

## Sexual Dimorphism of Craniodental Morphology in the Raccoon Dog *Nyctereutes procyonoides* from South Korea

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**ABSTRACT.** We examined sexual dimorphism in the craniodental traits of the raccoon dog *Nyctereutes procyonoides* from South Korea. Univariate comparisons of skull (cranium and mandible) and dental measurements revealed a small extent of sexual dimorphism in some measurements. The most indicative dimorphic measurements were the breadths of the upper and lower canines which were around 8% larger in male specimens on average. On the other hand, multivariate analyses using only skull traits showed slightly a clearer separation between sexes than those using only dental ones. This discrepancy may be derived from a higher variability in dental traits than in those of the skull. In conclusion, sexual dimorphism within *N. procyonoides* of South Korea is present, but was not so pronounced as for other local populations. However, measurements showing significant sexual dimorphism varied between different localities. This suggests that the selective forces acting upon craniodental morphology of each sex vary between populations of the species.

**KEY WORDS:** craniodental morphology, *Nyctereutes procyonoides koreensis*, raccoon dog, sexual dimorphism.

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Sexual size dimorphism (SSD) is a well-recognized phenomenon, which is observed in many taxa of mammals. Especially, most species in the order Carnivora show clear SSD [4, 12, 14, 22]. Therefore, this taxon has been regarded as a suitable model group to study sexual differentiation in morphology [4]. However, several species of Canidae exhibit exceptionally low to negligible SSD. In the raccoon dog *Nyctereutes procyonoides*, SSD has been studied by several authors [7, 10, 13, 16]. *Nyctereutes procyonoides* has originally held a wide distribution throughout East Asia, however, it has widely established itself throughout Eastern Europe, following introduction to the continent by man. The species shows remarkable geographic variation in the skull and teeth among both native and introduced populations [1, 5, 10, 17]. The sexual dimorphism is reported to be relatively small in raccoon dogs [5, 7, 10, 16], nevertheless, the degree of sexual dimorphism varies between its local populations [5, 16]. To elucidate the factors which have influenced sexual dimorphism within raccoon dogs, an assessment of the geographic variation in sexual dimorphism

should be helpful.

In *N. procyonoides*, there is only one study which has compared the regional differences in sexual dimorphism as noted above [16], though further authors have studied the dimorphism within one region [5, 6]. In this study, we examined sexual dimorphism of the craniodental traits among South Korean specimens, which are regarded as a distinct subspecies, *N. p. koreensis* [15]. This report is the first study to examine the sexual dimorphism of *N. p. koreensis* in South Korea, and should contribute to our understanding of factors relating to the evolution of sexual dimorphism.

### MATERIALS AND METHODS

We examined sexual dimorphism using craniodental measurements of 63 individuals of *N. p. koreensis* from South Korea (male: 37, female: 26). Only adult specimens of which the lower third molar (m3) is fully erupted, were used in order to eliminate age related variation. By using 17 cranial, 7 mandibular and 30 dental measurements (Table 1; Fig. 1), we conducted univariate and multivariate comparisons. These measurement techniques are those from Haba *et al.* [5], though the heights of the upper and lower canines (CH and cH) and the SIZE, the skull length independent of rostrum length (CBL–RL) were excluded. In univariate treatments, we compared the mean and variance values of each measurement by Welch's *t*-test and *F*-test, respectively. As multivariate treatments, we conducted principal component analysis (PCA) based on variance-covariance matrix and canonical variate analysis (CVA) using natural log-

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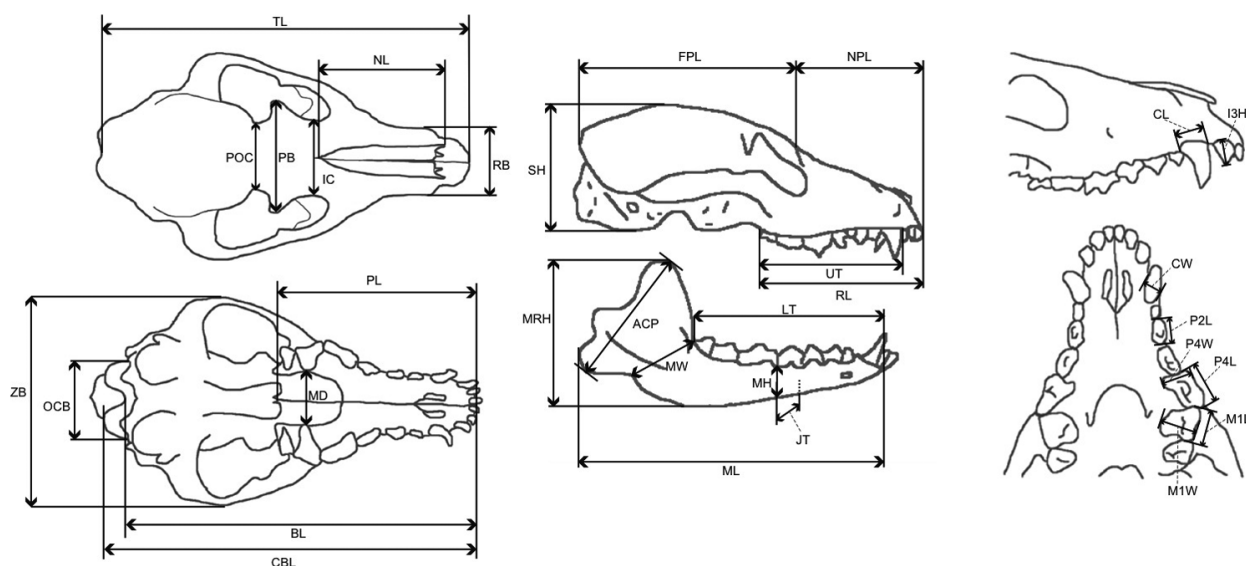


Fig. 1. Skull and tooth measurements of the raccoon dog used in this study.

transformed values of skull (cranium and mandible) (sPCA and sCVA) and dental measurements (tPCA and tCVA) separately. For these analyses, we used specimens without missing values (skull; male: 36, female: 25, teeth; male: 35, female: 24). All statistical analyses were conducted with the software R.2.13.2 [20].

## RESULTS

**Univariate analyses:** Mean values were different between sexes in 5 variables (POC, JT, cW, m3L and CW) (Table 2). Canine measurements (cW and CW) and POC were larger in male specimens, while JT and m3L were larger in females. Differences of variance were observed in 4 variables (RL, MW, p3L and I1H).

**Multivariate analyses:** In the sPCA, the first 3 axes (sPC1, sPC2 and sPC3) explained 36.6, 12.5, and 11.3% of the total variation, respectively (Table 3). Factor loadings for sPC1 were all positive except for POC, and therefore this variable indicated size variation and POC is not correlated with overall skull size. Factor loadings for sPC2 were large in POC (0.79), PB (0.62), IC (0.48) and MH (−0.45), and those for sPC3 were large in MW (0.69) and JT (−0.47). Scores of sPC1 were not different between the sexes ( $P=0.19$ ), and variance of the score was marginally significantly larger in female ( $P=0.077$ ) (Fig. 2A). On the other hand, sPC2 scores were larger in male ( $P=0.0052$ ), although the ranges overlapped to a high degree, and variances were not significantly different ( $P=0.35$ ).

In the tPCA, the first 3 axes accounted for 32.1, 15.4 and 10.0% of the total variation, respectively (Table 4). Factor loadings for tPC1 were larger in incisors. Those for tPC2 were large in canines, some premolars, m1 and M1, and those for tPC3 were larger in m3, followed by canine lengths (0.40 to 0.43). Cumulatively, the first 7 axes accounted for

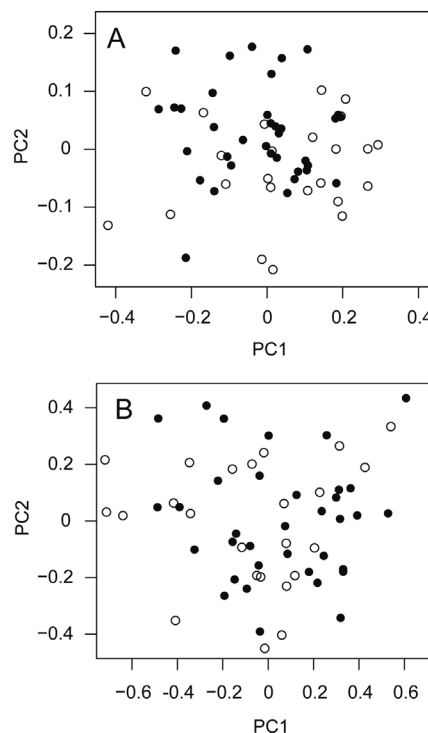


Fig. 2. Two dimensional plots of the first and second principal component axes in skull measurements (A) and dental measurements (B). Open circles: male, closed circles: female.

more than 80% in total. Each of these axes did not show significant difference of either mean or variance between sexes except for tPC4 which explains 8.0% of the total variation showing significant sexual difference of means ( $P=0.026$ )

Table 1. List of skull and tooth measurements of the raccoon dog used in this study

Category	Acronym	Measurement
Cranium	NPL	Nasal + premaxillary length
	NL	Nasal length
	FPL	Frontal + parietal length
	SH	Skull height
	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
	UT	Length of the upper toothrow
	RL	Rostrum length
Mandible	MRH	Height of the mandibular ramus
	ACP	Length from angular process to coronoid process
	LT	Length of the lower toothrow
	JT	Jaw thickness
	MH	Mandibular height
	ML	Mandible length
Tooth	MW	Mandible width
	i1H	Height of the lower first incisor
	i2H	Height of the lower second incisor
	i3H	Height of the lower third incisor
	cL	Length of the lower canine
	cW	Width of the lower canine
	p1L	Length of the lower first premolar
	p2L	Length of the lower second premolar
	p3L	Length of the lower third premolar
	p4L	Length of the lower fourth premolar
	p4W	Width of the lower fourth premolar
	m1L	Length of the lower first molar
	m1W	Width of the lower first molar
	m2L	Length of the lower second molar
	m2W	Width of the lower second molar
	m3L	Length of the lower third molar
	m3W	Width of the lower third molar
	I1H	Height of the upper first incisor
	I2H	Height of the upper second incisor
	I3H	Height of the upper third incisor
	CL	Length of the upper canine
	CW	Width of the upper canine
	P1L	Length of the upper first premolar
	P2L	Length of the upper second premolar
	P3L	Length of the upper third premolar
	P4L	Length of the upper fourth premolar
	P4W	Width of the upper fourth premolar
	M1L	Length of the upper first molar
	M1W	Width of the upper first molar
	M2L	Length of the upper second molar
	M2W	Width of the upper second molar

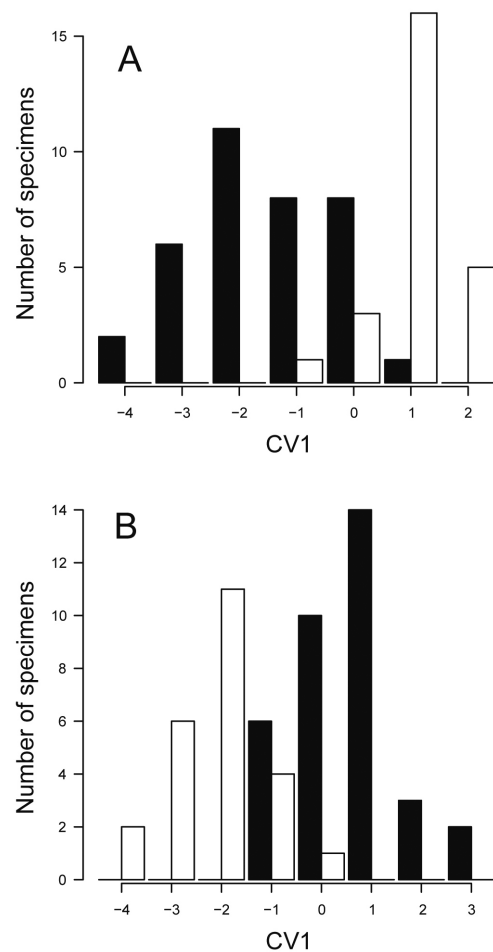


Fig. 3. Frequency distribution of CV1 scores by sCVA (A) and tCVA (B). Black: male, white: female.

(Fig. 2B).

By the CVA using skull and dental variables, 93.4 and 88.1% of specimens were correctly classified into each sex, respectively (Fig. 3). Standardized canonical coefficients for CV1 were large in TL (1.75), MRH (−1.53), MH (1.20), RL (−1.14) and BL (−1.13) in sCVA and large in CW (1.02), m1L (0.96), M1L (−0.92) and P4W (−0.85) in tCVA.

## DISCUSSION

In the present study, we found that sexual dimorphism of craniodental traits of *N. p. koreensis* in South Korea is not strongly pronounced. Similarly, several previous studies have shown that sexual dimorphism of craniodental traits in this species is quite low, or possibly absent in other regions [5, 7, 10, 13, 16]. Although both the current work and that of Haba *et al.* [5] which studied sexual dimorphism in 2 populations (Hokkaido and Honshu), similarly detected significant sexual dimorphism in several canine variables, those traits which showed sexual dimorphism were different between these 3 populations. The most dimorphic variables

Table 2. Descriptive statistics and results of comparison of skull and dental variables in each sex of the raccoon dog from South Korea

Variable	Sex	N	Mean	Ratio (%)	Welch's <i>t</i> -test		Variance	Ratio (%)	<i>F</i> -test	
					<i>t</i>	<i>P</i>			<i>F</i>	<i>P</i>
NPL	Male	37	54.68	98.78	-0.864	0.391	8.72	89.19	0.892	0.740
	Female	26	55.35				9.78			
NL	Male	37	43.99	98.59	-0.845	0.402	7.04	75.14	0.751	0.425
	Female	26	44.62				9.37			
FPL	Male	37	68.54	99.29	-0.640	0.525	8.43	91.31	0.913	0.789
	Female	26	69.03				9.23			
SH	Male	37	43.79	100.50	0.473	0.639	2.33	60.19	0.602	0.160
	Female	26	43.57				3.87			
BL	Male	37	110.47	100.36	0.410	0.683	11.68	70.18	0.702	0.325
	Female	26	110.07				16.64			
RB	Male	37	22.22	100.54	0.510	0.613	0.66	68.74	0.687	0.298
	Female	26	22.10				0.96			
POC	Male	37	20.42	104.44	2.245	<b>0.029</b>	2.15	90.63	0.906	0.773
	Female	26	19.55				2.37			
IC	Male	37	24.04	100.00	0.000	1.000	1.12	56.65	0.567	0.117
	Female	26	24.04				1.97			
PB	Male	37	33.37	101.77	1.261	0.213	2.67	74.27	0.743	0.407
	Female	26	32.79				3.60			
OCB	Male	37	22.35	99.07	-0.823	0.415	0.71	59.65	0.597	0.153
	Female	26	22.56				1.18			
ZB	Male	36	67.03	101.03	0.932	0.356	6.54	70.73	0.707	0.340
	Female	26	66.35				9.24			
TL	Male	37	118.77	99.35	-0.744	0.461	11.56	57.31	0.573	0.124
	Female	26	119.54				20.18			
PL	Male	37	57.88	100.50	0.472	0.639	6.30	122.37	1.224	0.605
	Female	26	57.59				5.15			
MD	Male	37	17.61	99.62	-0.228	0.820	1.58	134.43	1.344	0.443
	Female	26	17.67				1.17			
CBL	Male	37	116.53	99.83	-0.221	0.826	10.31	72.41	0.724	0.369
	Female	26	116.73				14.23			
UT	Male	37	44.99	101.35	1.180	0.245	2.46	49.09	0.491	0.050
	Female	26	44.39				5.01			
RL	Male	37	57.47	101.06	1.072	0.290	2.48	38.39	0.384	<b>0.009</b>
	Female	26	56.86				6.46			
MRH	Male	37	46.84	99.37	-0.507	0.615	4.23	70.57	0.706	0.333
	Female	26	47.13				5.99			
ACP	Male	37	36.84	99.17	-0.628	0.532	4.21	125.04	1.250	0.565
	Female	26	37.15				3.37			
LT	Male	37	52.62	100.92	1.005	0.320	2.65	68.61	0.686	0.300
	Female	25	52.15				3.86			
JT	Male	37	6.43	95.63	-2.217	<b>0.031</b>	0.22	72.79	0.728	0.377
	Female	26	6.73				0.30			
MH	Male	37	12.43	95.32	-1.899	0.064	1.06	54.43	0.544	0.093
	Female	26	13.04				1.94			
ML	Male	37	86.60	99.11	-0.701	0.487	12.28	52.27	0.523	0.074
	Female	26	87.38				23.50			
MW	Male	37	21.88	97.53	-1.188	0.240	5.54	315.11	3.151	<b>0.004</b>
	Female	26	22.43				1.76			
i1H	Male	36	4.03	107.93	1.995	0.051	0.34	105.30	1.053	0.906
	Female	26	3.73				0.32			
i2H	Male	36	4.29	106.34	1.400	0.167	0.53	107.95	1.080	0.854
	Female	26	4.03				0.49			
i3H	Male	37	5.11	103.14	0.786	0.435	0.62	105.54	1.055	0.902
	Female	26	4.96				0.59			

Table 2. (Continued)

Variable	Sex	N	Mean	Ratio (%)	Welch's <i>t</i> -test		Variance	Ratio (%)	<i>F</i> -test	
					<i>t</i>	<i>P</i>			<i>F</i>	<i>P</i>
cL	Male	37	5.54	103.59	1.649	0.105	0.18	77.98	0.780	0.486
	Female	26	5.35				0.23			
cW	Male	37	4.01	108.50	3.605	<b>0.001</b>	0.16	176.78	1.768	0.140
	Female	26	3.69				0.09			
p1L	Male	37	3.14	99.35	-0.217	0.829	0.12	83.22	0.832	0.603
	Female	26	3.17				0.15			
p2L	Male	36	5.54	99.01	-0.689	0.495	0.06	50.65	0.507	0.063
	Female	26	5.60				0.12			
p3L	Male	37	6.24	98.45	-1.055	0.297	0.08	46.23	0.462	<b>0.034</b>
	Female	26	6.34				0.17			
p4L	Male	37	7.49	100.13	0.107	0.915	0.12	88.35	0.884	0.721
	Female	26	7.48				0.14			
p4W	Male	37	3.60	100.57	0.285	0.777	0.07	80.95	0.810	0.552
	Female	26	3.58				0.09			
m1L	Male	37	12.64	101.33	1.240	0.221	0.24	82.64	0.826	0.590
	Female	26	12.47				0.30			
m1W	Male	37	5.15	98.58	-0.750	0.456	0.18	146.19	1.462	0.324
	Female	26	5.23				0.13			
m2L	Male	36	6.56	97.35	-1.934	0.058	0.13	100.25	1.002	0.989
	Female	26	6.74				0.13			
m2W	Male	36	4.30	103.08	1.419	0.161	0.15	144.06	1.441	0.345
	Female	26	4.17				0.10			
m3L	Male	37	3.05	93.55	-2.119	<b>0.038</b>	0.18	144.35	1.444	0.349
	Female	25	3.26				0.12			
m3W	Male	37	2.51	99.02	-0.322	0.748	0.12	198.71	1.987	0.081
	Female	25	2.53				0.06			
I1H	Male	36	3.35	97.91	-0.455	0.651	0.20	40.00	0.400	<b>0.013</b>
	Female	26	3.42				0.50			
I2H	Male	37	4.33	102.60	0.685	0.496	0.40	105.41	1.054	0.905
	Female	26	4.22				0.38			
I3H	Male	36	5.78	98.67	-0.427	0.671	0.47	88.95	0.890	0.738
	Female	26	5.86				0.53			
CL	Male	37	5.56	103.11	1.621	0.111	0.16	97.38	0.974	0.925
	Female	26	5.39				0.17			
CW	Male	37	3.98	107.21	3.003	<b>0.004</b>	0.17	205.05	2.050	0.064
	Female	26	3.71				0.08			
P1L	Male	37	3.49	96.78	-1.527	0.133	0.09	111.33	1.113	0.790
	Female	26	3.60				0.08			
P2L	Male	37	5.62	99.55	-0.385	0.702	0.07	113.17	1.132	0.762
	Female	25	5.65				0.06			
P3L	Male	37	6.73	99.62	-0.246	0.807	0.16	93.97	0.940	0.849
	Female	26	6.75				0.17			
P4L	Male	36	11.23	100.69	0.443	0.660	0.29	49.87	0.499	0.057
	Female	26	11.16				0.59			
P4W	Male	36	6.00	97.36	-1.279	0.206	0.30	141.81	1.418	0.366
	Female	26	6.17				0.21			
M1L	Male	36	8.76	99.11	-0.710	0.481	0.19	105.95	1.059	0.894
	Female	26	8.84				0.18			
M1W	Male	37	9.19	101.17	0.777	0.440	0.26	84.43	0.844	0.631
	Female	26	9.09				0.30			
M2L	Male	36	5.47	100.12	0.064	0.949	0.18	141.01	1.410	0.374
	Female	26	5.47				0.13			
M2W	Male	37	6.16	99.97	-0.018	0.986	0.24	132.76	1.328	0.463
	Female	26	6.16				0.18			

Ratio: ratios of mean and variance, male/female  $\times 100$  (%). Bold:  $P < 0.05$ .

Table 3. The first 6 principal components which account for more than 80% of total variation from the sPCA

Variable	PC1	PC2	PC3	PC4	PC5	PC6
NPL	<b>0.754</b>	0.128	0.239	-0.382	-0.295	0.264
NL	<b>0.684</b>	0.187	0.298	-0.386	-0.308	0.341
FPL	0.441	-0.153	-0.216	0.302	0.084	-0.513
SH	<b>0.637</b>	0.238	-0.056	0.013	0.307	-0.157
TL	<b>0.871</b>	0.058	0.152	-0.201	-0.081	-0.157
RB	0.493	0.275	-0.127	0.116	0.291	0.019
POC	-0.148	<b>0.790</b>	-0.376	0.303	-0.248	0.099
IC	0.478	0.480	-0.057	0.113	0.068	-0.166
PB	0.394	<b>0.622</b>	-0.215	0.387	-0.055	0.027
OCB	0.247	0.106	0.070	-0.091	-0.130	0.200
ZB	<b>0.722</b>	0.183	-0.055	0.185	0.070	-0.117
GL	<b>0.886</b>	0.039	0.090	-0.059	-0.141	-0.209
PL	<b>0.665</b>	0.228	0.140	-0.250	-0.228	-0.161
MD	0.413	0.346	0.020	-0.378	0.518	-0.311
CBL	<b>0.787</b>	0.081	0.174	-0.196	-0.103	-0.134
UT	<b>0.699</b>	0.250	-0.025	-0.345	-0.219	-0.282
RL	<b>0.723</b>	0.246	0.007	-0.371	-0.146	-0.237
MRH	<b>0.775</b>	-0.152	-0.182	0.146	0.145	-0.128
ACP	<b>0.703</b>	0.070	0.113	0.166	0.289	-0.128
LT	<b>0.706</b>	0.121	-0.160	-0.273	-0.213	-0.320
JT	<b>0.557</b>	-0.102	-0.468	-0.055	0.418	0.491
MH	<b>0.710</b>	-0.448	-0.348	0.194	-0.259	-0.078
ML	<b>0.896</b>	-0.165	-0.034	0.082	-0.113	0.012
MW	<b>0.501</b>	0.005	<b>0.691</b>	0.476	0.110	0.122
Eigenvalue	0.026	0.009	0.008	0.006	0.005	0.004
Proportion	36.639	12.456	11.281	8.270	7.140	5.897
Cumulative	36.639	49.094	60.375	68.645	75.786	81.682

Bold: absolute value >0.5.

were canine widths, followed by length of m3, jaw thickness and breadth of postorbital constriction. These results differ from that of Haba *et al.* [5], which reported significant differences in CBL and upper canine length among the specimens from Hokkaido, as well as differences in lower canine width, length of m3, upper canine length and width of M1 among specimens from Honshu.

It is known that species with prominently sexually dimorphic canines often have a polygynous mating system, and canines are often recruited for male-male competitions [3]. On the other hand, those with a more relaxed sexual dimorphism in the canines tend to exhibit monogamous mating systems [4]. The raccoon dog is reported to be monogamous in Korea, Japan and Finland [2, 8, 9, 23], although the mating systems of the species have not been studied in other populations. Future field observations of the interactions between males, especially on the use of canines for inter-male competitions or associated behavior, should shed further light on the evolution of arrested sexual dimorphism in the raccoon dogs.

The number and kinds of sexually dimorphic traits seem to be different between populations, as has been shown in our study as well as further previous studies [5, 16]. One explanation for this variability is that the selective forces acting upon the craniodental morphology of each sex may be different between populations. However, it should be

noted that many craniodental traits are often associated with one another [11, 18, 19]. If quantitative aspects of such traits are significantly integrated in a likewise manner, the apparent sexual dimorphism observed in some traits might be a byproduct of true sexual dimorphism. To investigate this possibility, geographically broader studies using comparable data from many distinct populations are required.

CVA using skull variables discriminated between the sexes more clearly than tCVA, despite using fewer skull variables than those of teeth. Scores of sPC2 and those of tPC4 were significantly different between sexes, but the total variation which we could account for was higher in the former. These results indicate that the overall sexual difference is more apparent from data relating to the skull than that relating to the teeth. In general, tooth measurements are more variable than skull measurements within a given population of carnivorous species [19, 21]. Therefore, although the clearest differences are found among canine widths, it is likely that the highly variable nature of the teeth may obscure the discrimination between sexes.

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Table 4. The first 7 principal components which account for more than 80% of total variation from the tPCA

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
i1H	<b>0.811</b>	-0.114	-0.135	-0.432	-0.042	0.129	0.036
i2H	<b>0.874</b>	-0.100	-0.167	-0.229	-0.183	0.081	-0.132
i3H	<b>0.904</b>	-0.112	0.055	0.018	0.060	0.081	0.067
cL	0.198	<b>0.579</b>	0.400	-0.241	0.078	-0.182	-0.396
cW	0.131	<b>0.698</b>	0.281	-0.228	0.269	-0.197	-0.031
p1L	0.244	<b>0.535</b>	0.098	0.046	<b>-0.635</b>	-0.044	0.216
p2L	0.177	<b>0.569</b>	0.192	0.198	-0.144	0.038	-0.122
p3L	0.075	0.428	0.045	0.239	-0.286	0.285	-0.132
p4L	0.106	<b>0.663</b>	0.017	0.053	-0.097	0.190	0.220
p4W	0.229	<b>0.683</b>	-0.045	-0.025	0.338	0.218	0.111
m1L	0.248	<b>0.709</b>	0.137	0.036	-0.146	0.204	0.029
m1W	0.201	<b>0.805</b>	0.009	0.082	0.065	0.139	0.172
m2L	0.047	0.333	-0.129	0.394	0.211	0.254	0.021
m2W	0.219	0.289	-0.226	-0.121	<b>0.609</b>	0.372	-0.068
m3L	-0.042	0.244	<b>-0.878</b>	0.150	-0.094	-0.192	0.009
m3W	0.157	0.328	<b>-0.769</b>	0.157	0.172	-0.250	-0.142
I1H	<b>0.699</b>	-0.086	0.131	<b>0.624</b>	0.002	0.198	-0.128
I2H	<b>0.748</b>	-0.203	0.055	0.115	0.330	-0.300	0.367
I3H	<b>0.548</b>	0.009	0.250	0.241	-0.160	<b>-0.602</b>	-0.146
CL	0.291	<b>0.514</b>	0.432	-0.234	0.165	-0.152	-0.364
CW	0.292	<b>0.672</b>	0.276	-0.275	0.268	-0.208	0.065
P1L	0.157	<b>0.551</b>	-0.031	-0.149	-0.413	-0.031	0.111
P2L	-0.012	<b>0.573</b>	0.298	0.060	-0.009	0.167	0.188
P3L	-0.083	0.314	0.139	0.330	-0.089	0.173	0.025
P4L	0.044	<b>0.743</b>	0.139	0.179	-0.083	0.108	0.015
P4W	0.116	<b>0.719</b>	-0.086	0.170	-0.051	-0.021	0.096
M1L	0.115	<b>0.648</b>	0.071	0.174	-0.199	0.289	0.315
M1W	0.176	<b>0.763</b>	0.106	0.033	0.144	0.175	0.014
M2L	0.040	0.380	-0.163	0.173	0.017	0.441	0.302
M2W	0.207	0.463	-0.089	0.074	0.388	0.192	-0.291
Eigenvalue	0.097	0.046	0.030	0.024	0.019	0.017	0.010
Proportion	32.084	15.403	10.019	7.981	6.223	5.511	3.155
Cumulative	32.084	47.487	57.506	65.487	71.709	77.220	80.375

Bold: absolute value >0.5.

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