Cranial morphological homogeneity in two subspecies of water deer in China and Korea

Yung Kun KIM1,3,4,*, Daisuke KOYABU2,*, Hang LEE3 and Junpei KIMURA3,*

1) Conservation Genome Resource Bank for Korean Wildlife, College of Veterinary Medicine, Seoul National University, Seoul 151–742, Korea
2) The University Museum, The University of Tokyo, 7–3–1 Hongo, Bunkyo-ku, Tokyo 113–0033, Japan
3) Department of Anatomy and Cell Biology, College of Veterinary Medicine, Seoul National University, Seoul 151–742, Korea
4) Marine Vertebrate Team, National Marine Biodiversity Institute of Korea, 101-75, Jangsan-ro, Janghang-eup, Seocheon-gun, Chungcheongnam-do, 33662, Korea

(Received 19 January 2015/Accepted 23 May 2015/Published online in J-STAGE 7 June 2015)

ABSTRACT. The water deer (Hydropotes inermis) has conventionally been classified into two subspecies according to geographic distribution and pelage color pattern: H. i. inermis from China and H. i. argyropus from Korea. However, the results of a recent molecular study have called this into question. To further reappraise this classification, we examined morphological variation in craniodental measurements of these 2 subspecies. Results of univariate and multivariate analyses demonstrated that these 2 subspecies are not well-differentiated, suggesting that individuals of the 2 populations share common morphological traits. Despite the distribution of the subspecies at different latitudes, no clear morphocline was detected, suggesting that Bergmann’s rule does not apply in this case. Discriminant analysis indicated that the characteristics of individuals are shared by both populations, suggesting that not all individuals can be assigned to their original population. Results of principal component analysis showed that the two populations shared more than 75% of individuals, congruent with the “75% rule” of subspecies classification. In both the neighbor-joining and unweighted pair group methods with arithmetic mean cluster analyses, specimens of H. i. argyropus and H. i. inermis were highly mixed within the cladograms. These results suggest that the overall morphological variation in the 2 subspecies overlaps considerably and that there is no coherent craniofacial difference between the 2 groups. The present findings combined with prior observations from molecular biogeography point out that the taxonomic division of water deer into 2 subspecies should be revisited.

KEY WORDS. Bergmann’s rule, biogeography, Hydropotes inermis, skull, taxonomy

The water deer (Hydropotes inermis) is the only species in the genus Hydropotes, subfamily Hydropotinae, family Cervidae. Two subspecies of water deer have traditionally been recognized. One is the Chinese water deer (H. i. inermis) [26], distributed in the lower Yangtze Basin, west to Hupeh in China [6]. The other is the Korean water deer (H. i. argyropus) [13], distributed throughout the whole of the Korean peninsula [1, 5]. The subspecies classification has been based solely on the pelage color differences between the two populations. The Korean subspecies is reported to have darker pelage, with more reddish coloring in the head region compared to the Chinese subspecies [28]. Otherwise, the 2 subspecies are very similar [28].

A recent molecular study has raised questions about this subspecies classification [17]. The authors studied the mitochondrial DNA (mtDNA) control region (927 bp) and cytochrome b gene (1,140 bp) sequences of both populations. A total of 30 samples from 3 sites in China and 45 samples from 5 sites in Korea were used. The authors demonstrated 2 sympatric mtDNA clades (a major clade from China and Korea and a minor clade from Korea) with an average genetic distance of 2.1% in the control region and 1.3% in the cytochrome b gene, respectively. A total of 35 haplotypes from the control region were detected with more than 50% bootstrap values; a major clade consisted of 27 haplotypes from China and Korea, and a minor clade had 8 haplotypes from Korea. Based on the cytochrome-b gene, 25 haplotypes were identified. A major clade had 17 haplotypes from China and Korea, and a minor clade had 8 haplotypes from Korea. From this finding, the authors concluded that the current subspecific classification based on pelage color cannot be supported and pointed out the need to morphologically reexamine the validity of the conventional subspecies classification.

In many cases, morphological variation related to adaptations to local climate is found between “subspecies” (i.e., Bergmann’s rule) [4]. Bergmann’s rule predicts that the average body size of a population in colder areas is generally larger than that in warmer regions due to physiological adaptations to colder environments. Numerous studies have tested Bergmann’s rule, and the results have been equivocal, with some observations being consistent and others being inconsistent with the rule. According to Meiri and Dayan...
[23], 97 of 149 mammal species from 12 orders (65.1%) follow Bergmann's rule. They reported that the validity of Bergmann’s rule differed depending on the taxon. For example, Artiodactyla (7 species), Carnivora (43 species), Cetacea (1 species), Chiroptera (13 species), Didelphimorphia (1 species), Diprotodontia (6 species), Hyracoidea (1 species), Insectivora (10 species), Primates (6 species) and Proboscidea (1 species) generally comply with the rule, whereas Rodentia (51 species) does not. Of the orders that do, some include fewer than 10 species or even only one species, which can be problematic for statistical analysis. That study included the order Artiodactyla, which includes the genus *Hydropotes*. The ranges of the two subspecies of water deer are at notably different latitudes (Chinese population: 30°N and Korean population: 35–38°N; Fig. 1), and the average lowest temperature differs considerably (about 2–8°C in January in the Zoushan archipelago and about −10°C in January in Korea). In this study, we used skull size as an indicator of Bergmann’s rule, instead of body mass, because skull size and body mass have high correlation [16]. If Bergmann’s rule holds, we would expect to find larger individuals in the Korean population.

Here, we report the first detailed morphological study of water deer. We examined geographical variation in the skull using 36 measurements and tested the validity of the conventional classification. The difference in sexual dimorphic patterns between the 2 populations was also examined. Based on the results, we suggest the need to reconsider the subspecies classification of water deer.

MATERIALS AND METHODS

Sample collection: In total, 95 crania were examined: 50 *H. i. inermis* (♀=30, ♂=20) and 45 *H. i. argyropus* (♀=28, ♂=17) (Table 1). The specimens were from museums including East China Normal University (ECNU), Shanghai; the Shanghai Science and Technology Museum (SSTM), Shanghai; and the Chinese Academy of Sciences (CAS), Beijing. As locality information for some of the Chinese specimens was missing, we considered all of these specimens as one Chinese population. For the Korean water deer, all specimens were collected by the Conservation Genome Resource Bank for Korean Wildlife (CGRB) and kept in the Department of Anatomy and Cell Biology, College of Veterinary Medicine, Seoul National University. Specimens were limited to adults with fully erupted teeth to avoid age-related bias.

Measurements and statistical analyses: Following the definitions of von den Driesch [9], 36 linear measurements (Fig. 2 and Table 2) were taken on the right side of each skull by one of the authors (Y.K.K.) to the nearest 0.01 mm with digital vernier calipers (Mitutoyo, Tokyo, Japan).

As geographical differences have not yet been reported in this species, we examined the differences in each skull measurement between males and females of both subspecies with a Student’s *t*-test using PASW Statistics v18 program (IBM, Chicago, IL, U.S.A.). All data were log-transformed before following multivariate analyses. Principal component analysis (PCA) and subsequent VARIMAX rotation were attempted to analyze the variation pattern using PASW Statistics v18 program (IBM) [8]. Standardized Cronbach’s alpha value was estimated to assess the reliability of the principal component analysis. The statistical certainty of assignment for individuals into their reference populations was evaluated by discriminant analysis (DA). These analyses were conducted using PAST version 2.12 for DA [11]. Results of PCA were applied to the “75% rule” that defines the criteria for subspecies classification [2].

The overall morphological similarities between and within the two populations were calculated using a Euclidean distance matrix by PopTools [14]. Each Euclidean morphological distance value (*Ed*) was recalculated with the formula \(1/(1+Ed)\) to set maximum and minimum values.

Using this formula, all morphological distance values were converted into the range 0–1. Here, the pairwise similarity value approaches 1 with increasing morphological similarity between the 2 populations. The hierarchical cluster diagram was drawn using measurement data in PAST version 2.12 [11]. In this clustering analysis, the neighbor-joining (NJ) clustering and the unweighted pair group method with arithmetic mean (UPGMA) clustering methods were conducted to test hierarchical topology among these specimens and were assessed by 1,000 bootstrap replicates.

RESULTS

Univariate analysis: Mean values of 7 skull measurements from female specimens (BFA, LMPR, GBOC, GBB, LFB, GBO and BC) and male specimens (GLN, LMPR, LPR, GBB, GBFM, LFB and BC) were significantly larger for *H. i. argyropus* than *H. i. inermis* (Table 3). In contrast, one measurement from females (BCA) and from males (GBN) was significantly larger for *H. i. inermis* than *H. i. argyropus*. In addition, most average values for all other measurements, which were not significantly different between subspecies,
were larger in *H. i. argyropus* than *H. i. inermis* in females.

PCA: In the PCA of cranium measurements, the first (F1) and second (F2) components explained 37.90% and 10.53% of the total variation in males (Table 5), and 32.86% and 14.43% of the variation in females (Table 6). The reliability of this analysis as tested by standardized Cronbach's alpha was 0.94 in males and 0.92 in females. Therefore, the reliability of the results was accepted as fairly high. The first
Y. KIM, D. KOYABU, H. LEE AND J. KIMURA

8 components which account for more than 1 eigenvalue explained 80.35% of total variance for males (Table 5). For the PC1 of males, values of thirteen components (TL, CBL, BL, SSL, PP, BFA, VCL, LP, AKI, SL, MPL, OPL and LLP) were significant. For females, the first 8 components which account for more than 1 eigenvalue explained 82.90% of total variance for females (Table 6). For the PC1 of females, values of thirteen components (TL, CBL, BL, PP, BFA, VCL, LR, LP, AKI, SL, MPL, OPL and LLP) were significant. In the scatter plots, individuals of 2 subspecies overlapped each other (Fig. 3). Factor loading values of males and females were not significantly different ($P > 0.05$).

DA: The result of DA could not discriminate populations significantly for males and females ($P = 0.359$ for males and $P = 0.487$ for females). From DA, 70.69% of males and 75.69% of females were correctly classified into their original population. Figure 4 is a bar plot of the DA between the two populations.

Morphological distance and cluster analysis: The within-population and inter-population morphological similarities computed by the Euclidean method were estimated for both

| Measurements | Male argyropus | Female argyropus | Female inermis |
|--------------|----------------|-----------------|----------------|
| Geometric Mean | 56.15 | 55.85 | 57.10 | 56.12 |
| TL | 168.33 | 4.87 | 169.22 | 3.96 | 173.26 | 3.56 | 172.54 | 4.78 |
| CBL | 158.24 | 5.19 | 158.59 | 3.67 | 163.13 | 3.31 | 162.25 | 4.79 |
| BL | 147.79 | 4.99 | 148.62 | 3.50 | 152.87 | 3.41 | 152.07 | 4.52 |
| SSL | 94.36 | 2.34 | 94.29 | 2.43 | 97.15 | 1.96 | 96.37 | 3.39 |
| PP | 53.39 | 3.07 | 54.24 | 1.92 | 55.67 | 2.65 | 55.44 | 2.35 |
| BFA | 113.31 | 3.81 | 113.81 | 3.60 | 117.11 | 2.17 | 114.38 | 3.99 |
| NCL | 93.21 | 3.33 | 93.78 | 3.41 | 94.58 | 1.99 | 93.18 | 3.74 |
| VCL | 81.26 | 3.56 | 81.29 | 3.06 | 84.79 | 3.39 | 84.05 | 3.17 |
| MFL | 95.80 | 3.23 | 94.54 | 2.39 | 95.10 | 2.17 | 94.38 | 3.35 |
| LN | 83.25 | 3.09 | 83.32 | 2.35 | 83.68 | 2.25 | 83.57 | 4.09 |
| LR | 135.56 | 3.86 | 133.34 | 4.76 | 138.02 | 3.84 | 135.93 | 3.80 |
| LP | 160.67 | 4.80 | 160.73 | 4.31 | 164.73 | 3.95 | 164.22 | 4.77 |
| AKI | 117.23 | 3.08 | 117.29 | 3.22 | 120.14 | 1.87 | 119.44 | 4.01 |
| GLN | 52.91 | 3.50 | 50.93 | 3.93 | 54.99 | 3.37 | 53.10 | 3.39 |
| SL | 80.67 | 2.82 | 81.13 | 2.63 | 84.15 | 2.95 | 83.48 | 2.96 |
| MPL | 95.61 | 4.38 | 97.40 | 3.54 | 100.18 | 3.36 | 99.56 | 2.97 |
| OPL | 72.40 | 3.46 | 73.20 | 2.31 | 75.38 | 2.92 | 74.47 | 2.71 |
| LLP | 46.72 | 3.06 | 46.69 | 3.00 | 49.04 | 3.16 | 48.34 | 2.64 |
| LMPR | 50.17 | 2.22 | 48.84 | 1.96 | 49.91 | 2.40 | 48.32 | 2.29 |
| LMR | 27.98 | 1.11 | 27.90 | 1.35 | 27.87 | 1.46 | 27.45 | 1.47 |
| LPR | 23.77 | 1.57 | 22.97 | 1.04 | 23.82 | 1.54 | 22.89 | 1.25 |
| LO1 | 25.44 | 1.04 | 25.51 | 0.79 | 26.05 | 0.86 | 25.86 | 1.08 |
| LO2 | 25.24 | 1.22 | 24.99 | 0.93 | 25.26 | 1.00 | 25.13 | 0.95 |
| GMB | 47.28 | 1.62 | 47.39 | 1.93 | 47.45 | 1.99 | 46.93 | 1.78 |
| GBF | 29.21 | 2.41 | 28.21 | 1.21 | 29.28 | 0.87 | 28.13 | 1.15 |
| GBG | 41.87 | 1.27 | 40.81 | 1.57 | 42.25 | 1.67 | 39.89 | 1.60 |
| GBFMM | 14.39 | 0.83 | 13.86 | 0.83 | 14.06 | 0.95 | 14.08 | 1.18 |
| GHB | 14.87 | 0.82 | 14.64 | 0.94 | 14.59 | 1.30 | 14.97 | 1.16 |
| LFB | 71.97 | 2.66 | 70.12 | 2.66 | 73.32 | 2.16 | 69.22 | 3.06 |
| ZB | 39.25 | 1.91 | 38.22 | 2.21 | 40.60 | 3.02 | 39.39 | 2.01 |
| LBO | 71.20 | 2.62 | 71.11 | 2.64 | 71.94 | 2.45 | 71.53 | 3.13 |
| GBO | 16.29 | 1.74 | 16.24 | 2.35 | 16.76 | 1.54 | 15.29 | 1.52 |
| GBN | 29.59 | 2.45 | 31.28 | 2.12 | 26.80 | 2.56 | 25.93 | 1.86 |
| GBP | 51.43 | 2.18 | 51.69 | 1.72 | 52.70 | 2.01 | 51.44 | 2.08 |
| BC | 41.72 | 1.54 | 40.92 | 1.48 | 42.07 | 1.30 | 40.82 | 1.59 |

Bold: significant difference between Korea and China.
sexes (Table 4). For males, the intra-population morphological similarity was 0.972 for both populations, and the inter-population distance was 0.971. For females, the intra-population similarity was 0.973 for the Korean population and 0.971 for the Chinese population. The inter-population similarity was 0.970. Figures 5 and 6 show the results of cluster analysis using the UPGMA and NJ methods, respectively, as well as the cladogram topology. Both methods showed that specimens from each population had mixed topologies in two cladograms; the morphological distance (=similarity, Y-axis) was <1% in the UPGMA cladogram.

### DISCUSSION

**Morphological differences between H. i. inermis and H. i. argyropus**: The present study investigated the 2 subspecies of water deer (*H. inermis*) distributed in Korea and China. The major goal of this research was to morphologically test the conventional subspecific classification of this species. The results of a Student’s *t*-test and PCA suggested that these 2 subspecies are not well-differentiated, meaning that individuals of the 2 populations share common morphological traits. DA results also indicated that some individuals share characteristics of both populations, suggesting that not all individuals can be assigned to their original population based on morphometrics. The results of cluster analysis using 2...
different algorithms, NJ and UPGMA, showed that specimens of the two populations had highly mixed topologies in the cladograms.

Previous research has confirmed that the 2 subspecies have a close genetic distance, with an average genetic distance of 2.1% in the control region and 1.3% in cytochrome b [17]. The topology of a phylogenetic NJ tree from the control region and cytochrome b showed that *H. i. inermis* and *H. i. argyropus* blended within a major clade. In the present study, it was found that the morphological distance between the populations was also very close. The inter-population similarity was almost the same as the intra-population similarity. These facts suggest that the 2 populations cannot be clearly distinguished genetically nor morphologically.

Bergmann’s rule posits that body size is negatively correlated with temperature among closely related species in mammals and birds [4, 15]. This pattern has been pointed out to be obvious, especially within species [19, 20] and has been regarded as one of the major factors producing within-species geographic variation [10, 25]. However, our results show that water deer do not follow Bergmann’s rule. TL, which represents skull size, was not significantly different between *H. i. inermis* and *H. i. argyropus* (Table 3). The Zhoushan Islands, the habitat of the Chinese water deer in central China (Fig. 1A), are located around 30°N latitude, and Korean water deer are distributed around 35–38°N latitude. Similar to the present results, others have demonstrated that this rule is not always applicable [3, 7, 22, 24, 27, 29].

| Variable | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|
| TL       | 0.865 | 0.402 | 0.113 | 0.008 | 0.098 | 0.046 | 0.119 | 0.114 |
| CBL      | 0.842 | 0.339 | 0.074 | −0.112 | 0.182 | −0.181 | 0.064 | 0.125 |
| BL       | 0.845 | 0.317 | 0.057 | −0.161 | 0.144 | −0.192 | 0.069 | 0.196 |
| SSL      | 0.497 | 0.468 | −0.063 | 0.186 | 0.233 | −0.336 | 0.187 | 0.460 |
| PP       | 0.808 | 0.011 | 0.173 | −0.415 | −0.010 | 0.084 | −0.129 | −0.178 |
| BCA      | 0.168 | 0.066 | 0.196 | −0.174 | −0.166 | −0.108 | 0.854 | −0.001 |
| BFA      | 0.627 | 0.272 | −0.071 | 0.008 | 0.269 | −0.081 | 0.572 | 0.197 |
| NCL      | 0.217 | 0.778 | 0.068 | 0.254 | 0.303 | −0.205 | −0.065 | −0.060 |
| VCL      | 0.889 | −0.325 | −0.021 | −0.036 | 0.091 | −0.015 | 0.046 | 0.168 |
| MFL      | 0.235 | 0.861 | 0.140 | 0.254 | 0.409 | 0.991 | 0.076 | −0.009 |
| LN       | 0.333 | 0.834 | 0.104 | 0.268 | −0.098 | 0.095 | 0.051 | −0.108 |
| LR       | 0.712 | 0.289 | 0.257 | 0.261 | 0.152 | 0.097 | 0.011 | 0.330 |
| LP       | 0.904 | 0.332 | 0.079 | 0.006 | 0.059 | 0.046 | 0.168 | 0.197 |
| AKI      | 0.586 | 0.613 | 0.181 | 0.131 | 0.124 | −0.043 | 0.184 | 0.240 |
| GLN      | 0.442 | −0.511 | 0.145 | 0.106 | 0.228 | 0.013 | −0.065 | 0.524 |
| SL       | 0.903 | 0.036 | −0.190 | −0.089 | 0.092 | −0.122 | −0.024 | −0.144 |
| MPL      | 0.823 | 0.078 | 0.157 | −0.070 | −0.194 | 0.092 | −0.086 | 0.102 |
| OPL      | 0.823 | 0.084 | 0.129 | −0.238 | −0.057 | −0.047 | −0.209 | −0.231 |
| LLP      | 0.635 | −0.040 | 0.233 | −0.069 | 0.095 | 0.196 | 0.170 | 0.114 |
| LMPR     | −0.125 | 0.178 | −0.034 | 0.939 | 0.108 | −0.036 | −0.136 | 0.050 |
| LMR      | −0.287 | 0.119 | −0.129 | 0.868 | 0.102 | −0.014 | 0.069 | 0.208 |
| LPR      | −0.104 | 0.079 | 0.094 | 0.884 | 0.109 | 0.071 | −0.104 | −0.119 |
| LO1      | 0.080 | 0.724 | 0.292 | −0.191 | −0.140 | −0.055 | −0.204 | 0.150 |
| LO2      | 0.401 | 0.064 | 0.357 | 0.090 | −0.063 | 0.147 | −0.146 | 0.501 |
| GMB      | 0.179 | 0.070 | 0.786 | 0.126 | 0.017 | 0.015 | 0.112 | −0.179 |
| GBC      | 0.056 | −0.026 | 0.014 | 0.136 | 0.795 | 0.237 | −0.223 | 3.036 |
| GBG      | 0.122 | 0.033 | 0.511 | 0.011 | 0.634 | −0.006 | 0.019 | 0.050 |
| GBFM     | −0.186 | 0.008 | 0.089 | −0.213 | 0.286 | 0.789 | 0.034 | 0.226 |
| GHFM     | 0.145 | 0.010 | −0.115 | 0.205 | 0.081 | 0.790 | −0.073 | 0.177 |
| LFB      | 0.187 | 0.243 | 0.810 | −0.019 | 0.077 | −0.054 | −0.108 | −0.001 |
| ZB       | −0.005 | 0.378 | 0.323 | 0.053 | 0.354 | −0.538 | 0.104 | −0.142 |
| LBO      | −0.134 | 0.171 | 0.786 | −0.272 | 0.018 | −0.095 | 0.227 | 0.206 |
| GBO      | 0.160 | −0.157 | 0.730 | −0.001 | 0.341 | 0.143 | 0.067 | 0.075 |
| GBN      | 0.025 | 0.544 | 0.499 | −0.144 | 0.221 | −0.312 | −0.034 | 0.058 |
| GBP      | 0.033 | 0.203 | 0.861 | 0.024 | 0.070 | −0.122 | 0.041 | 0.143 |
| BC       | 0.190 | 0.176 | 0.327 | 0.282 | 0.691 | −0.033 | −0.057 | 0.134 |

| Eigenvalue | Proportion | Cumulative |
|------------|------------|------------|
| 11.830     | 32.862     | 32.862     |
though the reason for the lack of clear morphcline in water deer is yet unclear, the establishment of current distribution of this species was perhaps a relatively recent event, producing the observed genetic and morphological homogeneity.

**Necessity to reconsider the subspecies classification of water deer:** Subspecies of water deer were initially designated by Swinhoe [26] and Heude [13]. Although the concept of subspecies has varied, it is generally defined as members of a polypytic species, not simply as a "slightly different" local population [21]. Results of PCA indicate that the 2 populations show more than 75% of overlap and reject the subspecies classification under the "75% rule" [2]. Phylogenetic analysis studying the mtDNA proposed that the subspecific classification may not be valid and indicated the need for examination of this issue from a morphological perspective [17]. Our results demonstrate that there is no clear difference in craniodental morphology between the 2 populations, lending further support to the reconsideration of the subspecific classification of water deer. The differences between the Chinese and Korean populations are thus not exceptional, other than their pelage color [28]. However, the pelage color variation has not been studied quantitatively and remains to be evaluated [18].

Although the Chinese water deer was originally distributed widely throughout China, these animals have gradually become rarer, and their distribution has been fragmented over the past century due to poaching for traditional medicine and habitat destruction by industrialization [12, 30, 32, 33]. Today, the Chinese water deer is classified as a vulnerable species by the International Union for Conservation of Nature (IUCN) [12]. In contrast to the situation in China, Korean water deer are distributed throughout the Korean peninsula, where its numbers are both stable and abundant [31]. If the population of Chinese water deer continues to decrease, plans for restoration will become more urgent. Given the homogeneity of Chinese and Korean water deer demonstrated by molecular evidence [17] and morphological evidence (this study), the introduction of Korean water deer into the Chinese population might be the most logical, and ultimately successful, restoration strategy.
ACKNOWLEDGMENTS. We thank the Shanghai Science and Technology Museum, Dr. Min Chen of East China Normal University and Dr. Chengming Huang of the Chinese Academy Sciences for allowing access to skull specimens for this study. This research was supported by the Basic Research Program of the National Research Foundation of Korea (NRF) funded by the Ministry of Education, Science and Technology (NRF-2012R1A1A3013561).

REFERENCES

1. Allen, J. 1940. Mammals of China and Mongolia. The American Museum of Natural History, New York.
2. Amadon, D. 1949. The seventy-five percent rule for subspecies. Condor 51: 250–258. [CrossRef]
3. Ashton, K. G., Tracy, M. C. and Queiroz, A. D. 2000. Is Bergmann’s rule valid for mammals? Am. Nat. 156: 390–415. [CrossRef]
4. Bergmann, C. 1847. Uber die Verhaltnisse der Warmekonomie der Thiere zu ihrer Grosse. Göttingen Studien 3: 595–708.
5. Butzler, W. 1990. Grzimek’s encyclopedia of mammals. McGraw-Hill Publishing, New York.
6. Corbet, G. B. 1978. The mammals of the Palaearctic region: a taxonomic review. British Museum of National History and Cornell University Press, London.
7. Dayan, T., Simberloff, D., Teichroew, E. and Yom-Tov, Y. 1991. Calibrating the paleothermometer: climate, communities, and the evolution of size. Paleobiology 17: 189–199.
8. Dixon, W. J. 1987. BMDP Statistical Software. University of California Press, Los Angeles.
9. von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. Harvard University Press, Cambridge.
10. Futuyma, D. J. 2009. Evolution. 2nd ed. Sinauer Associates Inc., Sunderland.
11. Hammer, Ø., Harper, D. A. T. and Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol. Electronica 4: 9 Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
12. Harris, R. B. and Duckworth, J. W. 2008. Hydropotes inermis. In: IUCN 2008. 2008 IUCN Red List of Threatened Species.
13. Heude. 1884. Hydropotes inermis argyropus. Comptes Rendus des Séances de l’Académie des Sciences 98: 1017–1018.
14. Hood, G. M. 2010. PopTools, Version 3.2.5. Pest Animal Control CRC, Canberra. Available at http://www.poptools.org.
15. James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365–390. [CrossRef]
16. Janis, C. M. 2005. Correlation of cranial and dental variables with body size in ungulates and macropodoids. pp. 255–300. In: Body Size in Mammalia Paleobiology: Estimation and Biological Implications (Damuth, J. and MacFadden, B. J. eds.), Cambridge University Press, New York.
17. Koh, H. S., Lee, B. K., Wang, J., Heo, S. W. and Jang, K. H. 2009. Two sympatric phylogroups of the Chinese water deer (Hydropotes inermis) identified by mitochondrial DNA control region and cytochrome b gene analyses. Biochem. Genet. 47: 860–867. [Medline] [CrossRef]
18. Koyabu, D. B., Maliivijitnond, S. and Hamada, Y. 2008. Pelage color variation of Macaca arctoides and its evolutionary implications. Int. J. Primatol. 29: 531–541. [CrossRef]
19. Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10: 105–108. [CrossRef]
20. Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge.
21. Mayr, E. 1982. Of what use are subspecies? Auk 99: 593–595.
22. McNab, B. K. 1971. On the ecological significance of Bergmann’s rule. Ecology 52: 845–854. [CrossRef]
23. Meiri, S. and Dayan, T. 2003. On the validity of Bergmann’s rule. J. Biogeogr. 30: 331–351. [CrossRef]
24. Oishi, T., Uraguchi, K., Abramov, A. V. and Masuda, R. 2010. Geographical variations of the skull in the red fox Vulpes vulpes on the Japanese Islands: An exception to Bergmann’s rule. Zoo- log. Sci. 27: 939–945. [Medline] [CrossRef]
25. Ridley, M. 1996. Evolution. 2nd ed. Blackwell Science, Cambridge.
26. Swinhoe, R. 1870. On a new deer from China (Plates VI. & VII.). In: Proceedings of the general meetings for scientific business of the Zoological Society of London. Zoological Science of London, London.
27. Takeuchi, M. 1995. Morphological and ecological study of the red fox Vulpes vulpes in Tochigi, central Japan: a biological monograph on morphology, age structure, sex ratio, mortality, population density, diet, daily activity pattern, and home range use. Ph. D. Thesis, Kanagawa University, Kanagawa.
28. Tate, G.H.H. 1940. Mammals of eastern Asia. MacMillan Co., New York.
29. Uraguchi, K. 2009. Vulpes vulpes (Linnaeus, 1758). In: The wild mammals of Japan. Shoukadoh Book Sellers, Kyoto.
30. Wang, S. 1998. China Red Data Book of Endangered Animals (Mammal Volume). Science Press, Beijing.
31. Won, C. M. and Smith, K. G. 1999. History and current status of mammals of the Korean peninsula. Mammal Rev. 29: 3–36. [CrossRef]
32. Xu, H. F., Zheng, X. Z. and Lu, H. J. 1998. Impact of human activities and habitat changes on distribution of Chinese water deer along the coast area in northern Jiangsu. Acta Theriol. Sin. 18: 161–167 (in Chinese with English abstract).
33. Zhang, E. 1996. Behavioural ecology of the Chinese water deer at Whipsnade Wild Animal Park, England. Ph. D. Thesis, University of Cambridge, Cambridge.