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Geographical Variations of the Skull in the Red Fox *Vulpes vulpes* on the Japanese Islands: An Exception to Bergmann's rule

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In order to clarify the morphological differences between two subspecies of the red fox (*Vulpes vulpes*) on the Japanese Islands and test the validity of Bergmann's rule, we examined geographical variations in 25 cranial and 24 dental characters in *V. v. schrencki* from Hokkaido and *V. v. japonica* from the other main islands of Japan (Honshu, Shikoku, and Kyushu). Many skull measurements, including the male greatest length, condylobasal length, and the length of upper and lower tooth rows, were significantly larger for *V. v. japonica* than for *V. v. schrencki*, whereas most tooth measurements, especially the length of molars and premolars, in *V. v. schrencki* were larger than those in *V. v. japonica*. Although the two subspecies were morphologically well-differentiated from each other, the results did not support that they have evolved following Bergmann's rule of adaptation to cold climates. Based on consideration of the relatively large differences of their tooth sizes, which are not easily influenced by food abundance, and previous genetic research on the different migration histories of the two subspecies, the morphological differences detected in the present study may have resulted not only from the present ecological differences between the two subspecies, but also from the difference of migration history and evolutionary constraints.

Key words: Bergmann's rule, Blakiston's line, morphology, red fox, skull, *Vulpes vulpes*

INTRODUCTION

The fauna of Hokkaido Island, the northernmost of the Japanese Islands, is separated from the other main islands of Japan (Honshu, Shikoku, and Kyushu) by Blakiston's line (referring to the Tsugaru strait) (Fig. 1; Blakiston and Pryer, 1880). This demarcation is thought to have played an important role in forming the unique faunal composition of the Japanese Islands (Dobson, 1994). Many species occurring in Hokkaido, such as the brown bear (*Ursus arctos*), the sika deer (*Cervus nippon*), and the Eurasian red squirrel (*Sciurus vulgaris*), are not considered to be endemic (Abe et al., 2005), whereas there are many endemic mammalian species on the other main islands of Japan located southward of Blakiston's line. These endemic species account for about 40% of all the Japanese mammalian fauna (Abe et al., 2005). On some species that are distributed across Blakiston's line, genetic divergences between Hokkaido and the other three main islands have been reported. For example, the subspecies of the red fox (*Vulpes vulpes*) are genetically

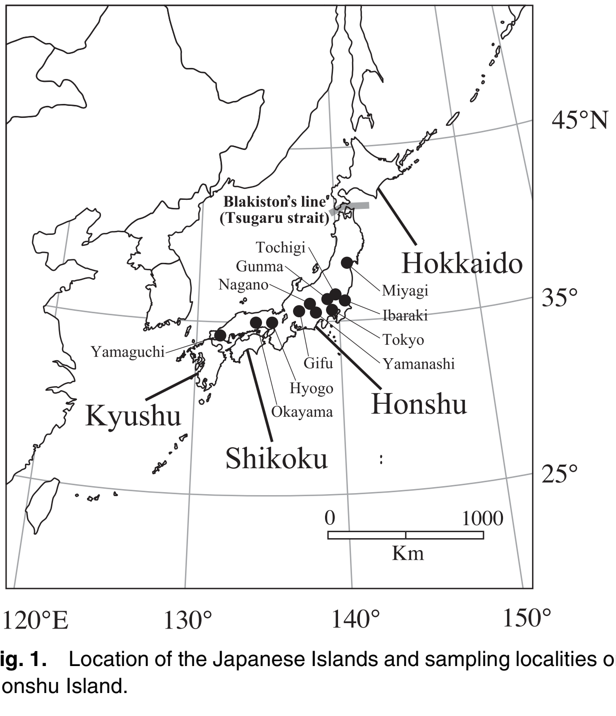

Fig. 1. Location of the Japanese Islands and sampling localities on Honshu Island.

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differentiated across Blakiston's line (Inoue et al., 2007).

Vulpes vulpes is widely distributed through almost entire northern hemisphere including even desert and tundra zones (Lariviere and Pasitschniak-Arts, 1996; Macdonald and Reynolds, 2004). Although 44 subspecies of this species were recognized by Lariviere and Pasitschniak-Arts (1996), their taxonomic status still requires reconsideration (Macdonald and Reynolds, 2004). In Japan, *V. vulpes* is distributed on all four main islands, and thus across Blakiston's line (Abe et al., 2005; Uraguchi, 2009). The Hokkaido population is classified as one subspecies *V. v. schrencki*, whereas those of in the other three main islands are classified a different subspecies, *V. v. japonica*. Based on a few samples, Imaizumi (1960) reported that *V. v. schrencki* had larger body sizes than *V. v. japonica* and that the coat colors were different between the two subspecies. In contrast, a comparison of body measurements of *V. vulpes* populations from several regions in Japan showed no clear differences between the two subspecies (Tsukada, 1997; Uraguchi, 2009). Although skulls of the subspecies were also measured in a relatively large numbers of samples, cranial values of the Japanese subspecies of *V. vulpes* often varied in different researches (Sasakawa, 1984; Takeuchi, 1995). Therefore, it is difficult to simply compare the results of these measurements. To our knowledge, there have been no reports on direct comparisons of the skulls between the two subspecies with large sample numbers to date.

Bergmann's rule states that the body size of a northern race is generally larger than that of a southern one, the result of adaptation to the colder climate (Bergmann, 1847). Because the Japanese Islands cover a wide expanse of latitude, morphological variations of many mammals in Japan follow Bergmann's rule. For example, Haba et al. (2008) reported that the raccoon dog (*Nyctereutes procyonoides*) in Japan follows the rule, with larger skulls in the northern subspecies *N. p. albus* in Hokkaido than those of *N. p. viverrinus* in the other main islands.

In the present study, to investigate effects of geographical isolation by Blakiston's line and clarify the morphological differences between the two subspecies of *V. vulpes* in Japan, especially from the view of testing Bergmann's rule, geographical variations in skull and tooth morphology were examined. We further discuss possible factors causing the differentiation, from ecological and natural historical viewpoints.

Table 1. Numbers and localities of samples examined in the present study.

Subspecies	Localities		Numbers			
	Island	Prefecture	Male	Female	Sex unknown	Total
V. v. schrencki	Hokkaido		44	41	4	89
V. v. japonica	Honshu		17	19	25	61
		Miyagi	0	0	1	1
		Tochigi	12	12	1	25
		Gunma	0	1	1	2
		Ibaraki	1	1	0	2
		Tokyo	0	2	0	2
		Yamanashi	1	0	0	1
		Nagano	2	2	5	9
		Gifu	0	0	9	9
		Hyogo	0	0	1	1
		Okayama	0	0	7	7
		Yamaguchi	1	1	0	2
	Shikoku		1	2	0	3
	Kyushu		4	2	1	7
	Subtotal		22	23	26	71
Total			66	64	30	160

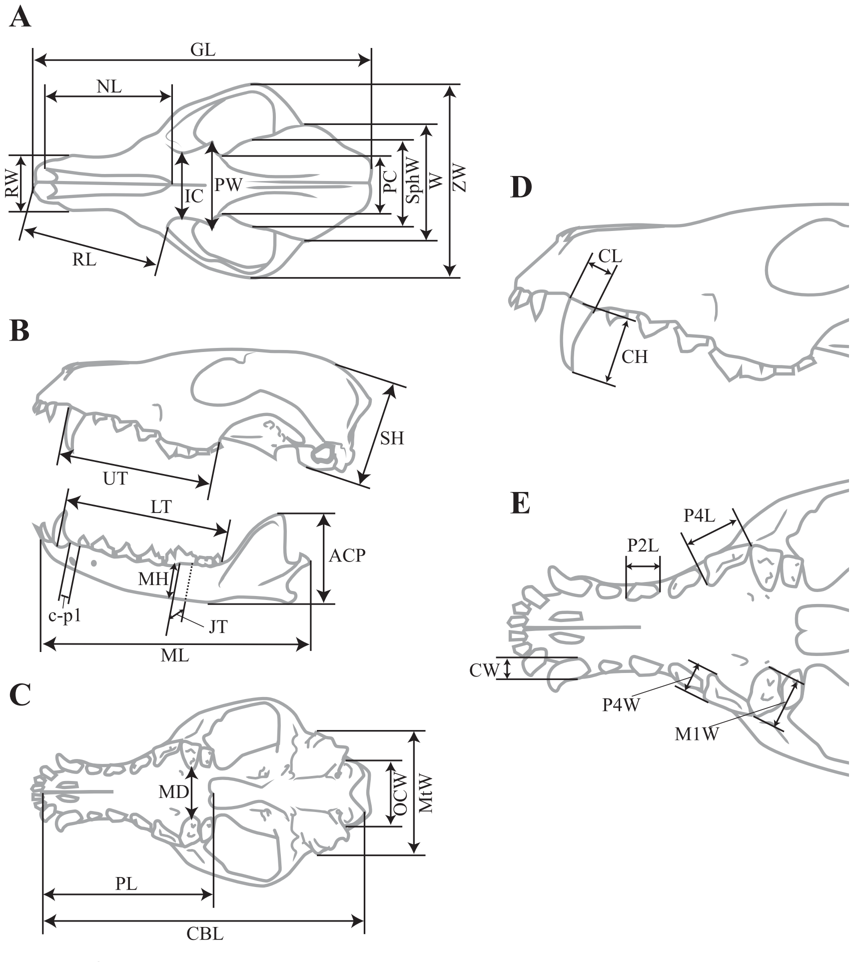

Fig. 2. Skull and tooth measurements of the red fox (*Vulpes vulpes*) used in the present study. **(A)** dorsal view of cranium, **(B)** lateral view of skull, **(C)** ventral view of cranium, **(D)** lateral view of maxilla, and **(E)** ventral view of maxilla. See text and Tables 2 and 4 for the abbreviations.

MATERIALS AND METHODS

Sample collection

A total of 89 skull specimens of *V. v. schrencki* (44 males; 41 females; and 4 sex unknown) and 71 of *V. v. japonica* (22 males; 23 females; and 26 sex unknown) were examined (Table 1). The specimens of subspecies *schrencki* were collected widely from Hokkaido by the Hokkaido prefectural government. Most *V. v. schrencki* specimens were caught during December of 2005 through February of 2006. The skulls of *V. v. japonica* were preserved in Ibaraki Nature Museum, Kyoto University Museum, Wildlife Community Center, Kitakyushu Museum of Natural History and Human History, Shikoku Institute of Natural History, Tochigi Prefectural Museum, and National Museum of Nature and Science, Tokyo. In both subspecies, individuals that were considered younger than one year old were eliminated from analysis after estimating their ages by the presence of crests, the closure of cranial structures, dentition, and the date of collection, as this species gives birth usually from March to May (Maekawa et al., 1980) and stops growing at 11 months old (Sasakawa, 1984).

Measurement points in skulls

Following the definitions of Saito (1963), Sasakawa (1984) and Haba et al. (2007), we measured 25 cranial and mandible variables (Fig. 2): rostrum length (RL), greatest length (GL), nasal length (NL), rostrum width (RW), interorbital constriction (IC), postorbital width (PW), postorbital constriction (PC), zygomatic width (ZW), sphenion width (SphW), cranial width (W), skull height (SH), condylobasal length (CBL), length of upper tooth row (UT), palatal length (PL), distance between the first upper molars (MD), mastoid width (MtW), occipital condyle width (OCW), mandible length (ML), length of lower tooth row (LT), mandibular height (MH), from angular process to coronoid process (ACP), jaw thickness (JT), distance between the alveoli of the canine and the p1 (c–p1), length of p1–p4 (p1–p4) and length of m1–m3 (m1–m3). A total of 24 dental variables were measured (Fig. 2): length of upper canine (CL), width of upper canine (CW), height of upper canine (CH), length of upper premolar (P1L, P2L, P3L and P4L), width of upper fourth premolar (P4W), length of upper molar (M1L and M2L), width of upper molar (M1W and M2W), length of lower canine (cL), width of lower canine (cW), height of lower canine (cH), length of lower premolar (p1L, p2L, p3L and p4L), width of lower fourth premolar (p4W), length of lower molar (m1L and m2L) and width of lower molar (m1W and m2W). All measurements were obtained to the nearest 0.01 mm by a digital caliper.

Sexual dimorphisms in skull dimensions have been reported in this species (Sasakawa, 1984), so we examined the differences of each measurement between the sexes of both subspecies with Aspin-Welch's *t*-test. Specimens without information on sex were not included to this test. Except for P1L, P2L, M2L, M2W, cW, p1L, m2L and m2W, there were significant sexual differences in *V. v. schrencki*, *V. v. japonica*, or both. For measurements without significant sexual differences, Aspin-Welch's *t*-test was used to compare differences between subspecies without sexual distinctions. For all other measurements, the differences were compared by Aspin-Welch's *t*-test for each sex. Principal component analysis (PCA) and stepwise discriminate analysis were used to clarify the intersubspecific variations for skull and tooth measurements for each sex. All analyses for Aspin-Welch's *t*-test were performed with Microsoft Excel X and the other statistical analyses were done with STATISTICA version 06J (StatSoft Japan).

Table 2. Skull measurements of the two Japanese subspecies of *Vulpes vulpes*, results of Aspin-Welch's *t*-test (*P*) and discriminant coefficient from stepwise discriminant analysis. “*”, “**” and “NS” indicate $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively. The bold letters in the rows of mean values indicate that they were significantly larger than the same measurement point in the other subspecies. [a]Hyphens show variables not selected for the stepwise discriminant analysis.

Abbreviations of the measurement	Full names of the measurement	Mean (SD)				*P* value		Discriminant coefficient[a]	
		V. v. schrencki		*V. v. japonica*		Female	Male	Female	Male
		Female	Male	Female	Male				
RL	Rostrum length	60.4 (2.6)	63.0 (3.3)	61.3 (2.7)	**65.8** (3.0)	NS	**	–	–1.057
GL	Gratest length	136.8 (5.3)	142.7 (6.3)	138.7 (4.7)	**147.3** (5.9)	NS	**	–	–
NL	Nasal length	53.2 (2.9)	56.4 (3.3)	**55.0** (2.6)	58.2 (3.6)	*	NS	–0.650	–
RW	Rostrum width	22.3 (1.0)	23.7 (1.3)	**23.2** (1.1)	**24.6** (1.5)	**	*	–0.388	–
IC	Interorbital constriction	25.8 (1.5)	27.6 (1.7)	25.4 (1.4)	27.0 (1.5)	NS	NS	1.468	–1.025
PW	Postorbital width	31.9 (2.6)	34.5 (2.9)	33.0 (2.0)	35.0 (2.6)	NS	NS	–	–
PC	Postorbital constriction	21.2 (1.1)	21.8 (1.4)	21.4 (1.0)	21.9 (1.2)	NS	NS	–1.285	1.326
ZW	Zygomatic width	71.3 (2.6)	74.9 (2.9)	**73.9** (2.3)	**78.5** (3.6)	**	**	–1.075	1.235
SphW	Sphenion width	35.7 (1.1)	36.7 (1.2)	35.7 (1.4)	36.2 (1.3)	NS	NS	–	–1.203
W	Cranial width	45.3 (1.1)	46.7 (1.3)	45.3 (1.1)	46.9 (1.1)	NS	NS	0.545	–
SH	Skull height	47.9 (1.4)	49.6 (1.2)	47.5 (1.0)	49.4 (1.6)	NS	NS	0.416	–1.092
CBL	Condylobasal length	133.6 (4.8)	138.8 (5.7)	135.7 (4.3)	**143.8** (5.3)	NS	**	–	2.628
UT	Upper tooth row length	61.4 (2.1)	63.4 (3.0)	60.8 (1.7)	64.2 (2.4)	NS	NS	–0.654	–1.068
PL	Palatal length	70.4 (2.7)	73.1 (3.5)	**72.9** (2.7)	75.2 (7.4)	**	NS	–	–
MD	Distance bitween upper M1s	17.1 (1.1)	17.5 (1.3)	**17.8** (0.7)	**19.1** (1.2)	**	**	–0.128	–
MtW	Mastoid width	44.3 (1.5)	45.2 (1.5)	43.9 (1.1)	46.0 (1.6)	NS	NS	1.425	–
OCW	Occipital condyle width	24.9 (0.9)	25.4 (1.2)	**25.7** (1.0)	**26.5** (0.7)	**	**	–0.476	0.360
ML	Mandible length	102.9 (3.9)	107.6 (4.6)	**105.2** (3.5)	**112.3** (4.7)	*	**	–1.148	1.964
LT	Lower tooth row length	68.7 (3.2)	71.5 (3.4)	68.7 (1.9)	72.6 (2.9)	NS	NS	–	–
MH	Mandibular height	14.5 (1.0)	15.2 (1.2)	14.8 (0.9)	**16.1** (1.2)	NS	**	–	–
ACP	angular - coronoid process	36.2 (1.8)	37.7 (2.2)	36.3 (1.6)	38.8 (2.3)	NS	NS	0.933	–1.424
JT	Jaw thickness	26.1 (1.6)	27.3 (1.8)	26.8 (1.0)	27.8 (2.4)	NS	NS	–0.445	–0.473
c–p1	Distance between canine and p1	3.6 (1.1)	3.8 (0.9)	**4.3** (0.6)	**4.8** (0.8)	**	**	–	–
p1–p4	Length of lower premolars	**32.9** (1.4)	33.9 (1.8)	32.2 (1.3)	34.5 (1.4)	*	NS	0.986	–
m1–m3	Length of lower molars	**24.8** (0.9)	**25.7** (1.3)	24.0 (1.2)	24.7 (1.1)	**	**	0.664	–0.650

RESULTS

Skull measurements

According to the Aspin-Welch's *t*-test between the two subspecies, two skull measurements from female specimens (NL and PL), four from male (RL, GL, CBL and MH), and six from both sexes (RW, ZW, MD, OCW, ML and c–p1) were significantly larger for *japonica* than *schrencki* ($P < 0.05$). In contrast, the length of lower premolars (p1–p4) in females and the length of lower molars (m1–m3) in both sexes were significantly larger in *schrencki* than *japonica* (Table 2). In addition, most average values for all other measurements, which were not significantly different between subspecies, were larger in *japonica* than *schrencki* (Table 2).

In PCA using skull measurements, the first (PC1) and second (PC2) principal component axes respectively explained 43.6% and 13.0% of the total variations in females, as well as 52.3% and 12.0% in males (Table 3). PC1 is loaded mainly on the length of skull in females, and the length and width of skull in males. PC2 expresses width positively, and length negatively in both sexes (Table 3). Fig. 3 shows the individual scores for the axes and the separation between the two subspecies.

In stepwise discriminant analysis of vixens, sixteen measurement points were selected in the following order: IC, MtW, PC, ML, ZW, p1–p4, ACP, m1–m3, UT, NL, W, OCW, JT, SH, RW, and MD (Table 2). These variables correctly classified 100% of female skulls by subspecies. Thirteen variables were selected for distinguishing subspecies of males in the following order: CBL, ML, ACP, PC, ZW, SphW, SH, UT, RL, IC, m1–m3, JT and OCW (Table 2). These variables also correctly classified 100% of male skulls between subspecies.

Table 3. Factor loading values for each measurement, eigenvalues, and contribution rates in principal component analyses.

Skull					Tooth				
Measurement point	Female		Male		Measurement point	Female		Male	
	PC1	PC2	PC1	PC2		PC1	PC2	PC1	PC2
RL	0.85	–0.39	0.89	–0.34	CL	0.57	0.56	0.64	0.19
GL	0.90	–0.30	0.93	–0.29	CW	0.60	0.50	0.74	0.27
NL	0.72	–0.28	0.79	–0.28	CH	0.29	0.44	0.72	0.21
RB	0.60	0.29	0.73	0.33	P1L	0.48	–0.05	0.75	–0.28
IC	0.55	0.34	0.41	0.73	P2L	0.84	–0.35	0.78	–0.47
PB	0.60	0.53	0.42	0.71	P3L	0.84	–0.26	0.88	–0.18
PC	0.33	0.65	0.07	0.71	P4L	0.65	–0.22	0.80	–0.21
ZB	0.77	0.41	0.83	0.33	P4W2	0.54	0.41	0.82	0.32
SphW	0.41	0.39	0.22	0.36	M1L	0.53	–0.10	0.81	0.05
W	0.52	0.32	0.59	0.14	M1W	0.78	–0.12	0.85	–0.03
SH	0.56	0.10	0.69	0.19	M2L	–0.17	0.02	0.47	0.51
CBL	0.90	–0.24	0.95	–0.23	M2W	0.56	–0.20	0.62	0.25
UT	0.79	–0.41	0.88	–0.26	cL	0.22	0.72	0.55	0.40
PL	0.86	–0.22	0.90	–0.24	cW	0.53	0.62	0.82	0.29
MD	0.54	0.42	0.57	0.28	cH	0.02	0.67	0.77	0.40
MtW	0.60	0.23	0.80	0.22	p1L	0.52	–0.28	0.64	–0.32
OCB	0.47	0.25	0.66	0.09	p2L	0.83	–0.35	0.81	–0.48
ML	0.89	–0.28	0.95	–0.21	p3L	0.79	–0.28	0.87	–0.37
LT	0.81	–0.36	0.90	–0.27	p4L	0.85	–0.29	0.85	–0.38
MH	0.61	0.17	0.72	0.12	p4W	0.43	0.67	0.75	0.20
ACP	0.73	–0.25	0.78	–0.11	m1L	0.73	–0.20	0.93	–0.15
JT	0.58	0.28	0.64	0.38	m1W	0.72	0.30	0.86	–0.07
c–p1	0.62	0.39	0.68	0.16	m2L	0.37	–0.04	0.62	0.24
p1–p4	0.46	–0.61	0.74	–0.36	m2W	0.63	0.05	0.75	0.17
m1–m3	0.17	–0.32	0.48	–0.11					
Eigenvalue	10.90	3.23	13.08	2.99		8.75	3.56	13.98	2.12
Contribution rate	0.44	0.13	0.52	0.12		0.36	0.15	0.58	0.09
Cummurative contribution rate	0.44	0.56	0.52	0.64		0.36	0.51	0.58	0.67

Tooth measurements

M1L of females, m1W of males and ten tooth measurements of both sexes (P2L, P3L, P4L, M1W, M2W, p1L, p2L, p3L, p4L and m1L) were significantly larger for *V. v. schrencki* than *V. v. japonica* ($P < 0.05$, Table 4). In contrast, cH and p4W of vixens and M2L and cL of both sexes were significantly larger for *V. v. japonica* than *V. v. schrencki* ($P < 0.05$, Table 4).

In PCA using tooth measurements, the first and second principal component axes respectively explained of the total variation 36.5% and 14.9% in females, 58.2% and 8.9% in males (Table 3). PC1 is loaded mainly on the length of molars and premolars in both sexes, and PC2 of both sexes expresses sizes of canine positively, and length of molars and premolars negatively (Table 3). These principle components adequately distinguished between the two subspecies in both sexes (Fig. 4).

In stepwise discriminant analysis of vixens, nine variables were selected in the following order: P2L, p4W, p4L, P4W, m1W, cL, P3L, CH and M2W (Table 4). These variables correctly classified 100% of female specimens

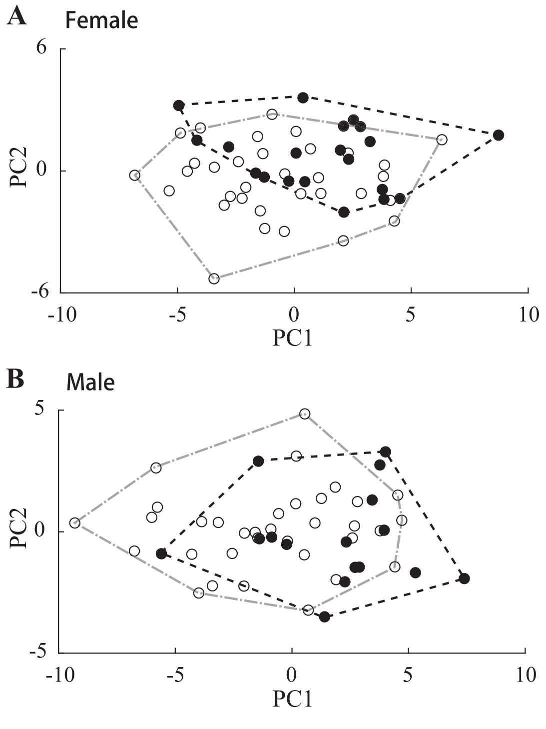

Fig. 3. Principal component analysis plots of female skulls **(A)** and male skulls **(B)** of *V. v. schrencki* (open circles) and *V. v. japonica* (closed circles).

Table 4. The tooth measurements of the two Japanese subspecies of *Vulpes vulpes*, results of Aspin-Welch's *t*-test (*P*), and discriminant coefficient from stepwise discriminant analysis. "*", "**" and "NS" indicate $P < 0.05$, $P < 0.01$ and $P > 0.05$, respectively. The bold letters in the rows of mean values indicate that the significantly larger than the same measurement point of another subspecies. P1L, P2L, M2L, M2W, cW, p1L, m2L, and m2W were not separated into sexes because these measurements show no significant differences between sexes. [a]Hyphens show the variables not selected for the stepwise discriminant analysis.

Abbreviations of the measument	Full names of the measurement	Mean (SD)				*P* value		Discriminant coefficient[a]	
		V. v. schrencki		*V. v. japonica*		Female	Male	Female	Male
		Female	Male	Female	Male				
CL	Upper canine length	6.21 (0.35)	6.73 (0.39)	6.29 (0.42)	6.76 (0.49)	NS	NS	–	–
CW	Upper canine width	4.04 (0.19)	4.39 (0.29)	4.05 (0.18)	4.50 (0.83)	NS	NS	–	0.745
CH	Upper canine height	17.09 (1.23)	18.65 (1.19)	17.19 (0.94)	17.42 (3.33)	NS	NS	0.305	–
P1L	Upper P1 length	4.63 (0.38)		4.70 (1.77)		NS		–	–
P2L	Upper P2 length	**8.77** (0.53)		7.94 (0.59)		**		–1.110	–
P3L	Upper P3 length	**9.44** (0.47)	**9.63** (0.62)	8.83 (0.39)	9.25 (0.43)	**	**	0.360	–
P4L	Upper P4 length	**14.58** (0.51)	**15.10** (0.76)	13.80 (0.70)	14.17 (1.37)	**	**	–	0.842
P4W	Upper P4 width	6.67 (0.39)	6.99 (0.65)	6.88 (0.49)	7.01 (0.55)	NS	NS	0.698	–
M1L	Upper M1 length	**9.31** (0.38)	9.53 (0.54)	9.04 (0.40)	9.31 (0.69)	**	NS	–	–0.772
M1W	Upper M1 width	**12.41** (0.57)	**12.86** (0.73)	11.81 (0.72)	12.10 (0.93)	**	**	–	0.485
M2L	Upper M2 length	5.20 (0.41)		**5.63** (0.94)		**		–	–0.707
M2W	Upper M2 width	**8.48** (0.50)		8.19 (0.66)		**		0.208	0.604
cL	Lower canine length	6.42 (0.48)	6.95 (0.48)	**6.90** (0.61)	**7.37** (0.74)	**	*	0.444	–0.690
cW	Lower canine width	4.26 (0.31)		4.35 (0.38)		NS		–	–
cH	Lower canine height	15.67 (0.87)	16.84 (0.98)	**16.50** (1.38)	16.82 (1.33)	*	NS	–	–0.667
p1L	Lower P1 length	**3.99** (0.33)		**3.81** (0.24)		**		–	–
p2L	Lower P2 length	**8.49** (0.39)	**8.72** (0.67)	7.62 (0.52)	7.97 (0.43)	**	**	–	0.767
p3L	Lower P3 length	**8.87** (0.35)	**9.19** (0.54)	8.32 (0.40)	8.63 (0.50)	**	**	–	–
p4L	Lower P4 length	**9.75** (0.38)	**10.16** (0.55)	9.15 (0.37)	9.51 (0.45)	**	**	–0.978	–
p4W	Lower P4 width	3.74 (0.19)	4.00 (0.26)	**3.93** (0.23)	4.06 (0.29)	**	NS	1.016	–1.062
m1L	Lower M1 length	**15.00** (0.47)	**15.48** (0.85)	14.46 (0.55)	14.74 (0.73)	**	**	–	–
m1W	Lower M1 width	5.33 (0.25)	**5.61** (0.35)	5.24 (0.23)	5.37 (0.30)	NS	**	–0.583	0.490
m2L	Lower M2 length	7.00 (0.39)		6.97 (0.45)		NS		–	–
m2W	Lower M2 width	5.00 (0.35)		4.96 (0.32)		NS		–	–

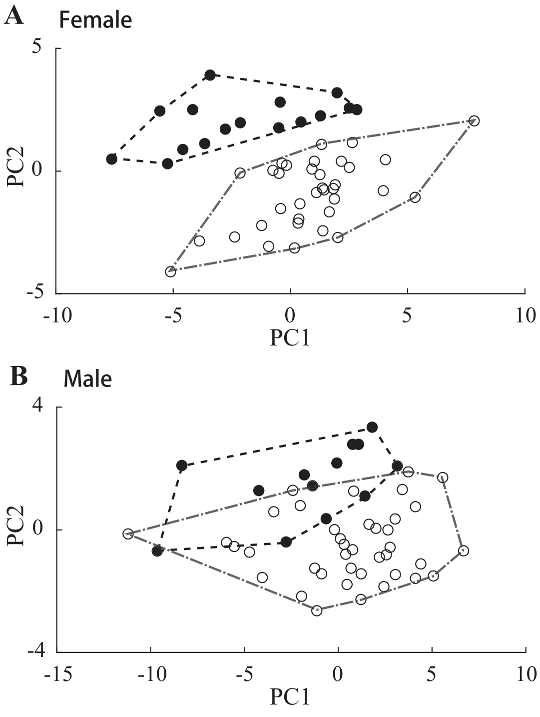

Fig. 4. Principal component analysis plots of female teeth **(A)** and male teeth **(B)** of *V. v. schrencki* (open circles) and *V. v. japonica* (closed circles).

between subspecies. In contrast, eleven variables were selected for distinguishing subspecies of males in the following order: p4W, P4L, M1L, p2L, CW, M2L, cL, cH, M2W, m1W and M1W (Table 4). These male dental variables also correctly classified 100% of the two subspecies.

DISCUSSION

Morphological differences between the two subspecies of *V. vulpes*

The present study demonstrated that two Japanese subspecies of *V. vulpes* are morphologically differentiated from each other. The skull measurements, which were chosen by the discriminant analyses in both sexes with significant differences between subspecies by *t*-test, were rostrum width (RW), zygomatic width (ZW), the distance between the first upper molars (MD), occipital condyle width (OCW), mandible length (ML), distance between the alveoli of the canine and the p1 (c–p1), and length of lower molars (m1–m3). Many tooth measurements, except for those of upper canines and lower molars, were significantly smaller in *V. v. japonica*. Discriminant analyses also identified such measurements as useful in distinguishing the two subspecies. The differences between the two subspecies are summarized as follows: *V. v. schrencki* from Hokkaido has a narrower cranium and shorter mandible, with long molars and premolars, whereas *V. v. japonica,* of the other main islands of Japan, is characterized by a wider skull and smaller molars and premolars. In addition, no significant differences were indicated on the sizes related to braincases such as sphenion width (SphW), cranial width (W), and skull height (SH).

***Vulpes vulpes* on the Japanese islands, an exception to Bergmann's rule**

Many skull measurements, including male greatest and condylobasal length (GL and CBL, respectively), were significantly larger for *V. v. japonica* than *V. v. schrencki*, and the average values of the other skull measurements were also relatively larger in *japonica* (Table 2). The results show that *V. vulpes* in Japan does not follow Bergmann's rule. According to Ashton et al. (2000), 78 out of 110 mammalian species show positive correlations between sizes and latitudes, indicating that Bergmann's rule is certainly a valid generalization for mammals. Meiri and Dayan (2003) reported that 57.4% (skull length) and 63.3% (dental length) of mammalian measurements comply with Bergmann's rule, and that 82.1% of mammals follow the rule in their body weight. Significant positive correlations between skull lengths and latitudes were found in 50% of carnivore species, while significant negative correlation was found in only 11% of species (Meiri et al., 2004). The previous studies show that *V. vulpes* also followed Bergmann's rule (see Meiri et al., 2004). Meanwhile, some exceptions of Bergmann's rule have been also reported on the Japanese mammals (e.g. Yoneda and Abe, 1976; Kaneko, 1988), including *V. vulpes*. Takeuchi (1995) compared the skull measurements of *japonica* from Tochigi Prefecture, central Honshu, with those from other regions, and showed that their skulls increase in size with decreasing latitudes. In addition, Uraguchi (2009) reported that the total body length of *V. v. schrencki* is slightly larger than that of *V. v. japonica*, but that the average body weight of males was not different between subspecies, and relatively smaller in female *V. v. schrencki*. The present study agrees with the above previous studies of Takeuchi (1995) and Uraguchi (2009) on the point of negative correlation.

Why does *V. vulpes* in Japan not follow the Bergmann's rule?

Bergmann's rule is an empirical generalization, and exceptions may occur (Mayr, 1956). Species that do not follow Bergmann's rule may be affected more by the following elements than by latitude. Mayr (1963) and King (1989) suggested that burrowing mammals often fail to follow Bergmann's rule as the microhabitat of a burrow protects them from cold. Nearctic populations of *Mustela* species in the family Mustelidae also deviate from the rule, due to the negative correlation between latitude and size in *Microtus*, the main prey of *Mustela* species (Ralls and Harvey, 1985). Ashton et al. (2000) considered that, in *Mustela*, relationships with prey may override other selective factors in determining body size. One of the key factors that determines body size is likely to be food availability, and the spatial distribution of key resources within the species range constitutes a significant predictor of carnivore body size (see Meiri et al., 2007). Factors influencing food availability may also affect *V. vulpes*. However, because this species is omnivorous and its diet habit varies extremely by season and region (Tsukada, 1997), it is difficult to simply compare food availability and quality between the subspecies.

Moreover, the present study showed that most tooth measurements, especially the length of molars and premolars, were larger in *V. v. schrencki* than *V. v. japonica*, whereas the average length of upper and lower tooth rows (UT and LT, respectively) were not significantly different between the two subspecies (Tables 2 and 4). In the raccoon dogs in Japan, molars and premolars are larger in the Honshu population, which is more omnivorous than the Hokkaido population (Haba et al., 2008). In the present study, however, the molars and premolars were developed more in *V. v. schrencki* (Table 3), despite the fact that fibrous foods are more frequently found in feces of *V. v. japonica* than *V. v. schrencki* (Tsukada, 1997).

Morphological differences may have resulted from both ecological differences and evolutionary processes (e.g. Futuyma, 1998; Newton, 2003). It may however be more plausible that the morphological differences between the two Japanese subspecies of *V. vulpes* are related to differences in their migration histories. Two sets of evidence support this idea. First, a previous study using the analysis of mtDNA variation revealed that the Japanese subspecies of *V. vulpes* were genetically isolated by Blakiston's line (Inoue et al., 2007). In addition, Inoue et al. (2007) reported that there were two clusters in Japan: one cluster was composed of *V. v. japonica* and partial populations of *V. v. schrenki*, and the other consisted of other populations of *V. v. schrencki.* The mean sequence divergence between the two clusters for the entire cytochrome *b* gene was about 3%, and *V. v. schrencki* was considered to have a different genetic background from *V. v. japonica* (Inoue et al., 2007). The second reason is the difference of tooth sizes between the two subspecies. Dental measurements separated the two subspecies in the PCA more accurately than did skull measurements (Figs. 3 and 4). Nutrition abundance easily affects the growth of many skull parts in *V. vulpes*, whereas tooth sizes are not strongly influenced by food abundance (Englund, 2006). It is difficult to view this difference as solely the result of environmental factors, and it may be caused by genetic differences between the subspecies. By considering both of these factors, we can conclude that the morphological features detected in the present study are not only influenced by present ecological differences of the locality, but also affected by evolutionary processes, such as migration history.

This is the first study revealing detailed skull differences between the two subspecies of *V. vulpes* in Japan. The findings provide an opposing insight to those of a previous study using a limited sample number, which suggested that this species in Japan follows Bergmann's rule (Imaizumi, 1960). In order to clarify the certain reason why they do not obey Bergmann's rule, however, an examination of the differences of food abundance between the subspecies and phylogeographical analysis of paternally and biparentally inherited genes through a wide habitat range, in addition to the previous genetic study, will be necessary.

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