.35	I	1.16	-0.99	I	1.43	-1.57	P	1.17	-1.00	I
PB	1.38	-1.43	P	1.30	-1.26	ns	2.06	-2.88	P	0.87	-0.32	ns	1.58	-1.81	P	1.75	-2.18	P	2.16	-3.06	P
OCB	0.94	-0.59	I	0.87	-0.43	I	0.93	-0.59	I	0.94	-0.59	I	1.02	-0.78	I	1.00	-0.72	I	0.99	-0.72	ns
PL	1.05	-0.38	I	0.97	-0.20	I	1.12	-0.54	P	1.14	-0.58	I	1.22	-0.74	P	1.19	-0.67	I	0.92	-0.09	I
MD	1.63	-2.24	P	1.51	-1.96	ns	1.60	-2.17	P	0.90	-0.66	ns	1.51	-1.96	P	1.51	-1.99	P	1.50	-1.95	I
CML	1.17	-0.70	P	0.80	0.08	N	1.07	-0.49	I	1.07	-0.49	I	1.06	-0.46	I	1.07	-0.47	I	1.12	-0.60	I
RL	0.98	-0.21	I	0.73	0.31	N	1.05	-0.36	I	0.93	-0.11	I	1.04	-0.34	I	1.01	-0.28	I	0.97	-0.20	I
ACP	1.05	-0.67	I	0.98	-0.51	I	1.22	-1.04	P	1.35	-1.32	I	1.22	-1.03	P	1.58	-1.80	P	1.21	-1.00	I
LT	1.28	-0.88	I	0.84	0.06	I	1.05	-0.37	I	1.08	-0.43	I	1.03	-0.32	I	1.09	-0.45	I	0.76	0.26	I
JT	1.33	-2.01	I	1.41	-2.21	I	1.59	-2.58	P	1.65	-2.72	ns	1.56	-2.52	P	1.96	-3.39	P	1.65	-2.69	ns
MH	1.63	-2.36	P	1.77	-2.62	P	1.64	-2.36	P	1.47	-2.00	P	1.65	-2.37	P	1.99	-3.11	P	1.94	-3.00	ns
ML	1.06	-0.24	I	0.92	0.05	I	1.07	-0.27	P	1.27	-0.69	P	1.10	-0.32	P	1.17	-0.48	P	1.02	-0.16	I
MW	1.33	-1.66	P	1.47	-1.96	ns	1.49	-2.03	P	1.27	-1.54	P	1.60	-2.24	P	1.48	-2.00	P	1.51	-2.07	I

α, indicates slope of the allometric regression line; β, indicates intercept of the allometric regression line; AR, mode of allometric relation; I, indicates isometry; P, indicates positive allometry; N, indicates negative allometry; M, indicates mainland; I, indicates island; NS, no significant difference on slopes among populations or no significant difference of *α* from 1; ns, indicates no significant slope.

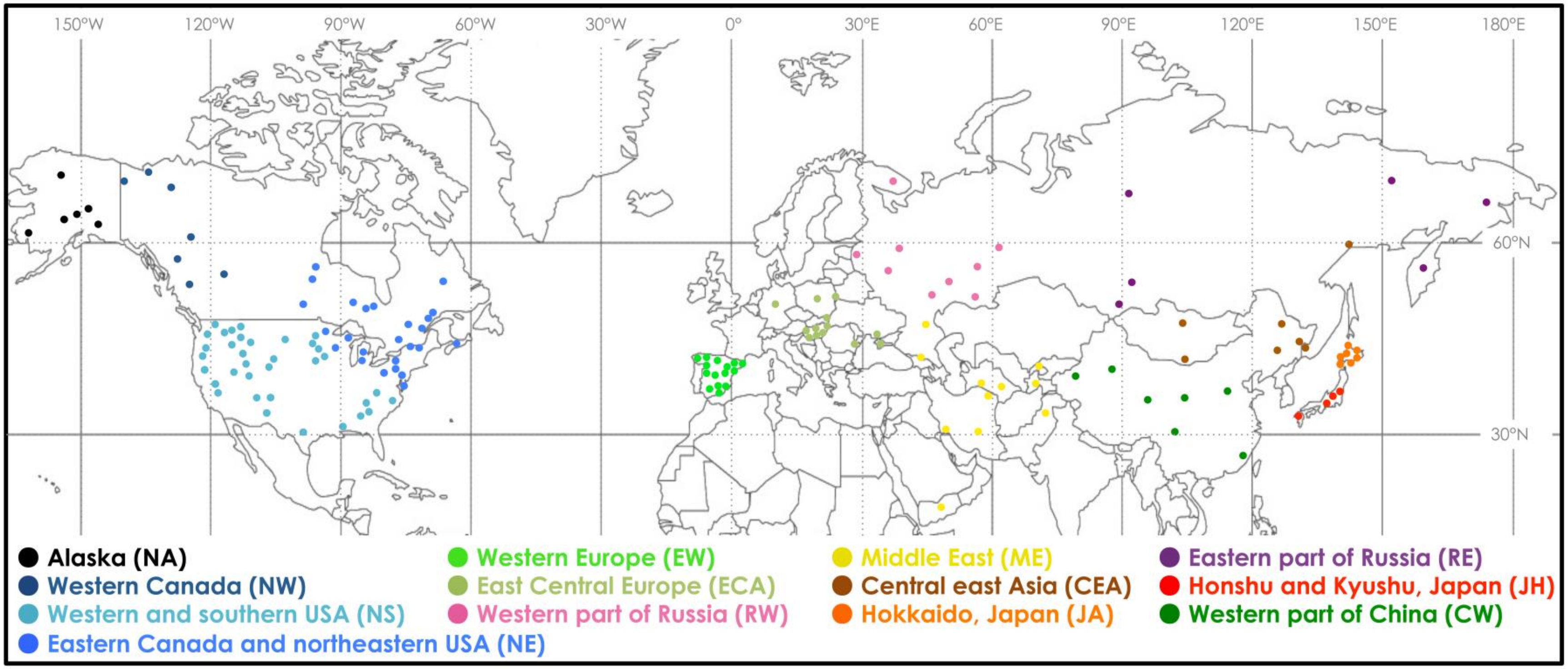


Fig. 1. Locality of red fox specimens obtained across the Northern Hemisphere. 13 geographic populations are designated as different colors. Totally 180 geographic zones are designated as each circle.

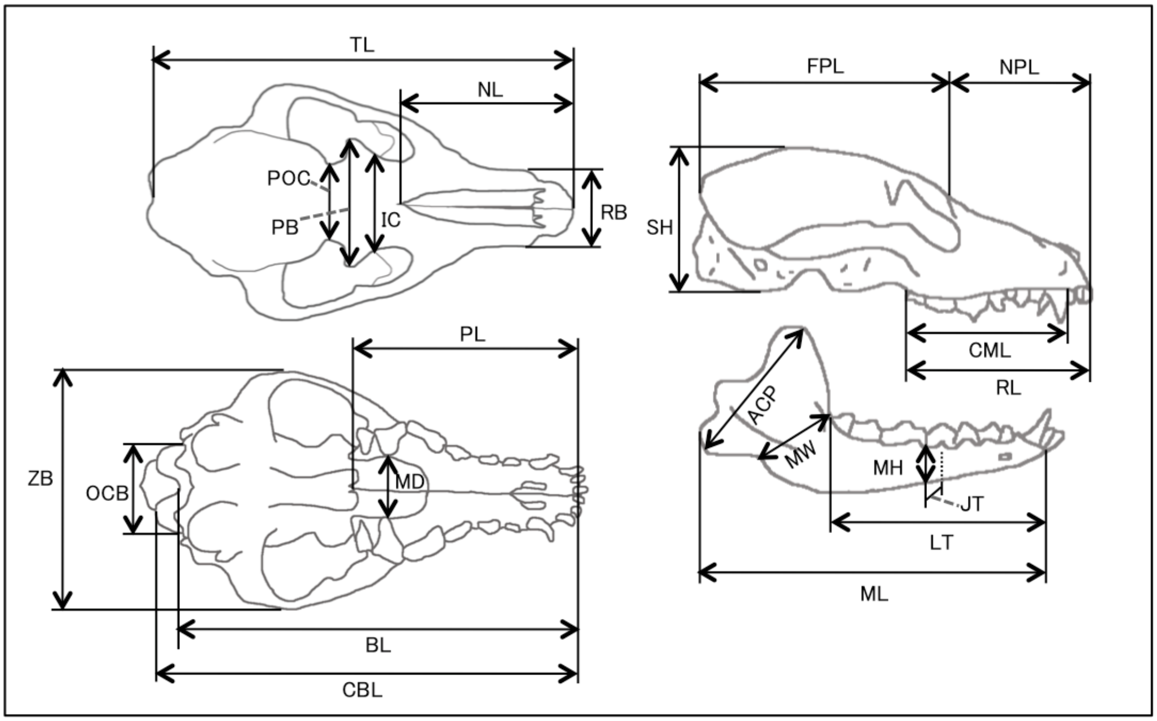


Fig. 2. Cranium and mandible measurements of the raccoon dogs used in this study. Abbreviations are defined in Table 2.

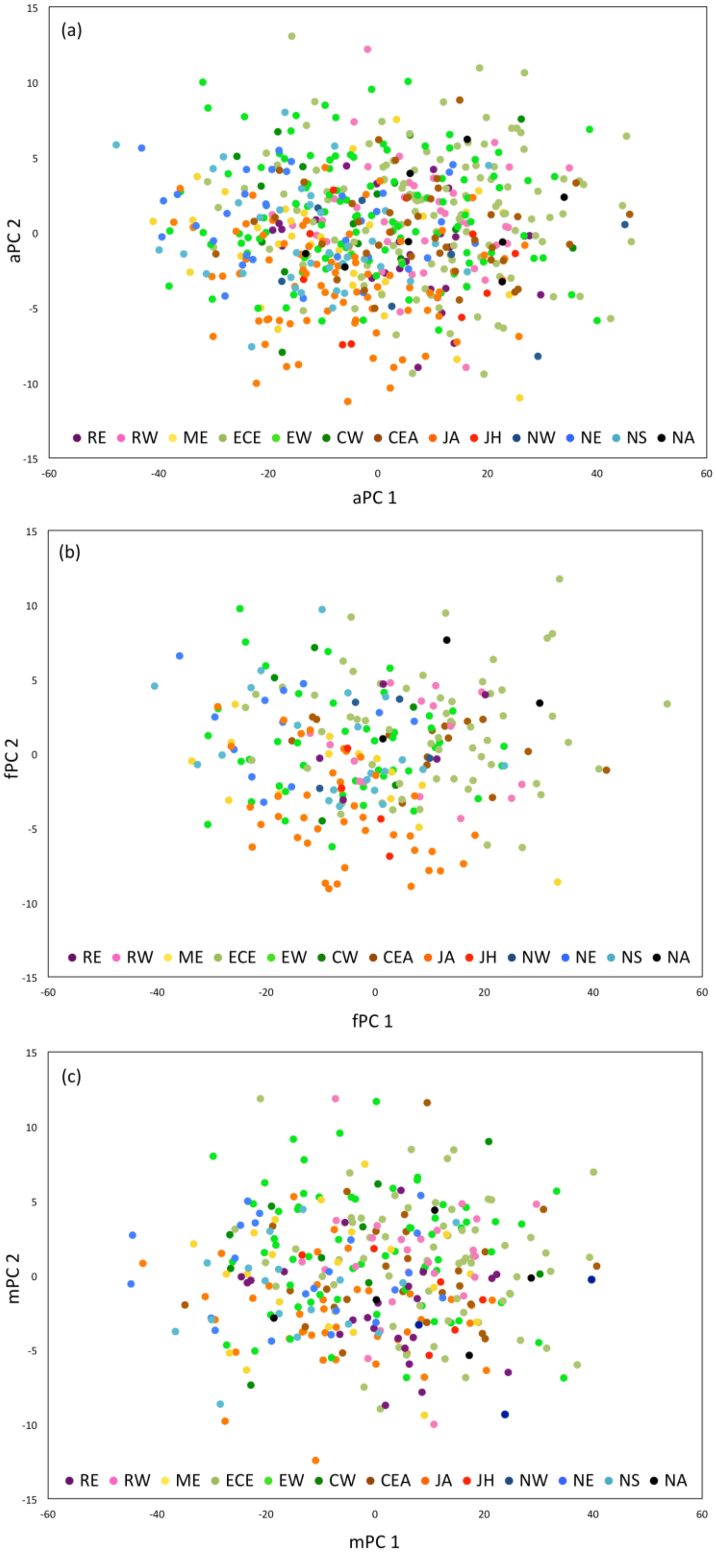


Fig. 3. Results of principal component analysis indicated first against second principal component axes on (a) total red fox populations (aPCA); (b) female red fox populations (fPCA); (c) male red fox population (mPCA) of 13 geographic populations.

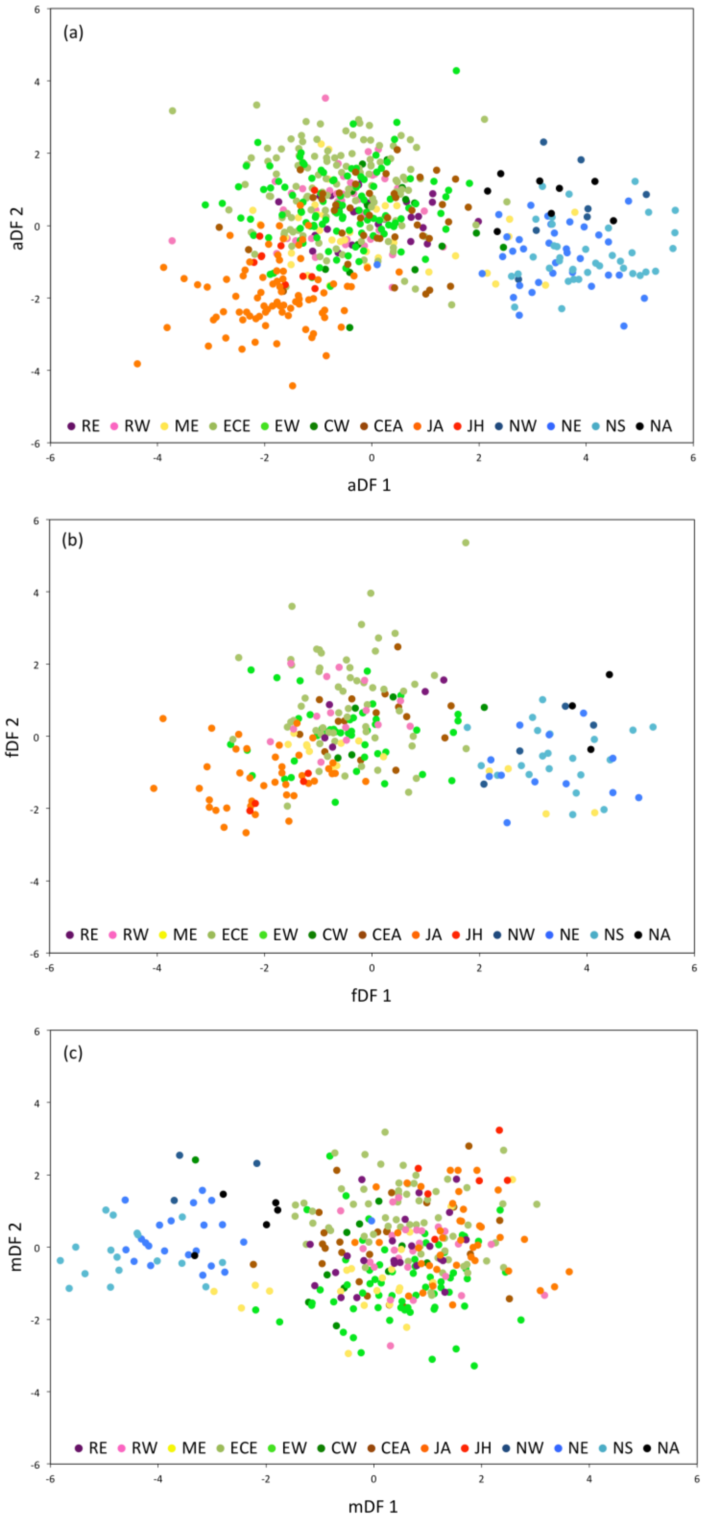


Fig. 4. First against second canonical discriminant functions of (a) total red fox populations (aDFA); (b) female red fox populations (fDFA); (c) male red fox population (mDFA) regarding crania and mandible measurements of all 13 red fox populations.

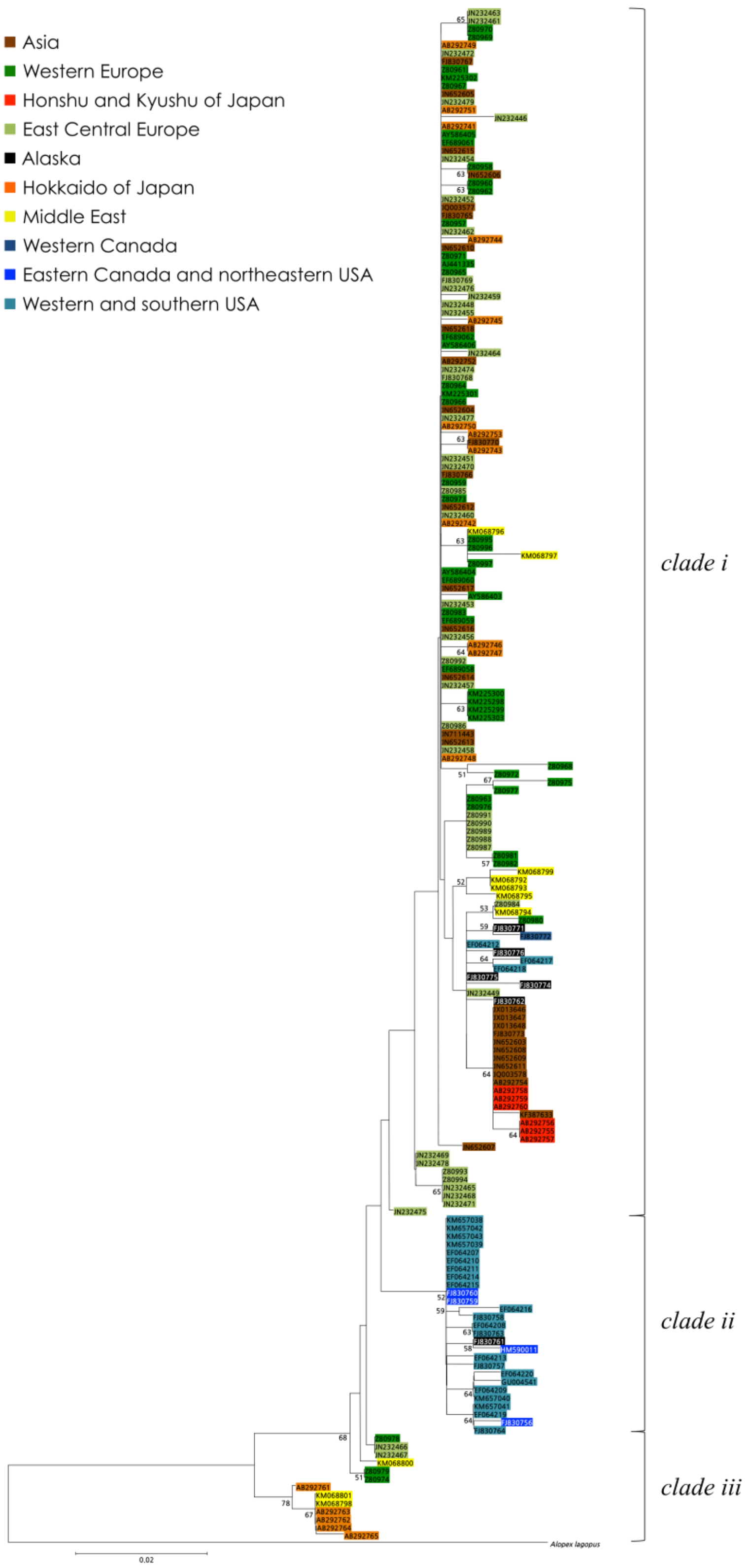
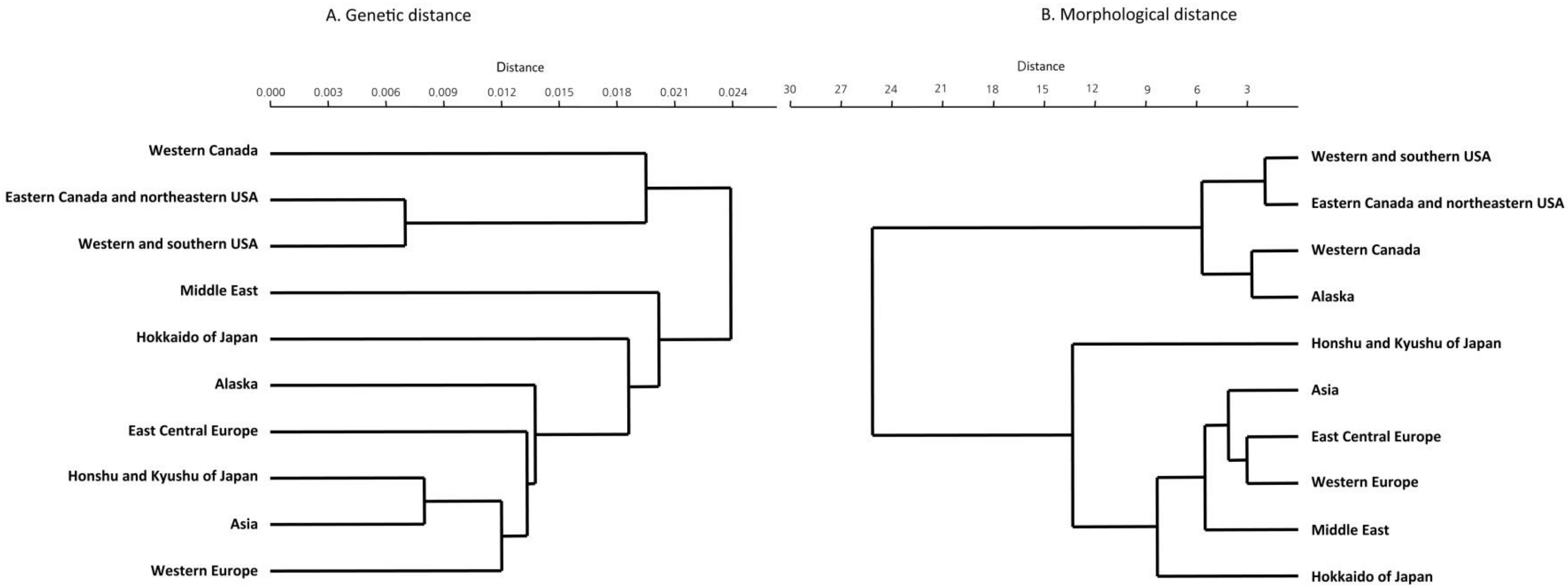


Fig. 5. Phylogenetic trees for red foxes *Vulpes vulpes* reconstructed by neighbour joining method using cytochrome *b* nucleotide sequences (250 bp) obtained from Genbank. The numbers at the branches indicate bootstrap values (%) derived from 5,000 replications.


A. Genetic distance

B. Morphological distance

Fig. 6. Comparison between A. dendrogram of phylogenetic tree reconstructed by pairwise genetic distance matrix calculated with Kimura-2-parameter method using cytochrome *b* nucleotide sequences (250 bp) obtained from Genbank and B. UPGMA dendrogram of 23 skull morphological characteristics derived from squared Mahalanobis distance of 10 red fox populations.

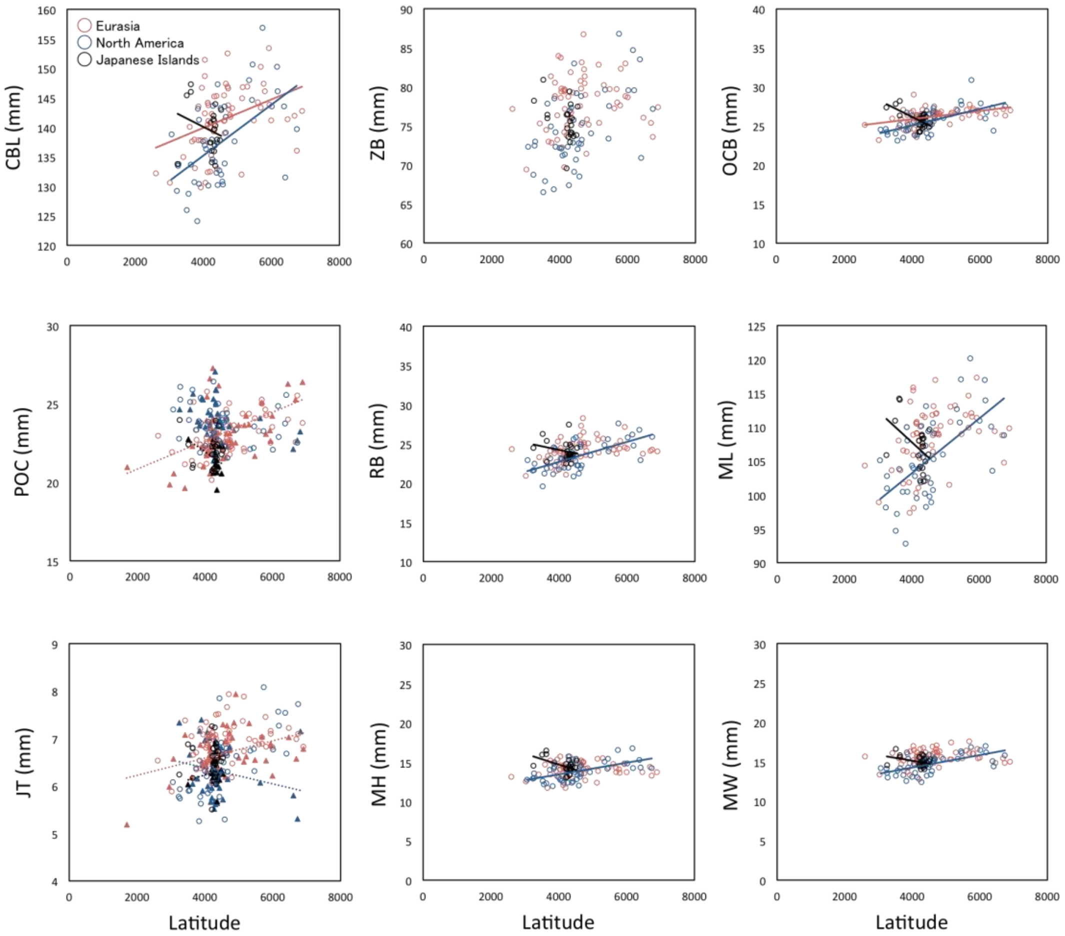


Fig. 7. Size variation of nine skull measurements (mm) with latitude (x-axis) of male (open circle) and female (closed triangle) red foxes populations regarding 180 zones. Three land types, Eurasia, North America, and Island populations are indicated as red, blue, and black colors, respectively. Regression lines of male (solid line) and female (dashed line) describe significant influence of interaction depending on the land type. (Female individuals are designated in POC and JT that showed significant influence of latitude)

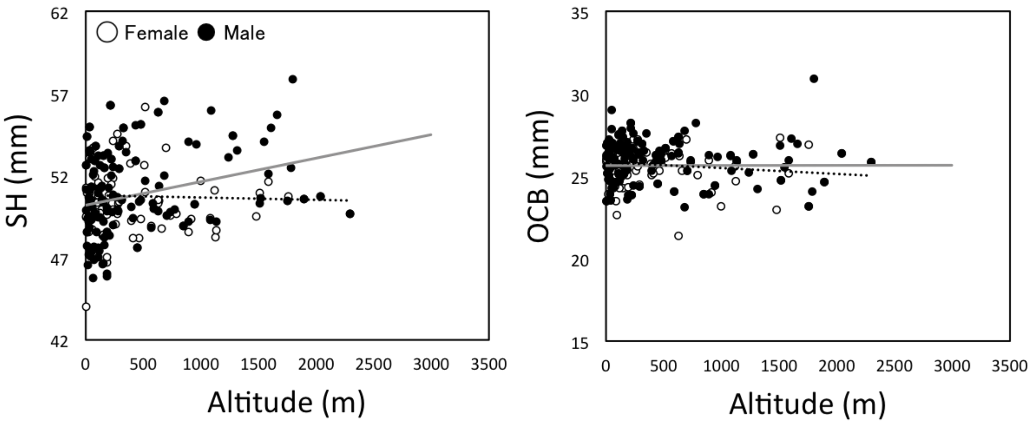


Fig. 8. Size variation of two skull measurements (mm) with altitude (x-axis) of red fox populations regarding 180 zones. Female and male red foxes are indicated as white and black circles, respectively. Regression lines of all (gray line) and female red foxes (dashed black line) describe significant morphological influence on the altitude (m).

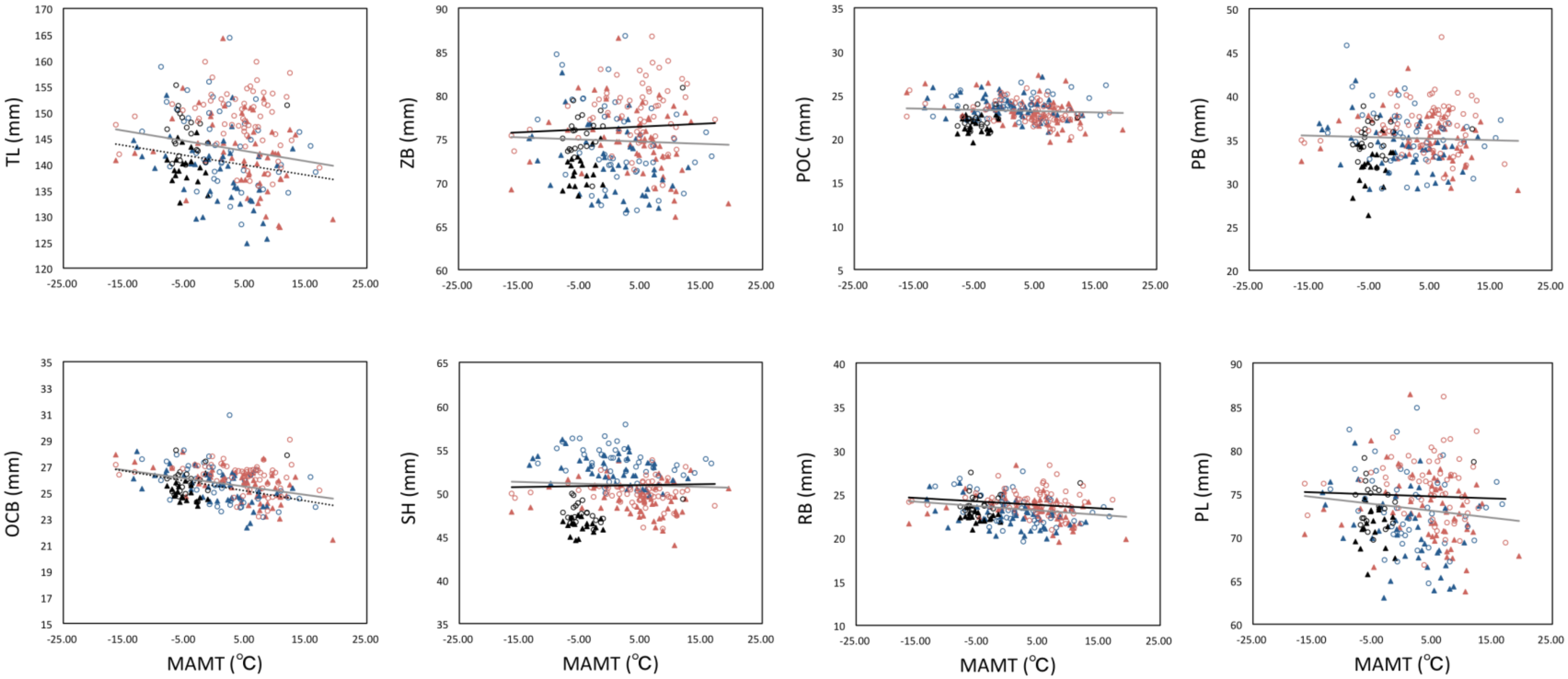


Fig. 9. Size variation of nine skull measurements (mm) with MAMT (x-axis) of female (closed triangle) and male (open circle) red foxes regarding 180 zones. Three land types, Eurasia, North America, and Island populations are indicated as red, blue, and black colors, respectively. Female and male red foxes are indicated as white and black circles, respectively. Regression lines of all (solid gray line), female (dashed black line), and male (solid black line) red foxes describe significant morphological influence on the MAMT (℃).

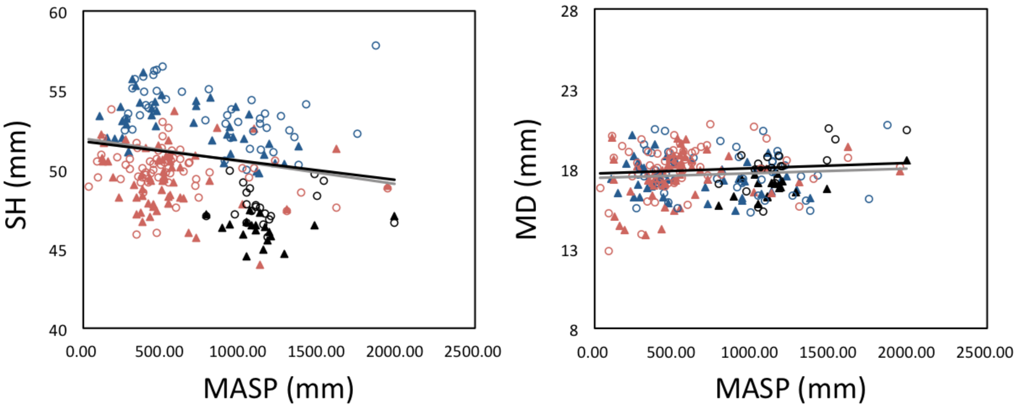


Fig. 10. Size variation of four skull measurements (mm) with MASP (x-axis) of male (open circle) and female (closed triangle) red foxes populations regarding 180 zones. Three land types, Eurasia, North America, and Island populations are indicated as red, blue, and black, respectively. Regression lines of all (solid gray line) and male (solid black line) red foxes describe significant morphological influence on the MASP (mm).

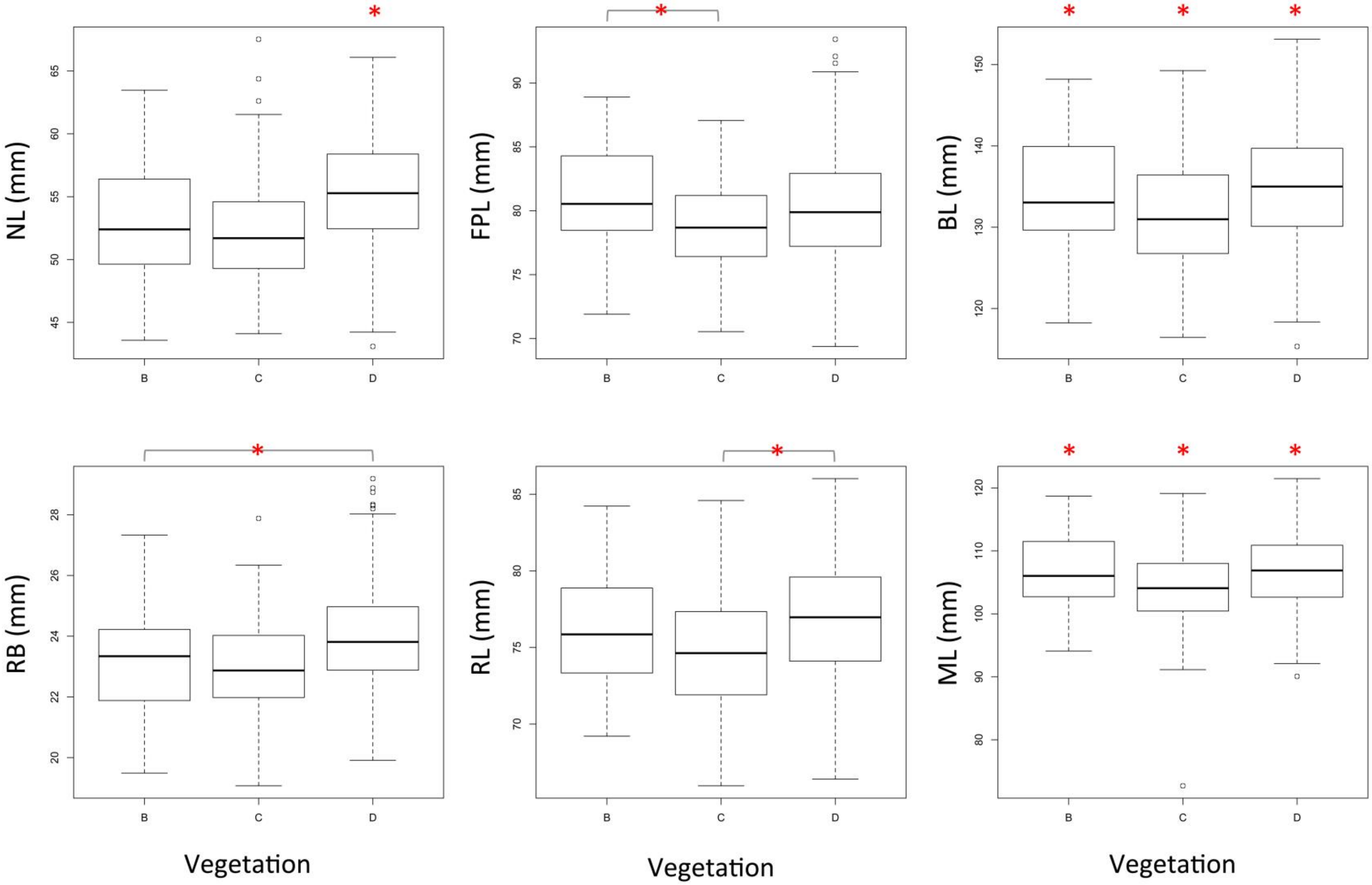


Fig. 11. Size variation of six measurements (mm) with vegetation differences (x-axis) in the red foxes. Vegetation B indicates arid desert or steep, vegetation C indicates temperate forest and vegetation D indicates boreal or taiga. (* indicates significant morphological difference on vegetation difference.)

CONCLUSION

Integrated approaches to the biogeographic study of raccoon dog and red fox were conducted in the present study for the first time. I found that the skull morphological patterns of these two middle-sized carnivore species are affected with the complicated environmental factors consisting of biotic and abiotic elements. They have different distributional ranges, although their ranges are partially overlapped (Larivière & Pasitschniak-Arts, 1996; Kauhala & Saeki, 2004). Nevertheless, the similar environmental determinants had a great influence on their craniomandibular variations.

Morphological variation reflects evolutionary history of raccoon dog and red fox

This study demonstrated the phylogeographic patterns were reflected in the morphogeographic patterns of both species. Raccoon dog and red fox originated from Eurasia and expanded to current distribution, East Asia and the Northern Hemisphere, respectively (Pei, 1934; Kurtén, 1968; Tedford & Qiu, 1991; de Bonis *et al*., 2007; Szuma, 2008; Kutschera *et al*., 2013). Extant Japanese raccoon dogs were colonized after the migration of ancestral species from adjacent continent (Korea or southern part of China) to southern part of Japan during the Middle Pleistocene (Shikama, 1949; Kawamura, 1991; Kim *et al*., 2015). Previous studies suggested that there might be no further gene flow between mainland and Japanese Islands (Kawamura, 1991; Harunari, 2001; Kim *et al*., 2013). This long isolation period implies that the morphological differences between mainland and island were formed with clear geographic differences.

Traveling distances of raccoon dogs and red foxes are quite changeable depending on the region, season, or environmental situation. In Russia, the dispersal distances of raccoon dogs are usually from 2 to 20 km (Heptner *et al*., 1998). Red foxes have greater mobility than raccoon dogs. Their general traveling distances range from 15 to 40 km and individual emigrated more than 100 km has been observed (Nasimovich, 1948; Popov, 1956). This high mobility might be related to the multiple migrations of red fox between Eurasian Continent and Japanese Islands or North American Continent during glacial periods (e.g., Kutschera *et al*., 2013). Most recent migration to both Japanese Islands and North America occurred in LGM. Through the present study, the repeated colonization of red fox is reflected in the phylogenetic pattern than morphological distance while obvious geographic difference was observed both in the phylogenetic and morphological patterns of raccoon dogs. It is due to the different mobility and adaptability to severe winter between red fox and raccoon dog. In comparison with the red fox, relatively low mobility and adaptability of raccoon dogs showed clear geographic difference especially between mainland and island. Red foxes were morphologically different, but were not phylogenetically diverged on land types due to the intimate relation between Eurasian Continent and Alaskan or Japanese populations. Alaskan and Japanese populations underwent colonization and expansion repeatedly according to the multiple migrations from adjacent continents (e.g., Kutschera *et al*., 2013). This ambiguous geographic difference of phylogenetic pattern could be explained by relatively high mobility and adaptability of red fox. Intraspecific relationship was not simply explained by geographic difference especially in the red fox that are proper to apply various species concepts. Based on the phylogenetic and morphogeographic differences between the land types, however, it is apparent that these two species are undergoing speciation. Therefore, raccoon dog and red fox are suitable for speciation model, which could be applied to other middle-sized carnivore species.

Morphological variation reflecting ecogeographic rules by adaptation of geographic gradient, climate, and vegetation

Morphogeographic patterns of raccoon dog and red fox showed strong conformity to Bergmann’s rule and Island rule. Especially in the continental populations, Bergmann’s rule was supported by the clear negative effect of ecological factor, MAMT on skull measurements related to body size. Although the present study demonstrated strong influence of Bergmann’s rule in the endemic population of raccoon dog and red fox, I found different influence between male and female in both species. Interestingly, this tendency differed in skull measurements between two species. While Bergmann’s rule had an influence on the skull size in male and muzzle size and breadth of orbital constriction in female of raccoon dogs, it was observed in most of measurements such as skull length, skull width, nasal length, and muzzle length in male and skull size in female of red foxes. Unfortunately, plausible reason to explain the difference is still ambiguous. Present study demonstrated that larger skull measurements in cold condition were more clearly recognized in the male raccoon dog and red fox~~,~~. Therefore, disparate effect of MAMT on different skull measurements depending on the sex may have resulted from the relatively high susceptibility to the cold condition of male raccoon dog and red fox.

The tendency for skull size variation among the populations of particular mammal species varies with island. The island rule is an emergent pattern resulting from a combination of selective forces whose importance and influence on insular populations vary in a predictable manner along a gradient from relatively small to large species (Lomolino, 2005). Kim *et al.*, (2015) reported that smaller skull size of raccoon dogs on Japanese populations influenced by island effect. The present study also demonstrated island effect on raccoon dogs and red foxes occurring in Japanese Islands. Skull morphological difference and different ecological effect on the difference between the Eurasian Continent and Japan were observed in both species; especially in the raccoon dogs, these features appeared more clearly. In island populations of both species, Japanese raccoon dogs showed larger skull size in Hokkaido populations but red foxes were not. The different morphogeographic pattern observed here between raccoon dog and red fox might be influenced by different ecological strategy after they moved from continent to Japanese Islands. I observed that Japanese raccoon dogs were negatively influenced by the MAMT as the other continental populations. On the other hand, Japanese red foxes were positively influenced by the MAMT different from the other continental populations due to the island dwarfism of Hokkaido red foxes.

Validity of Bergmann's rule and island rule has been discussed on many terrestrial carnivorous species and those tendency of body size of particular species was varied with characteristics of environmental situations (e.g,. Meiri *et al.*, 2004a;

Lomolino, 2005). Present study demonstrated influence of Bergmann's rule on the raccoon dogs of East Asia and red foxes of continents. Also island effect was reflected in the raccoon dogs of Japanese Islands and red foxes of Hokkaido Island. The argument on the reliability of these ecogeographic rules regarding the regional scaled data of carnivore species could establish confidence and support Bergmann's rule and island rule by the broad data.

Can the similar allometric scaling be interpreted as convergence within a species?

Morphological affinity of mandibular shape among solitary carnivore species in similar hunting manners was observed (Meloro, Clauss & Raia, 2015). The convergent evolution of skull morphology of southern populations may reflect the similar environmental condition within a species, raccoon dogs and red foxes. Allometric scaling of mandible measurements in raccoon dogs implies convergent evolution. Raccoon dogs of southern populations (both mainland and island) had relatively smaller mandible size (mandible ramus, lower tooth low, jaw thickness, mandible height, and mandible width) compared to skull length. Although it was not clearly demonstrated in all red fox populations, relatively larger mandible measurements (mandible length, mandible ramus, and jaw thickness) regarding skull length were observed in the southern populations of two continents. Also, the relatively smaller mandible measurements (lower tooth low, jaw thickness, and mandible width) were observed in the East Asian populations and its adjacent populations (southern islands of Japan and Alaskan populations), which are genetically closer to each other. Therefore, unique allometric pattern in mandible measurements of southern raccoon dogs could be interpreted as putatively convergent taxa that are not overlapped but are closer to each other than their relatives (northern populations of mainland and island). Red fox also showed different allometric pattern of mandible in southern populations but less clearly applied in the Asian relatives. This might be affected by multiple migrations of red foxes between the Eurasian Continent and Japanese Islands or Alaska. However, limitation of gene flow among three land types after the LGM cannot be ignored as the period of morphological adaptation.

Unique allometric pattern in the mandible of broadly distributed terrestrial mammal species might be related to convergence evolution by similar environmental pressures, but not always reflect the phylogenetic background. I demonstrated that each species has an unique allometric scaling. The pattern of morphospace was flexible depending on the environmental conditions or species as shown in raccoon dog and red fox. Documentation of the repeated or iterative evolution of given form in similar environmental conditions is important to demonstrate adaptation especially on the ecomorphological variation at the multispecies level (Van Valkenburgh, 1994). Morphological convergence between phylogenetically distinct taxa is powerful evidence for adaptation. Species that have wide distribution range according to high ability of adaptation show various morphological variations. This could be interpreted as consequence of convergent evolution within a species. This study will contribute to understand other mammal species, which have extensive distribution range and have not been fully resolved their biogeographic history by various viewpoints.

ABSTRACT

Morphological characteristic is one of important phenotypes that reflect on geographic differences of organisms and their adaptations to varying environmental conditions. Of the external morphological characteristics, body size difference is often linked to specific environmental factors, such as climate, food availability, and geographic range. Ecogeographic variation in body size of homeotherms has been demonstrated by skull length as an index of body size. Terrestrial carnivore species occurring in wide geographic ranges have remarkable geographic variation in body size due to their high mobility and generalist habits. These species are the most challenging groups to resolve biogeographic patterns. Their high adaptability to various environmental conditions influenced on polymorphic characteristics and variety of phylogeographic outcomes. Of carnivores, raccoon dog (*Nyctereutes procyonoides*) and red fox (*Vulpes vulpes*) have opportunistic feeding habits depending on food availability in various geographic areas. Therefore, raccoon dogs and red foxes could be the most ideal model to demonstrate patterns of historical biogeography and ecomorphology influenced by various environmental factors. This study focused on two generalist, raccoon dog and red fox that are distributed in the Northern Hemisphere.

First, to estimate biogeographic and ecomorphological patterns of raccoon dogs influenced by various environmental factors, I compared skull morphological variation to phylogeographic pattern, geographic gradients, and climatic factors based on the following four hypotheses.

1. Skull morphological variation of raccoon dogs in East Asia might be influenced by phylogenetic patterns.
2. Diversity pattern of skull morphology might be influenced by clinal variation due to the geographic gradients.
3. Skull morphological variation of raccoon dogs might have specific geographic patterns influenced by specific ecological factors.
4. Influence of environmental factors to the morphological adaptation might be different depending on the land type (mainland or island), according to the island effect).

Second, to estimate biogeographic and ecomorphological patterns of red foxes influenced by various environmental factors, I compared skull morphological variation to phylogeographic pattern, geographic gradients, climatic factors, and vegetation types based on the following four hypotheses.

1. Morphogeographic pattern of red fox in the Northern Hemisphere might be reflected by the effect of phylogenetic constraints.
2. Morphogeographic differences in the skull characteristics might be explained by the clinal variation.
3. Skull morphological variation of red fox may show specific geographic pattern influenced by climatic differences due to their various habitats across the Northern Hemisphere.
4. Various habitat types with the extensive vegetational differences might affect the skull morphological variation pattern.

This study demonstrated environmental factors that determine the morphogeographic pattern of skull on both species. Firstly, phylogeographic pattern was reflected in the morphogeographic difference of raccoon dog and red fox. Significant correlation between genetic and morphological distances was observed especially between land types. Also, the disparity between phylogenetic and morphological patterns within the land types was interpreted as strong influence on morphological distance with geographic difference. It might be due to the multiple migrations of red foxes, which have high mobility and adaptability to severe winter. This study supports that the raccoon dog and red fox are suitable for speciation model due to the phylogenetic and morphogeographic differences between the land types. Secondly, morphogeographic patterns of raccoon dog and red fox showed strong conformity to Bergmann's rule and island rule by significant relation to ecological determinants such as latitude, mean annual minimum temperature, mean annual sum of precipitation, and vegetation. Larger skull size of raccoon dog and red fox in cold conditions in continental populations strongly reflected Bergmann's rule. In Japanese Islands, clear influence of Bergmann's rule was observed in the raccoon dogs. However, red foxes showed opposite tendency on the temperature difference between continental and island populations with relatively smaller skull size of Hokkaido population due to the island dwarfism. Although these two species of Japanese Islands had distinct skull morphological characteristics on the temperature, the significantly different influence between continents and islands on the temperature reflects on island effect on Japanese raccoon dogs and Japanese red foxes. These ecogeographic rules for carnivore species could be supported by the present results that cover wide distribution range. Lastly, allometric scaling of mandible measurements in southern populations of raccoon dogs implies convergent evolution. Raccoon dogs of southern populations both in mainland and island had relatively smaller mandible size compared to skull length. Also, relatively larger mandible measurements compared with skull length were observed in the southern populations of red foxes in two continents (the Eurasian and North American Continents). Unique allometric pattern in the mandible of broadly distributed terrestrial mammal species might be related to convergence evolution by similar environmental pressures, but not always reflect the phylogenetic background. Species that have wide distribution range according to high ability of adaptation show various morphological variations. This could be interpreted as consequence of convergent evolution within a species. The present study will contribute to understand other mammal species, which are extensively distributed and have not been fully resolved their biogeographic history.

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