

## NATURAL SELECTION, MORPHOLOGIC DIVERGENCE AND PHENOTYPIC EVOLUTION IN *Proechimys dimidiatus* (RODENTIA: ECHIMYIDAE)

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### ABSTRACT

Models of evolutionary quantitative genetics were employed to study cranial morphologic differentiation in two populations of the echimyid rodent *Proechimys dimidiatus* from Tijuca and Teresópolis in the state of Rio de Janeiro. Under the assumption that the deterministic process of natural selection has acted to differentiate the two populations, the net selection gradient and minimum intensities of selection necessary to account for evolutionary divergence were calculated. The vector of selection coefficients indicated that some cranial traits evolved in the direction contrary to the force of selection, acting to increase mean values for cranial traits in the population from Tijuca. Minimum selective mortality per generation was low ( $10^{-3}$ ) suggesting that weak selection can explain the observed morphologic differentiation.

### INTRODUCTION

The theory of quantitative genetics (Bulmer, 1980; Falconer, 1989) has recently been adapted to study evolution in natural populations (Lofsvold, 1986). The models of evolutionary quantitative genetics were developed by Lande (1976, 1979, 1988) and can be used to examine the hypothesis that phenotypic divergence has occurred by random genetic drift or to reconstruct the hypothetical forces of direc-

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tional selection acting to differentiate populations. These models have been used to test the hypothesis of morphological differentiation under genetic drift (Lande, 1976; Reyment, 1983; Lofsvold, 1988) and to assess the role of selection to account for the observed morphologic divergence among populations and higher taxa (Lande, 1976; Price *et al.*, 1984; Schluter, 1984; Grant, 1986; Arnold, 1988; Lofsvold, 1988; Grant and Grant, 1989; Bryant and Meffert, 1990).

In this paper we apply the mathematical models of evolutionary quantitative genetics (Lande, 1988; Hartl and Clark, 1989) to study morphologic divergence and phenotypic evolution in two populations of the echimyid rodent *Proechimys dimidiatus* that have diverged significantly in overall cranial size (Pessôa and Reis, in press). We worked under the hypothesis that the deterministic process of natural selection has acted to differentiate the two populations and estimate the gradient of selection and the minimum intensities of selection that might have been necessary to account for the observed morphologic differences between the two populations.

## MATERIAL AND METHODS

Forty-two specimens of *P. dimidiatus* from the following localities in the state of Rio de Janeiro (Brazil) were examined: Tijuca [22°56'S 43°17'W (n = 24)] and Teresópolis [22°26'S 42°59'W (n = 18)]. All specimens utilized in this study were adults according to the criteria of Patton and Rogers (1983) and sexes were pooled to increase sample sizes since sexual size dimorphism is limited to few cranial characters in *P. dimidiatus* (Pessôa and Reis, in press).

The following cranial morphometric characters defined in Patton and Rogers (1983) were measured in all individuals with electronic digital calipers: bulla length, palatal length, nasal length, interorbital constriction, rostral length, diastema, rostral depth, skull length, basilar length, and pos-palatal length. An additional measurement, mandible length, was also taken from all specimens studied.

Morphologic divergence in cranial traits between the two populations was assessed by univariate and multivariate procedures (Morrison, 1976; Sokal and Rohlf, 1981). All character values were transformed to their natural logarithms prior to analysis. The null hypothesis of no difference in vector means of cranial characters in the two populations was tested by multivariate analysis of variance (MANOVA). The *F*-value, transformed from Wilks' Lambda was employed to test the significance of the MANOVA (Harris, 1975). Univariate analysis of variance (ANOVA) was performed to determine which cranial characters contribute significantly to the morphologic differentiation of the two populations of *P. dimidiatus*.

The net selection gradient describing the response of a cranial character to the hypothetical forces of selection was computed from  $\sum_{i=1}^k \nabla \ln \bar{W} = G^{-1} [\bar{z}_1 - \bar{z}_2]$ ,

obtained from the summation over  $t - 1$  generations of  $\Delta \bar{z} = G \nabla \ln \bar{W}$  (Lande, 1979, 1988; Manly, 1985; Caswell, 1989). The latter expression describes the evolution of the mean vector of characters in one generation, where  $G$  is the additive genetic covariance matrix,  $\nabla = (\partial / \partial \bar{z}_1, \dots, \partial / \partial \bar{z}_n)^T$  is the gradient operator, and  $\bar{W}$  is the mean fitness. The genetic covariance matrix was approximated by the mean phenotypic covariance matrix of the two populations (Arnold, 1988; Lofsvold, 1988).

In Lande's (1979, 1988) model, natural selection acting on the multivariate phenotype is approximated by truncation selection (Bulmer, 1980; Falconer, 1989), and the intensities of selection represented by the net gradient can be estimated by a selection index. For the multivariate case, a selection index can be computed as a linear combination of the original characters and the selection gradient (Lande, 1979; Lofsvold, 1988).

A time scale for the divergence between the two populations has to be chosen in order to calculate the truncation point. The truncation point was computed from  $b = \pm \sqrt{-2 \ln \left[ \sqrt{2 \pi} \{ I(\sqrt{P}/Gt) \}} \right]}$  (Lande, 1976), where  $P = (\nabla \ln \bar{W})^T P (\nabla \ln \bar{W})$  and  $G = (\nabla \ln \bar{W})^T G (\nabla \ln \bar{W})$  are the phenotypic and additive genetic variances of the index of selection, respectively (Lofsvold, 1988). In this study we used time scales of the order  $10^3$ ,  $10^4$ ,  $10^5$ , and  $10^6$  generations (Lofsvold, 1988). The values of  $b$  were then entered in a table of integrals of the standard normal distribution to calculate the proportion of the population culled each generation.

## RESULTS

The two populations of *P. dimidiatus* differ in the cranial traits measured, with individuals from Tijuca being larger than those from Teresópolis for all characters (Table I). The vectors of means for cranial characters differ significantly in the two populations (MANOVA: Wilks' Lambda = 0.168,  $F = 13.50$ ,  $P < 0.0001$ ). Univariate ANOVA's indicate that all characters are significantly different in the two populations (Table I).

We calculated the net gradient of selection, arbitrarily letting the divergence be from the larger to the smaller mean values for the cranial traits measured, and the results are shown in Table I. Bulla length and skull length are the characters subjected to the greatest intensity of selection, whereas nasal length, interorbital constriction, and basilar length show intermediate selection intensities.

The values for the intensities of selection approximated by truncation selection are shown in Table II. The results indicate, as expected, a correlation between the time available for differentiation between the two populations of *P. dimidiatus* and the magnitude of selection intensities.

Table I - Cranial character variation in the populations of *Proechimys dimidiatus* from Tijuca (T) and Teresópolis (E).

Character	(T) Mean (SD)	(E) Mean (SD)	F	$\nabla \ln \bar{W}$
Bulla length	11.98 (0.49)	9.54 (0.47)	92.27**	73.43
Palatal length	16.22 (0.64)	14.87 (0.99)	28.90**	4.91
Nasal length	19.72 (0.84)	18.58 (1.19)	13.28*	-30.36
Interorbital constriction	12.40 (0.63)	11.64 (0.75)	12.63*	26.68
Rostral length	8.49 (0.61)	7.57 (0.70)	20.62**	8.93
Diastema	10.94 (0.53)	9.70 (0.76)	38.63**	9.53
Rostral depth	10.91 (0.40)	10.13 (0.47)	34.74**	-4.29
Skull length	53.38 (1.48)	50.07 (2.19)	34.13**	61.29
Basilar length	36.42 (1.21)	34.74 (1.87)	12.49**	-18.17
Pos-palatal length	24.67 (0.78)	23.76 (0.93)	20.62**	-3.56
Mandible length	26.11 (1.30)	24.29 (1.36)	38.63**	2.38

Statistics given are mean, standard deviation (SD), F-value of an analysis of variance, and the net selection gradient ( $\nabla \ln \bar{W}$ ).

\*, \*\* =  $P < 0.001, 0.0001$  respectively.

Table II - Estimates of truncation points, b, and the corresponding proportion of selective mortality necessary to account for the observed mean differences in the two populations of *Proechimys dimidiatus* since divergence given different number of generations (t).

Number of generations (t)	b	Selective mortality (per generation)
$10^3$	3.037	$1.3 \times 10^{-3}$
$10^4$	3.720	$1.1 \times 10^{-4}$
$10^5$	4.294	$8.5 \times 10^{-5}$
$10^6$	4.800	$7.9 \times 10^{-6}$

## DISCUSSION

The univariate and multivariate procedures employed in this study showed that significant differentiation in cranial morphology has occurred between the two populations of *P. dimidiatus*, which inhabit sub-tropical forest environments located

66 km apart in southeastern Brazil (Pessôa and Reis, in press). The pattern of selection uncovered by the net selection gradient indicates that certain traits were under stronger selection intensities whereas others were little affected by selection (Table I). The multivariate analysis of selection intensities also shows that although individuals from the Tijuca population are larger for all cranial measurements the direct forces of selection have acted to decrease the means of nasal length, rostral depth, basilar length, and pos-palatal length, as indicated by the negative signs of the coefficients (Table I).

Lande (1979) derived an equation [ $\Delta \bar{z} = G \nabla \ln \bar{W}$ ] that shows that the response of the multivariate phenotype to selection is jointly governed by the genetic covariance among traits and the selection gradient. It is clear from this study that the covariance among cranial traits in the populations of *P. dimidiatus* has caused some traits to evolve toward smaller (mean) values contrary to the forces of selection acting to increase mean cranial size in the population from Tijuca. Similar results were obtained by Lofsvold (1988) in a study of morphologic differentiation among subspecies and species of the cricetid rodent genus *Peromyscus*.

The results obtained here and in other studies (Lande and Arnold, 1983; Lande, 1988; Lofsvold, 1988) underscore the importance of multivariate models of selection to study evolution in natural populations since an univariate analysis of selection would fail to reveal the effect of selection acting on correlated characters. The covariance among characters can change the magnitude and even the sign of selection differentials since the evolution of a particular character depends on the indirect selection on all genetically correlated characters as demonstrated by the expression  $\Delta \bar{z}_i = \sum G_{ij} \partial \ln \bar{W} / \partial z_j$  (Lande, 1988, p.73).

The intensities of natural selection necessary to account for the phenotypic differentiation between the two populations of *P. dimidiatus* were low. The minimum selective mortality required under rapid divergence (1000 generations) was of the order of  $10^{-3}$  indicating that only 0.1% of the population would have to be culled each generation for 1000 generations to produce the observed morphologic differentiation. The necessary minimum selective mortality is thus quite low and these figures are of the same order of magnitude as those estimated by Lofsvold (1988) for the rates of divergence in *Peromyscus* for a similar number of generations.

The values of minimum selective mortalities reported here for *P. dimidiatus* and those obtained for *Peromyscus* (Lofsvold, 1988) are lower than those computed for selection favoring large size in the bird species *Geospiza fortis* and the pentatomid bug *Euschistus variolarius*, although they are of comparable magnitudes to estimates of minimum selective mortalities calculated for *Passer domesticus* (Lofsvold, 1988). The results reported in this paper and those found in the literature [reviewed in Lofsvold (1988)] indicate that morphologic divergence can be accounted for by weak

selection acting on small quantitative differences and can explain microevolution in natural populations.

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### RESUMO

Os modelos da genética quantitativa desenvolvidos por R. Lande (1976, 1979, 1988) foram aplicados em um estudo de diferenciação na morfologia craniana de duas populações do roedor equimídeo *Proechimys dimidiatus* das localidades de Tijuca e Teresópolis no estado do Rio de Janeiro. Foram estimados o gradiente de seleção e as intensidades seletivas mínimas necessárias para causar as diferenças observadas entre as duas populações. O vetor de coeficientes de seleção mostrou que alguns caracteres cranianos evoluíram na direção contrária à força da seleção natural que teria atuado para aumentar os valores médios das dimensões cranianas na população da Tijuca. A mortalidade seletiva mínima por geração foi baixa ( $10^{-3}$ ), sugerindo que seleção fraca agindo sobre diferenças quantitativas pode explicar as diferenças morfológicas observadas.

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