Morphological variation in deer mice in relation to sex and habitat

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Received June 20, 1986

XIA, X., and J. S. MILLAR. 1987. Morphological variation in deer mice in relation to sex and habitat. Can. J. Zool. **65**: 527–533.

Peromyscus maniculatus borealis were collected in two habitats with contrasting physiognomic features in the Kananaskis Valley, Alberta, in the summer of 1983. We tested for differences between sexes and habitats using 4 body measurements (body length, tail length, hind foot length, and ear length) and 10 cranial (including mandibular) measurements of 222 and 192 adult *P. m. borealis*, respectively. Body measurements of 132 juveniles and five cranial (including mandibular) measurements from 124 juvenile skulls were analysed similarly. When differences in body length were controlled, adult males had significantly longer hind feet than adult females. The mandible was also significantly longer in adult males than in adult females. We interpreted the longer hind foot length in adult males as an adaptation to provide greater mobility, and the differences in mandibular morphology as a consequence of differential habitat use between the two sexes. No significant differences were found between juvenile males and females. Sexual dimorphism appeared to be age dependent rather than size dependent when adults and juveniles of similar body size were analysed.

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Des *Peromyscus maniculatus borealis* ont été capturés en deux habitats à structures physiognomoniques distinctes dans la vallée de Kananaskis, Alberta, au cours de l'été 1983. La mesure de quatre structures corporelles (longueur du corps, longueur de la queue, longueur de la patte arrière et longueur de l'oreille) chez 222 adultes et de 10 mesures craniennes (y compris la mesure de la mandibule) chez 192 adultes ont servi à établir les différences reliées au sexe et à l'habitat. De même, les mesures corporelles de 132 jeunes et cinq mesures crâniennes (y compris celle de la mandibule) de 124 crânes de jeunes souris ont été analysées. Pour une même longueur totale, les mâles adultes ont des pattes postérieures significativement plus longues que les femelles adultes. La mandibule est aussi significativement plus longue chez les mâles adultes que chez les femelles adultes. Nous croyons que la croissance de plus grandes pattes postérieures chez les mâles constitue une adaptation à une plus grande mobilité et que les différences dans la morphologie des mandibules chez les mâles et les femelles sont une conséquence d'une utilisation différente de l'habitat. Il n'y a pas de différences significatives entre jeunes mâles et jeunes femelles. Le dimorphisme sexuel semble donc une fonction de l'âge plutôt que de la taille lorsque des adultes et des jeunes de même taille sont comparés.

[Traduit par la revue]

Introduction

Many interspecific and intraspecific studies have demonstrated predictable relationships between morphology and ecology in species of *Peromyscus*. Forest-dwelling *Peromyscus maniculatus* have longer tails and longer hind feet than their prairie realtives (Dice 1940; Horner 1954; Baker 1968), and *Peromyscus polionotus* living on sandy beaches have longer hind feet than those living inland (review in Klingener 1968). Species that inhibit arid land, particularly *Peromyscus truei*, have relatively large pinnae, supposedly an adaptation to detect approaching predators in habitats with sparse cover (review in Klingener 1968). Smartt and Lemen (1980) showed a correlation between morphological variables and food habits of *Peronyscus boylii* and *P. truei*, and Holbrook (1982) found that *P. maniculatus* in woodland habitats had longer mandibles than animals from open habitats, which she attributed to differences in food habits.

Although sexual dimorphism in *P. maniculatus* is poorly documented, recent studies have suggested that males and females may differ both ecologically and morphologically. Bowers and Smith (1979) documented differential habitat use between the sexes: females tended to occupy more mesic sites, with denser vegetation, than males. Dewsbury *et al.* (1980*a*) found male *P. m. blandus* and *P. m. bairdii* to be significantly heavier than females at 35 and 90 days of age. This was consistent with the findings of Drickamer and Bernstein (1972) for *P. m. labecula* and *P. m. nebrascensis*. According to Whitaker's Vigo County data (Mumford and Whitaker 1982), male *P. maniculatus* tended to have longer hind feet than females ier than males in his samples.

Both sex and habitat may affect morphological variation in *P. maniculatus*, but this cannot be assessed when the data from both sexes are pooled to test habitat effects or when the data from different habitats are pooled to test sex effects. For example, in cases where the effect of sex is important while the effect of habitat is not, the morphological differences between the sexes would be attributed to habitat if the effect of sex was ignored and sex ratios differed between samples from different habitats. Similarly, in cases where the effect of habitat is important while the effect of sex is not, the difference between habitats would be attributed to sex if the effect of habitat was ignored and sex ratios differed between habitats. The most serious problem arises when sex and habitat interact significantly. Both effects would be obscured if data were pooled over one factor.

The objective of this study was to examine the effect of both sex and habitat on morphological variation in *Peromyscus maniculatus borealis*.

Materials and methods

Extensive snap-trapping of small mammals in the Kananaskis Valley, Alberta (Millar *et al.* 1985), resulted in a large sample ($N = 384$) of *P. m. borealis* from two habitat types during the summer (May through August) of 1983. Density of *P. m. borealis* in the two habitat types varies synchronously, reaching peak density in July. There is no significant deviation from a 1:1 sex ratio with respect to age and habitat. A brief description of the two habitat types (riparian–deciduous and talus–cliffs) with respect to vegetation is given in Millar *et al.* (1985). The riparian–deciduous habitat consisted of trapping sites along the Kananaskis River and its tributaries. These trapping sites are connected by the river system and the habitat is characterized by balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), and

dense ground cover. The talus–cliff habitat consisted of rock fields, talus slopes, and cliffs on mountain slopes away from the river system. All the trapping sites were located within an area about 40 km long and 8 km wide. The shortest distance between the two habitat types was about 750 m, so the habitat effect should not have been significantly diluted by immigration from areas of a different habitat type. The two habitat types were trapped alternately. Traps were spaced at intervals of about 10 m, baited with peanut butter, set on day 1, checked on days 2, 3, and 4, and removed on day 4. Trapping sites were not resampled.

All *P. m. borealis* were sexed, weighed, and aged on the basis of size and pelage characteristics (Layne 1968). Adults were defined as animals that had overwintered. Juveniles were defined as those animals captured during the summer of their birth. Complete records of habitat, sex, age, weight, reproductive status, and four standard external body measurements (total length (BL), tail length (TAL), hind foot length (HFL), and ear length (EL)) were obtained for 222 adult and 132 juvenile *P. m. borealis*. Two assistants (referred to hereafter as assistant A and assistant B) measured the external characteristics. Skulls were prepared using the method described in Lightbody and Millar (1983). Ten skull measurements (including mandible) were taken by the senior author from 192 adults, using a dial caliper with a precision of 0.02 mm. Cranial measurements for adults consisted of (*i*) condylobasal length (CL), (*i*) width of braincase (BW), (*iii*) bullae – brain case height (BBH), (*iv*) height of braincase (HB), (*v*) width of interorbital constriction (WIC), (*vi*) length of incisive foramen (LIF), (*vii*) greatest length between the anterior edge of the crown of the lower incisors and the anterior margin of the alveolus of the first lower molar (LX), (*viii*) length of ramus (LR), (*ix*) length of upper tooth row (LUTR), and (*x*) length of lower tooth row (LLTR).

Only five cranial measurements were taken for each of 124 juveniles. Skulls of juveniles were fragile and five measurements permitted a relatively large sample to be used. The five measurements (symbols as before) were (*i*) CL, (*ii*) WIC, (*iii*) LIF, (*iv*) LX, and (*v*) LR.

External and cranial measurements were analysed separately. Measurements for adults and juveniles were also analysed separately because of heteroscedasticity. Normality and linearity of the data were checked with normal plotting, bivariate scatter plotting, and residual plotting. Log-transformation was not used because bivariate plotting did not show any curvilinear relationship between any pair of variables, implying that no apparent shape change occurred in *P. m. borealis* within the size range we worked with. For external measurements, three factors (sex, habitat, and assistant) were considered. For cranial measurements, two factors (sex and habitat) were considered. Three-way and two-way MANOVAs were the main statistical procedures. The method of weighted squares of means (generalized least square analysis) for analysis of variance (Barcikowski 1983; Berenson *et al.* 1983, pp. 352–368) was used in all analysis of variance procedures because of unequal cell sizes (appendix Tables A1, A2). The Box-*M* test was used to test homoscedasticity. Discriminant function analyses and analyses of covariance were used to assist interpretation.

Results

The number of animals in different data sets are presented in appendix Tables A1 and A2, together with means and standard errors for each morphological variable.

External body measurements of adults

The three-way MANOVA (assistant, sex, and habitat) revealed significant differences between the sexes ($p = 0.006$) and assistants ($p < 0.0001$) but habitat effect was not significant ($p = 0.090$). A discriminant analysis showed that the two sexes differed most in hind foot length and the two assistants differed most in measuring hind foot length and ear length. The assumption of homoscedasticity, however, was violated (Box-*M* test, $p < 0.0001$). The values of the generalized variance of the eight cells were much smaller for assistant A than for assistant B, implying that the heteroscedasticity was caused by differences in measurements between the two assistants. For assistant A, the generalized variances were 191 (males in riparian–deciduous), 76 (males in talus–cliffs), 29 (females in riparian–deciduous), and 69 (females in talus–cliffs). The corresponding values for assistant B were 336, 160, 1457, and 114. Because heteroscedasticity degrades the multivariate analysis of variance (Tabachnick and Fidell 1983) and smaller generalized variance implies better precision, the data recorded by assistant A only were analysed by a two-way (sex by habitat) MANOVA to see if the result was consistent with the previous three-way MANOVA. The pattern remained the same (Table 1). Sexes differed significantly ($p = 0.007$); discriminant function analysis again revealed that hind foot length contributed most to the differences between the sexes. A two-way MANCOVA on HFL, TAL, and EL with BL as a covariate (Table 2) indicated that adult males had significantly longer (2%) hind feet than adult females ($p = 0.007$) when body length was held constant.

External measurements of juveniles

For the same reasons mentioned with respect to the analysis of external measurements of adults, we ran a two-way MANOVA on the four variables of juveniles measured by assistant A only. The Box-*M* test was significant ($p = 0.02$), but this is not a serious violation of homoscedasticity for a two-way MANOVA (Tabachnick and Fidell 1983, and literature cited therein). The results of the MANOVA (Table 3) revealed no significant difference between the sexes ($p = 0.447$) or habitat types ($p = 0.140$), but univariate tests showed that ear length differed between habitat types ($p = 0.010$). Because age, and consequently size, of juveniles might differ between the two habitats, we used body length as a covariate and tested the effect of sex and habitat on the other three variables. Neither multivariate nor univariate tests revealed any significant sex or habitat effects. Therefore, no significant differences existed between sexes or habitat types in the three external measurements (tail length, hind foot length, and ear length) of juveniles when body length was held constant.

Development of sexual dimorphism in external measurements

Development of sexual dimorphism may provide clues to the interpretation of the dimorphism, e.g., if sexual dimorphism is related to mating activity, it should be more apparent in adults than in juveniles, and should depend more on age than on size. We tested this hypothesis by using adults and juveniles of similar body size to see if the pattern of sexual dimorphism differed between these two groups. Animals with body lengths ranging from 75.1 to 86.0 mm, which included 43 large juveniles and 31 small adults, were chosen for this analysis. This range did not include a few extremely small adults and extremely large juveniles. We hypothesized that, if the small-sized adults differed between sexes while the large-sized juveniles did not, the interaction between sex and age would account for a substantial proportion of variance. This hypothesis was supported (Table 4). The interaction term was significant and accounted for 13.2% of the variance.

Cranial measurements of adults

Correlation coefficients among cranial measurements showed that these measurements were not all highly correlated with each other. Length measurements were correlated among themselves but only weakly correlated with width and height measurements, except for brain width (BW). Because there is little point in doing multivariate analysis of variance and covariance on weakly correlated variables (Tabachinick and Fidell 1983), the 10 skull measurements were classified into two groups: (*i*) length measurements (including BW) and (*ii*) width and height

TABLE 1. Two-way (sex and habitat) MANOVA on body length (BL), tail length (TAL), hindfoot length (HFL), and ear length (EL) of adults measured by assistant A

Source of variation	Multivariate: Wilk's lambda	df	F (significance)	n^2	Standard discriminant function coefficients: BL	TAL	HFL	EL
Sex	0.886	4,115	3.69(0.007)	11.4%	0.147	0.710	−0.988	−0.269
Habitat	0.964	4,115	1.07(ns)	—	—	—	—	—
Sex × habitat	0.943	4,115	1.74(ns)	—	—	—	—	—

NOTE: n^2 (1 − Wilk's Lambda) shows the strength of association between the dependent variables and the model (the variance explained by the model). n^2 and standardized discriminant function coefficients are presented only for effects with $p < 0.10$

TABLE 2. Two-way (sex and habitat) MANCOVA on tail length (TAL), hind foot length (HFL), and ear length (EL) using body length (BL) as a covariate for adults measured by assistant A (see Table 1 for explanation of symbols)

Source of variation	Multivariate: Wilk's lambda	df	F (significance)	n^2	Univariate (df 1,117): F (significance) TAL	HFL	EL
Parallelism	0.899	9,272	1.35(0.211)				
Regression	0.760	3,115	12.09(0.000)	24.0%	29.20(0.000)	20.41(0.000)	9.65(0.002)
Sex	0.906	3,115	3.99(0.009)	9.4%	—	7.49(0.007)[a]	—
Habitat	0.973	3,115	1.07(ns)	—	—	—	—
Sex × habitat	0.974	3,115	1.04(ns)	—	—	—	—

[a]Adjusted marginal means for HFL between the two sexes (in mm): males, 19.4174, females, 19.0452.

TABLE 3. Two-way (sex and habitat) MANOVA on body length (BL), tail length (TAL), hind foot length (HFL), and ear length (EL) for juveniles measured by assistance A (F value and the corresponding significance level for univariate analyses are presented only for effects with $p < 0.05$)

Source of variation	Multivariate: Wilk's lambda	df	F (significance)	n^2	Univariate (df 1,66): F (significance) BL	TAL	HFL	EL
Sex	0.944	4,63	0.94(0.447)	—	—	—	—	—
Habitat	0.898	4,63	1.80(0.140)	10.3%	—	—	—	7.05(0.010)
Sex × habitat	0.964	4,121	1.13(0.594)	—	—	—	—	—

TABLE 4. Two-way (sex by age) MANOVA on tail length (TAL), hind foot length (HFL), and ear length (EL) for animals measured by assistant A (see Table 1 for explanations of symbols)

Source of variation	Multivariate: Wilk's lambda	df	F (significance)	n^2	Univariate (significance of F) TAL	HFL	EL
Sex	0.951	3,68	1.16(0.331)	4.9%	NI[a]	NI	NI
Age	0.622	3,68	13.76(0.000)	37.8%	NI	NI	NI
Sex × age	0.868	3,68	3.43(0.022)	13.2%	0.338	0.060	0.193

NOTE: The data were homoscedastic (Box-M test, $p = 0.763$).
[a]Not of interest.

measurements. The following analyses were done separately on these two groups of variables.

A two-way (sex by habitat) MANOVA revealed neither a significant interaction effect nor a significant effect of habitat, but sex had a significant influence on length measurements of the skull (Table 5). Univariate tests revealed that only the two mandibular measurements (LX and LR) were significantly different between the two sexes (Table 5). A step-down analysis was used to examine whether some variables showed sex or habitat effects when other variables were held constant. LR was longer in males than in females given the same LX, and LIF was shorter in males than in females when LX, LR, CL, and BW were held constant (Table 6).

Width and height measurements of the skull did not differ

TABLE 5. Two-way MANOVA for testing the influnces of sex and habitat on the six length measurements and one width measurement

Source of variation	Multivariate			Univariate							
					F						
	Hottelling's *T*	df	*F*	df	CL	BW	LUTR	LIF	LX	LR	LLTR
Sex	0.082	7,182	2.13* (0.043)	1,188	1.99 (0.160)	0.16 (0.689)	0.01 (0.911)	0.98 (0.323)	4.83* (0.029)	5.21* (0.024)	0.01 (0.915)
Habitat	0.042	7,182	1.09 (0.371)	1,188	0.58 (0.488)	3.41 (0.067)	2.16 (0.143)	2.91 (0.090)	0.46 (0.500)	2.67 (0.104)	1.43 (0.233)
Sex × habitat	0.006	7,182	0.16 (0.993)	1,188	0.02 (0.894)	0.01 (0.912)	0.22 (0.640)	0.45 (0.504)	0.00 (0.992)	0.05 (0.824)	0.03 (0.864)

NOTE: Only adults were used in the analysis. See text for definitions of symbols for measurements. Values in parentheses represent the significance of the *F* values. The strength of association (see Table 2) between the dependent variables and the effect sex is 0.076. No significant violation of homoscedasticity is present (Box-*M* test, $p = 0.14$).
*$p < 0.05$.

TABLE 6. Step-down analysis on the seven skull measurement of adult deer mice

(A) Table of statistical test

Source of variance	LX				LR				CL	BW	LIF				LUTR	LLTR
	SS	df	*F*	n^2	SS	df	*F*	n^2			SS	df	*F*	n^2		
Sex	0.466	1	4.83* (0.029)	0.03	0.301	1	4.16* (0.043)	0.02	ns	ns	0.18	1	4.06* (0.045)	0.02	ns	ns
Habitat	0.044	1	ns	—	0.178	1	ns	—	ns	ns	0.09	1	ns	—	ns	ns
Sex × habitat	0.000	1	ns	—	0.004	1	ns	—	ns	ns	0.00	1	—	ns	ns	
Error	18.142	188			13.464	187					8.03	184				

(B) Comparison of adjusted marginal means (in mm) between the two sexes

	LX	LR	LIF
Males	6.52	7.63	5.24
Females	6.42	7.55	5.31

NOTE: Strength of association between the dependent variable and the model was calculated for significant effects, and was denoted by n^2 (see Table 3). Values in parentheses represent the significance of the *F* values. Table 6B compares the adjusted marginal means for LX; for LR with LX as a covariate; and for LIF with LX, LR, Cl, and BW as covariates. Parallelism was checked for each step. None of the tests showed significant violation of the assumption at the 0.05 level.
*$p < 0.05$.

between the sexes or between the habitats. The interaction term and main effects were not significant at the 5% significance level.

Cranial measurements of juveniles

A two-way (sex by habitat) MANOVA was run on the five cranial measurements of juveniles. Neither main nor interaction effects were significant (sex effect, $p = 0.482$; habitat effect, $p = 0.335$; sex by habitat, $p = 0.687$). Univariate tests on each variable also failed to reveal any significant sex or habitat effect at the 5% significance level. We therefore conclude that for the measurements used in this study, sexual dimorphism in *P. m. borealis* was exhibited only in adults.

We did not analyse the development of sexual dimporphism in cranial measurements because: (*i*) the size (CL) range was very small for both adults and juveniles, (*ii*) there was little overlap in size of cranial measurements between adults and juveniles, and (*iii*) there was serious heteroscedasticity when age was introduced as a factor.

Discussion

This study revealed consistent morphological differences between the sexes, with adult males having longer hind feet (Table 2) and longer mandibles than adult females (Tables 5, 6). These findings indicate that data from both sexes should not be pooled to test differences between or among habitats. For example, Smartt and Lemen (1980) demonstrated a significant canonical correlation between morphological traits and food habits in *Peromyscus maniculatus* of the same population. Sexes were not separated because differences between sexes were said to be "not important." In their study, animals eating more tree-related food had longer hind feet than animals eating food unrelated to trees. Similarly, Holbrook (1982) found that animals from woodland habitats had "slightly" longer mandibles than animals from neighbouring open habitats. Based on Bowers and Smith's (1979) observation that the sexes of *Peromyscus maniculatus* showed differential microhabitat utilization and our observation that males had longer mandibles and longer hind feet, it is possible that the morphological differences in *P. maniculatus*

between microhabitats as revealed by Smartt and Lemen (1980) and Holbrook (1982) are attributable to differences between sexes if biased sex ratio existed in their samples.

A further source of spurious results in studying morphological variation is measurement error between observers. Investigators seldom consider individual differences in taking standard museum measurements. For example, Koh and Peterson (1983) used museum records of external measurements of *P. maniculatus*. Because these specimens were from many parts of North America, they were collected by many different people. If discripancies between observers are great enough, we may mistakenly attribute the difference between observers to other effects. Van Valen (1965) believed that the same morphological traits measured by different people using different techniques could differ in means but would not differ in variance. Our data suggest that this may not be true.

We failed to find any significant differences in morphological variation of both adult and juvenile *P. maniculatus* between two habitat types. The riparian–deciduous habitat had more trees than the talus–cliff habitat, so we expected *P. m. borealis* caught in the riparian–deciduous habitat to have longer tails than those caught in the talus–cliff habitat. Tail length appeared not to be a sensitive indicator of ecology of *P. maniculatus* in this study although it has been repeatedly suggested to be positively correlated with climbing ability (Dice 1940; Horner 1954; Dewsbury *et al.* 1980*b*). However, McShea and Francq (1984) found that tail length in *Peromyscus leucopus* had no value in discriminating animals caught in trees and animals caught on the ground. *Peromyscus maniculatus* nest more often in trees than *leucopus* (Wolff and Hurlbutt 1982), although the latter have longer tails than the former. Therefore, the relationship between tail length and arboreality in *Peromyscus* is not well established.

Sexual dimorphism has often been suggested to have ecological significance, especially in energy partitioning between males and females (Selander 1966; Storer 1966; Mayr 1972; Schoener 1967; Schoener *et al.* 1982; Carothers 1984). Our findings do not contradict the finding of Bowers and Smith (1979) that different sexes of *P. maniculatus* may have differential microhabitat use. Mandibular morphology has been shown or suggested to be sensitive to differences in food (Watt and Williams 1951; Holbrook 1982, and literature cited therein). Hypofunction can reduce the growth of the mandible while tough food can stimulate its growth (Watt and Williams 1951; Moore 1973; Riesenfeld 1969). It has been recorded that adult males occupy more xeric, presumably less favourable, habitats and may eat poorer food than adult females (Bowers and Smith 1979). This may also be true in other areas.

Daly and Daly (1974) observed in the Saharan gerbil, *Psammomys obesus*, that adult males visited females around them constantly, presumably to encounter each female on her infrequent days of sexual receptivity. To make this surveillance most efficient, males inhabit sites that are resource poor but centrally located relative to several females living in scattered food-rich areas. This spatial distribution is very similar to the dispersion pattern of breeding *Peromyscus maniculatus* (Bowers and Smith 1979; Metzgar 1979; Xia and Miller 1986). Adult male *P. maniculatus* are known to travel much more than adult females (Blair 1940, 1942; White 1964; Stickel 1968; Fairbairn 1977, 1978). Adult males should have longer hind feet than adult females if hind foot length is correlated with locomotion and climbing abilities, as has been proposed by Dice (1940), Baker (1968), and Smartt and Lemen (1980).

It is not known whether the above morphological differences are phenotypic or genotypic. The difference in mandibular morphology between adult males and females may be genotypic if (*i*) longer mandible is adaptive to tough food, (*ii*) males have to eat tougher food than do females, and (*iii*) some of the genes promoting mandibular growth are on the Y chromosome. Phenotypic plasticity would be more likely if the last condition is not met. The same argument applies to the difference in hind foot length between the sexes.

We found no significant differences between juvenile males and females. This was to be expected since, according to the previous inference, sexual dimorphism is likely related to breeding activities. Juvenile males do not have to continuously track the reproductive status of females and occupy poor habitats. There is thus no reason to believe that sexual dimorphism should exist in juveniles.

Although these interpretations are consistent with present knowledge of deer mouse ecology, we found it difficult to speculate on how important those differences between the sexes really are, because the differences are very small (no larger than 2%). Specific experiments focusing on food choice and mating systems are needed to establish the biological meaning of the difference.

Acknowledgements

This study was supported by the Natural Sciences and Engineering Research Council of Canada and the University of Western Ontario. Drs. C. D. Ankney, R. H. Green, L. Harder, and R. C. Jancey provided useful comments on earlier drafts of the manuscript. J. Falk, G. Hickling, S. Lusk, and S. Sharpe provided valuable assistance and suggestions. We are grateful to two anonymous reveiwers for constructive comments.

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Appendix 1

TABLE A1. Sample size, mean, and standard error of morphological variables used in this study (*N* represents sample size; all measurements are presented as mean ± SE (in mm))

	Assistant	Sex	Habitat[a]	*N*	BL	TAL	HFL	EL
Adults	A	M	R–D	31	87.23±3.83	76.58±5.69	19.31±0.95	17.53±1.05
			T–C	38	89.47±3.54	75.97±5.37	19.45±0.71	17.50±0.93
		F	R–D	20	89.90±3.42	78.05±7.64	19.05±0.90	17.25±1.03
			T–C	33	89.18±4.43	77.33±4.43	19.12±0.73	17.62±0.89
	B	M	R–D	35	87.43±5.18	74.20±5.47	20.47±1.01	14.46±0.90
			T–C	16	89.14±5.61	75.75±3.82	20.39±1.05	14.79±0.88
		F	R–D	39	88.38±6.95	76.00±4.62	20.11±1.07	14.56±1.28
			T–C	10	92.10±4.75	76.40±4.65	20.34±0.84	14.97±0.93
Juveniles	A	M	R–D	6	74.33±4.51	65.83±4.14	18.75±0.58	15.50±0.51
			T–C	31	78.35±0.94	70.42±1.19	19.40±0.13	16.75±0.19
		F	R–D	9	74.67±1.90	66.78±1.25	19.06±0.26	16.28±0.21
			T–C	24	77.00±1.19	66.92±1.26	19.33±0.17	16.71±0.24
	B	M	R–D	15	74.73±2.15	68.73±1.65	20.01±0.19	14.44±0.35
			T–C	9	79.22±1.65	70.00±2.28	20.26±0.31	14.84±0.29
		F	R–D	23	76.17±1.31	69.83±1.11	19.84±0.78	14.27±0.23
			T–C	15	76.73±6.39	64.87±7.67	19.44±1.08	14.61±1.04

[a]R–D riparian–deciduous; T–C, talus–cliffs.

TABLE A2. Sample size, mean, and standard error of skull variables used in this study (*N* represents sample size; all measurements are presented as mean ± SE (in mm))

Variables[a]	M:R–D (59)[b]	M:T–C (43)	F:R–D (50)	F:T–C (40)
CL	23.21±0.07	23.26±0.08	23.08±0.09	23.15±0.09
BW	11.84±0.04	11.92±0.05	11.82±0.04	11.90±0.05
BBH	8.57±0.03	8.65±0.04	8.59±0.04	8.59±0.04
HB	7.55±0.03	7.62±0.02	7.55±0.04	7.58±0.04
WIC	3.99±0.02	3.99±0.02	4.00±0.02	3.99±0.02
LUTR	3.55±0.02	3.59±0.03	3.55±0.02	3.58±0.02
IF	5.22±0.04	5.30±0.02	5.28±0.03	5.31±0.04
LX	6.50±0.04	6.54±0.04	6.41±0.05	6.44±0.06
LR	7.61±0.04	7.66±0.04	7.51±0.04	7.58±0.04
LLTR	3.63±0.14	3.66±0.03	3.63±0.02	3.66±0.02

[a]See text for the meaning of symbols.
[b]M, male; F, female; R–D, riparian–diciduous; T–C, talus–cliffs. Numbers within parentheses indicate cell sizes.