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Sexual dimorphism and age variability in cranial characters of *Oryzomys subflavus* (Wagner, 1842) (Rodentia: Sigmodontinae) from northeastern Brazil

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Abstract. Sex and age variation in a population sample of *Oryzomys subflavus* from the state of Alagoas (northeastern Brazil) was morphometrically examined. Fifteen cranial characters were measured in a total of 366 specimens, and analyzed using univariate and multivariate statistical procedures. Age variation was highly significant, occurring in fourteen characters, and most of the skull variation was due to growth effect throughout development. Significant secondary sexual dimorphism was found for all age classes by Univariate and Multivariate Analysis of Variance. Our results were compared with those found in a previous study of a population from the state of Pernambuco, northeastern Brazil, revealing a stronger pattern of sexual dimorphism in cranial characters for the Alagoas population. They suggested a possible intraspecific association between variation in size and strength of secondary sexual dimorphism.

Key words. *Oryzomys subflavus,* cranial variability, sexual dimorphism, morphometrics, bootstrap, Anova, Manova.

Introduction

The genus *Oryzomys* Baird, 1858 is the most diversified among Neotropical sigmodont rodents (Reig 1984) and is taxonomically complex but poorly understood. The difficulty to identify taxonomic units in *Oryzomys* has been attributed to high morphological variation both at intrapopulational and specific levels (Carleton & Musser 1989).

Oryzomys subflavus (Wagner, 1842) occurs in a large area encompassing east Brazil (Musser & Carleton 1993), the north of Minas Gerais state (Moojen 1952) and central Brazil (Alho & Villela 1984). Despite its wide geographical distribution, *O. subflavus* is regarded as a monotypic species and no study of interpopulational variation has been conducted so far.

Recently, Brandt & Pessôa (1994) demonstrated that sexual size dimorphism in young adults (age class 3) can be a source of intrapopulational variation in *O. subflavus* and that there are significant differences among age classes of adults. The results of Brandt & Pessôa (1994) are valid for a population from Pernambuco, northeastern Brazil, but their generality remains to be determined.

Although studies of geographic variation and sexual dimorphism are available for rodents, the study of the interaction of these two sources of variation is not so common. The objective of this study was to assess the contribution of sex and age variation in cranial morphometric traits of *O. subflavus* in a population from the Alagoas state, and to compare the results with those found for the population from Pernambuco (Brandt & Pessôa 1994), as a step towards the understanding of the patterns of geographic variation in this species.

Material and techniques

A total of 366 specimens of *O. subflavus* collected in the vicinity of Viçosa (9°24'S and 36°14'W) and Palmeira dos Indios (9°25'S and 36°37'W), state of Alagoas, was used in this study. This is part of a large survey of small mammals collected between 1952 and 1955 by the 'Serviço Nacional da Peste' (SNP — 'National Plague Service', Brazil), and deposited in the mammal collection of the Museu Nacional (UFRJ), in Rio de Janeiro. Specimens were allocated according to the five age classes defined by Brandt & Pessôa (1994) on the basis of the occlusal surface wear of molars.

Fifteen cranial dimensions, fourteen of which as defined in Brandt & Pessôa (1994), were measured in all individuals as follows: greatest length of skull (GLS); basilar length (BL) (here measured from the posterior margins of the alveoli of the upper incisors to the anteriormost point of the lower border of the foramen magnum); nasal length (NL); zygomatic breadth (ZB); diastema length (D); maxillary toothrow length (MTRL); palatal length (PL); incisive foramen length (IFL); rostral depth (RD); rostral length (RL); rostral breadth (RB); maxillary breadth (MaxB); braincase depth (BD); least interorbital constriction (IOC); mandibular length (ML) (Fig. 1).

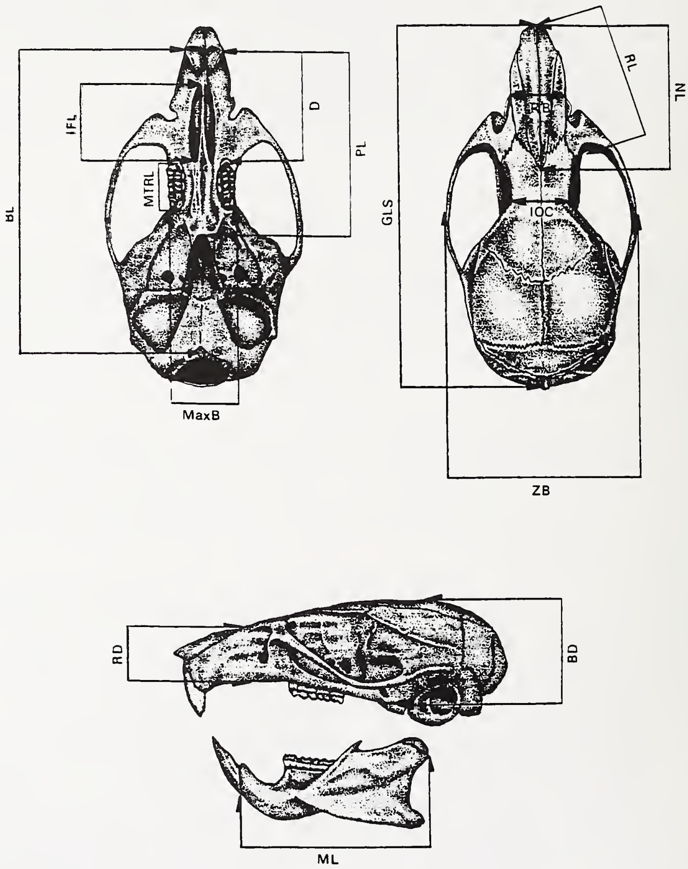

Fig 1: Fifteen measurements taken from the skulls of *Oryzomys subflavus* from Alagoas (see text for explanation of measurement abbreviations).

Descriptive statistics, including arithmetic means and standard deviations, were calculated for the fifteen cranial traits for individuals of both sexes and all different age classes. Gender data were obtained from the SNP original files. Preliminary morphometric analyses were performed to test the null hypothesis that individuals from both localities belong to the same population. Univariate Analysis of Variance showed non-significant differences between the samples for all cranial characters ($P < 0.05$), and Multivariate Analysis of Variance cor-

Table 1: Anova for age variation for 15 cranial characters, in four age classes. Statistics are: F=(F-value of univariate analysis of variance), P=(significance level of an Anova), AVC=(among age classes added variance component, in percentage).

Character	Males			Females		
	F	P	AVC	F	P	AVC
GLS	74.20	***	61	38.91	***	62
BL	78.57	***	62	38.34	***	61
NL	55.22	***	54	34.55	***	59
ZB	73.18	***	60	19.28	***	44
D	93.96	***	66	34.18	***	58
MTRL	3.84	***	5	0.44	ns	0
PL	63.26	***	57	26.58	***	52
IFL	54.93	***	53	14.28	***	36
RD	76.95	***	62	33.84	***	58
RL	64.78	***	57	42.29	***	64
RB	40.59	***	46	17.75	***	41
MaxB	22.09	***	31	7.50	***	21
BD	21.55	***	30	4.11	***	21
IOC	25.59	***	34	9.55	***	27
ML	57.74	***	55	36.73	***	60

* = P<0.05; ** = P<0.01; *** = P<0.001; ns = non significant

Table 2: Variation in means (mm) for 15 cranial characters in four age classes, with pooled sexes. Indistinguishable subsets of means are united by horizontal lines.

Age classes Character	2	3	4	5
GLS	31.43	33.85	35.01	35.83
BL	24.20	26.42	27.56	28.50
NL	12.05	13.20	13.87	14.25
ZB	16.21	17.36	18.08	18.42
D	8.28	9.19	9.77	10.15
MTRL	5.03	5.04	5.02	4.96
PL	13.29	14.30	14.86	15.26
IFL	6.49	6.96	7.21	7.40
RD	6.15	6.73	7.06	7.32
RL	11.38	12.50	13.08	13.48
RB	5.41	5.81	6.01	6.26
MaxB	5.26	5.46	5.59	5.68
BD	9.18	9.48	9.68	9.81
IOC	5.25	5.55	5.71	5.82
ML	16.29	17.67	18.24	18.74

roborated this result (F=1.44, P>0.15). Univariate and Multivariate Analysis of Variance were thus employed to investigate secondary sexual dimorphism and age effects on the same cranial characters. Age class 1 was excluded from all analyses due to its small sample size. A possible violation to the premise of homogeneity of variances is the presence of unbalanced samples in this study, which can cause sample test statistics to be artificially inflated. For this reason, for all Anovas a bootstrap procedure (1000 interactions) was used to derive empirical sampling distributions of the F–ratio and thus to obtain realistic probabilities of rejecting the null hypothesis of equality of means. Tukey HSD multiple comparison test (Norman & Streiner 1994) identified maximally non-significant subsets of means among age classes for characters that showed significant differences in the anovas for age effects. Variation in cranial characters was further partitioned into components of variance and their magnitude for the effects studied were calculated following Sokal & Rohlf (1981). Missing values (0.6 %) were estimated by multiple regression on principal components obtained from a matrix of complete individuals (the subset of the entire dataset containing only individuals that showed no missing characters). This estimation and the bootstrapped anovas were implemented by use of routines written for Matlab (version 4.2c, The MathWorks 1992) and available upon request. All other analyses were conducted using the statistical package Systat, version 5 (Wilkinson 1992).

Results

Age variation — Bootstrapped anovas on separated samples of males and females revealed highly significant (P<0.001) age effects for most characters except for maxillary toothrow length (MTRL), which was not statistically distinct throughout age classes (P>0.999) of females (Table 1). Multivariate analysis of variance showed significant differences among age classes (males, F=96.46, P<0.001; females, F=56.94, P<0.001).

The Tukey HSD multiple comparisons test with pooled sexes indicated that most measurements differed significantly (P<0.05) among the four age classes analyzed. Maxillary toothrow length (MTRL) was not significantly distinct between any pair of age classes. Individuals of age classes 4 and 5 overlapped in five other characters (Table 2). When sexes were analyzed separately age classes 4 and 5 were even less distinguishable.

Results of the added variance component showed that average 49 % of cranial variation of males and 44 % of females are due to growth. In eleven cranial characters the magnitude of the added component of age variation is larger for males than for females (Table 1).

Secondary sexual dimorphism — Males averaged larger than females for thirteen measurements in age classes 1 and 2, twelve of which being the same characters in both classes. Anova showed significant differences (P<0.001) between sexes in ten characters in age class 2 (Table 3). Males from age class 3 are larger than females in mean values for fourteen cranial characters, eleven of which being significantly dimorphic (P<0.001). In age class 4, males are larger in twelve cranial characters, six being statistically significant (P<0.001). Males are larger than females in mean values for twelve cranial characters in age class 5, but only three of these were significantly dimorphic. Manova revealed significant sex differences (P<0.001) for all age classes (Tables 3 and 4).

The added component of sexual variation was estimated for class 3, because this age category exhibited the largest number of sexually dimorphic characters. The results indicated that relatively more variation occurs within groups. An average of

4 % of variation in cranial traits is accounted for by the differences between sexes, and 96 % is due to residual variability within sexes (Table 4). Only maxillary toothrow length (MTRL) showed more than 10 % of the variation due to sex differences.

Table 3: Anova of sexual variation for the four age classes separately. Statistics are: F=(F-value of Anova), P=(significance level of Anova).

Character	2		3		4		5	
	F	P	F	P	F	P	F	P
GLS	1.98	***	10.74	***	0.28	ns	2.07	ns
BL	0.97	***	5.97	***	1.62	***	0.42	ns
NL	1.17	***	1.83	**	0.05	ns	0.29	ns
ZB	0.04	ns	5.34	***	2.19	ns	2.09	ns
D	0.18	ns	1.58	ns	0.59	ns	2.58	ns
MTRL	4.79	***	16.88	***	0.66	ns	0.02	ns
PL	0.79	***	6.53	***	4.08	***	1.65	ns
IFL	1.50	***	2.84	***	3.82	***	5.96	***
RD	1.81	***	5.76	ns	2.67	***	2.75	ns
RL	2.05	***	5.68	***	0.04	ns	0.03	ns
RB	0.26	ns	4.69	***	1.25	ns	0.58	ns
MaxB	0.05	ns	0.42	ns	0.01	ns	0.03	ns
BD	0.09	ns	5.84	***	4.69	***	2.38	***
IOC	1.68	***	9.89	***	2.27	***	3.55	***
ML	1.87	***	2.37	ns	0.78	ns	0.49	ns

* = P<0.05; ** = P<0.01; *** = P<0.001; ns = non significant

Table 4: Statistics of sexual variation, in age category 3, for 15 cranial characters. Statistics are: M=(mean), SD=(standard deviation), P=(significance level of Anova), AVC=(added variance component among sexes), and WVC=(added variance component within sexes).

Character	Males		Females		P	AVC	WVC
	M	SD	M	SD			
GLS	34.11	1.206	33.54	1.29	0.001	9	91
BL	26.60	1.153	26.19	1.20	0.001	5	95
NL	13.26	0.693	13.13	0.72	0.002	1	99
ZB	17.46	0.675	17.24	0.75	0.001	4	96
D	9.23	0.485	9.14	0.54	0.999	0	100
MTRL	5.08	0.159	4.99	0.14	0.001	15	85
PL	14.40	0.585	14.18	0.64	0.001	5	95
IFL	6.99	0.306	6.91	0.39	0.001	2	98
RD	6.78	0.319	6.67	0.35	0.999	4	96
RL	12.59	0.612	12.39	0.61	0.001	4	96
RB	5.85	0.301	5.75	0.33	0.001	3	97
MaxB	5.45	0.214	5.47	0.25	0.999	0	100
BD	9.53	0.326	9.42	0.30	0.001	5	95
IOC	5.61	0.288	5.48	0.30	0.001	8	92
ML	17.75	0.736	17.58	0.78	0.999	1	99

Discussion

The analysis of geographic patterns of variation is an important step in understanding the mechanisms involved in the process of differentiation within a species. It is nevertheless important to assess properly the magnitude of within-population variability before evaluating the extent of geographic variation (Patton & Rogers 1983; Thorpe 1983; Pessôa & Dos Reis 1991). Variation within populations can usually be ascribed to ontogenetic, sexual, environmental, and random factors (Straney 1978).

The ontogenetic and sexual variation found here for a population of *O. subflavus* from Alagoas state was different from that shown in the morphometric analyses of Brandt & Pessôa (1994), for a population from Pernambuco state. The two populations are from northeastern Brazil, and are geographically separated by approximately 240 km. The age criteria and the measurements are the same in both studies, therefore the results are comparable.

Although results of age variation provided similar results in univariate and multivariate analyses, the values of the added component of variance were different for the two samples. In the population from Alagoas there is more variation due to age in males than in females (49 % and 44 % respectively), whereas in the Pernambuco sample variation due to age is greater in females (56 %) than in males (32 %). In the Sergipe population, the Tukey HSD multiple comparison test for pooled sex samples showed significant differences between age classes 2—3, and 3—4 for all characters, except for maxillary toothrow length. Age classes 4—5 showed significant differences in nine characters. For the population from Pernambuco, however, individuals of age classes 4 and 5 are not distinguishable, forming an overlapping subset for all characters. Such results indicate that variability in skull dimensions due to indeterminate growth may confound the analysis of geographic variation and taxonomic studies in *O. subflavus.*

Significant sexual dimorphism in cranial characters of *O. subflavus* was found for both populations but a more conspicuous pattern was revealed for the population from Alagoas. In age class 1, males averaged larger than females for thirteen characters in both samples, but the characters are not exactly the same. In age class 2, ten characters were statistically significant for the Alagoas population but none in Pernambuco. Age class 3 exhibited the greatest number of dimorphic characters; eleven characters differed significantly in the Alagoas sample and seven in Pernambuco, five of these being the same in both studies. In the Alagoas sample, age class 4 showed significant dimorphism in six characters and in Pernambuco only one was significant. In age class 5 males averaged larger for twelve cranial traits in Alagoas, but in Pernambuco females were larger for eleven cranial characters. No character showed significant sex differences in the population from Pernambuco. Notwithstanding only three characters being significant for the sample of age class 5 from Alagoas, it is interesting to note that they sample different and independent dimensions of the skull. This independence is corroborated by the results of Manova, which showed significant sex differences for all age classes in the Alagoas population. For the population of Pernambuco, only age class 3 had shown significant sexual dimorphism (Brandt & Pessôa 1994). In spite of the mean percentage of the

Table 5: Statistics of sexual variation, in age category 3, for 15 cranial characters of *O. subflavus*, from Pernambuco state. Modified from Brandt & Pessôa 1994.

Character	Males		Females	
	M	SD	M	SD
GLS	34.05	1.18	33.55	1.30
BL	31.30	1.10	30.87	1.25
NL	13.01	0.61	12.84	0.71
ZB	17.19	0.66	16.98	0.62
D	8.84	0.43	8.64	0.50
MTRL	5.15	0.16	5.07	0.20
PL	14.29	0.61	13.97	0.66
IFL	6.81	0.41	6.59	0.40
RD	6.41	0.34	6.26	0.34
RL	12.85	0.66	12.71	0.70
RB	5.60	0.32	5.56	0.28
MaxB	4.87	0.22	4.81	0.20
BD	9.54	0.28	9.33	0.21
IOC	5.71	0.30	5.30	0.25
ML	17.27	0.65	17.15	0.64

sexual component of variation for all characters in age class 3 being similar, the values of each character were quite different among the two populations (Table 5).

Sexual dimorphism in mammals is very common, generally with males being larger than females (Ralls 1977; Shine 1989). In rodents, the magnitude of sexual dimorphism is relatively low, especially in the smaller species (Da Fonseca & Kierulff 1989; McLain 1993). However, sexual size differences have been found in external and cranial characters of many taxa, such as phylotine rodents (Provensal & Polop 1993), kangaroo rats (Kennedy & Schnell 1978; Robertson et al. 1992), voles (Heske & Ostfeld 1990; Ostfeld & Heske 1993), chipmunks (Levenson 1990), deer mice (Xia & Millar 1987), pocket gophers (Daly & Patton 1986), muskrats (Pankakoski 1983), tuco-tucos (Malizia & Busch 1991; Gastal 1994), and bandicoot rats (Hussain et al. 1992). In the tribe Oryzomyini, sexual size dimorphism is a conspicuous feature in cranial characters of *Oligoryzomys nigripes* (Olfers, 1818), *O. chacoensis* (Myers & Carleton, 1981) and *O. fornesi* Massoia, 1973 (Myers & Carleton 1981), and in external and cranial measurements of *O. longicaudatus* (Bennett, 1832) (Gallardo & Palma 1990). In *Oryzomys argentatus* (Spitzer & Lazell, 1978) and *O. palustris* (Harlan, 1837) the males are larger than the females and usually have the characters more accentuated (Goodyear 1991).

Two main theories are commonly used to explain the evolution of sexual size dimorphism in mammals, namely sexual selection and intraspecific niche divergence (Shine 1989; Dayan & Simberloff 1994). Sexual selection may evolve from intrasexual contests for mates and intersexual mating preferences, usually in the males, producing sexual dimorphism which is maladaptive to natural selection (Lande 1980). The alternative idea is that sexual differences in body size or morphology may evolve for ecological causes, that is, to adapt the sexes to different ecological niches, decreasing intersexual competition (Shine 1989).

Among rodents, the two explanations were utilized, depending on the taxa, but it is very difficult to reconcile the evolution of sexual dimorphism. Sexual selection is the more utilized theory (Pankakoski 1983; Daly & Patton 1986; Heske & Ostfeld 1990; Levenson 1990), but niche divergence is preferred when different sexes have differential microhabitat use or when significant sex differences exist in the trophic apparatus (Kennedy & Schnell 1978; Xia & Millar 1987). For *O. subflavus* we found significant sexual dimorphism in at least one character of the trophic apparatus (maxillary toothrow length), however there is no knowledge of niche utilization in this species.

In our intraspecific comparisons of *O. subflavus* we found evidence that local variation in magnitudes of sexual dimorphism may be associated with geographical variation in size, as can be inferred from the comparisons of mean values of males and females for each character between the two populations (Tables 4 and 5). Such a pattern of intraspecific variability could constitute an extrapolation of a trend of variation in magnitudes of sexual dimorphism that has already been noticed in comparisons between small and large rodent species (McLain 1993).

Age variation and sexual dimorphism were significant and may be variable in the populations of *O. subflavus,* suggesting that individuals of all age classes and different sexes must be separated in further studies of geographic variation. The findings showed here are preliminary and studies of other populations along the range of distribution are needed to understand and evaluate the magnitude and extension of these sources of variation before assessing geographic variation in this species.

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Zusammenfassung

Die Geschlechts- und Altersvariation einer Population von *Oryzomys subflavus* von Alagoas, Nordost-Brasilien, wurde morphometrisch studiert. Fünfzehn Schädelmerkmale wurden bei 366 Exemplaren gemessen und mit univariaten oder multivariaten Techniken analysiert. Die Altersvariation war in vierzehn Merkmalen sehr auffällig; der größte Anteil der Schädelvariation ist auf Wachstumseffekte zurückzuführen. Ein bedeutsamer sekundärer Geschlechtsdimorphismus wurde mit Hilfe von univariaten und multivariaten Varianzanalysen in allen Altersklassen gefunden. Unsere Ergebnisse wurden mit früheren Studien an einer Population in Pernambuco, Brasilien, verglichen. Im Vergleich dazu wies die Alagoas Population einen stärkeren Geschlechtsdimorphismus der Schädelmerkmale auf. Der Befund legt einen Zusammenhang zwischen intraspezifischer Größenvariation und Ausprägung des sekundären Geschlechtsdimorphismus nahe.

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