Application of nonlinear mixed models to describe growth patterns and sexual dimorphism in capybaras (*Hydrochoerus hydrochaeris*).

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Abstract

In this paper a von Bertalanffy functions was fitted to describe long-term changes in body mass of capybaras (*Hydrochoerus hydrochaerys*). A multilevel nonlinear mixed effects model was employed because it allowed for estimation of all growth profiles simultaneously, and different sources of variation (i.e., sex, individuals, and litter effects) were incorporated directly into the parameters. Furthermore, variance in-homogeneity and within-individuals correlation were introduced to the functions. Inclusion of a variance of power function and a continuous autoregressive process of first order rendered a substantially improved fit to data. The sample consisted of 673 weight data obtained from 33 females and 37 males. Significant variance components were recorded for both individuals and litters. Also significant differences were observed in growth patterns between sexes. Males showed asymptotic weights and age at the inflection point significantly higher than females, while the constant growth rate was lower. These differences could be interpreted in terms of mating system of this species since males have chances to mate only when they reach a large enough size to compete with other males. For females, however, the possibility of mating does not depend on aggressive confrontations, so if they reach sexual maturity earlier, they may extend the period when they are sexually active.

Keywords: capybaras; body mass; nlme.

1. Introduction

The period of time an individual grows may change with age or size are important elements in a species' life history (Bartareau et al. 2011). One method of examining growth is the use of empirical models that summarize size-at-age data in a number of numeric parameters having physical meaning. This gives one the opportunity to assist comparison of different sexes and environmental conditions (Bartareau et al. 2011).

Capybara , *Hydrochoerus hydrochaeris*, is the largest living rodent, with adults weighing 49–50 kg, (range 35–65 kg) (Moreira et al. 2013). They live in stable groups of 5–14 adult individuals, usually including a dominant male, one or two subordinate males, and several (probably related) females (Herrera and Macdonald 1993, Moreira et al. 2013). The dominant male in each group are significantly heavier than any of the subordinates (Herrera and Macdonald 1993). Dominant males , on average, obtain more matings than subordinate males (Herrera and Macdonald 1993). This intrasexual competition between males of capybaras for access to females should result in male- biased size dimorphisms as was observed in many mammals' species (Lindenfors et al. 2007). However, until the present no evidence of sexual size dimorphism was recorded for this species.

Few studies have modeled the growth of capybaras. Usually the descriptions were based on short periods of time, assuming a linear growth function (Moreira et al., 2013). There is at present a unique description of the growth of capybara done by setting a sigmoid function more realistic (Zullinger et al., 1984), although based on only 6 individuals.

The goal of this work is to fit and validate a nonlinear model to describe the growth of capybaras, incorporating sex as fixed factor, to establish whether there are differences in growth patterns between males and females. On the other hand, random factors (litters and individuals) to describe the hierarchical structure of the data will be incorporated.

2. Methods

The work was carried out in the capybara breeding and husbandry at the "Módulo Experimental de Cría de Carpinchos," located in the Experimental Station of the Paraná Delta (Province of Buenos Aires, Argentina in the "Experimental module of breeding capybaras" located in the Experimental Station "Delta del Paraná" (INTA), located in Buenos Aires Province, Argentina.
The sample consisted of 673 weight data obtained from of 33 females and 37 males. Individuals were weighed at birth and at different ages. The amount of data per animal was variable, with a median of 8 (range 3-21). The median of the age was 3 months (range 0-37). Only weights of live specimens were used and those obtained from pregnant females were discarded. Were used. Sigmoid growth model proposed by von Bertalanffy (Bertalanffy 1960; Zullinger et al 1984) was fitted:

$$W_t = A \cdot \left(1 - \frac{1}{3} \cdot e^{-k \cdot (t - I)}\right)^3$$

where W_t is the body weight (kg) at age t; A the asymptotic or mature weight (kg) when age (t) approaches infinity; k the growth rate constant (days^{-1}); t the age in days and I is the age at the inflection point (days).
In order to study the differences between sexes and to take into account the variation provided by litters and individuals and dependence between observations, a mixed nonlinear model was developed (Pinheiro and Bates, 2000). The proposed full model was as follows:

$$y_{ijk} = A_i \cdot \left(1 - \frac{1}{3} \cdot e^{-k_i \cdot (t_{ijk} - I_i)}\right)^3 + \varepsilon_{ijk}$$

$$A_i = \beta_1 + \gamma_1 x + b_{1i} + b_{1j(i)}$$

$$k_i = \beta_2 + \gamma_2 x + b_{2i} + b_{2j(i)}$$

$$I_i = \beta_3 + \gamma_3 x + b_{3i} + b_{3j(i)}$$

$$b_i \approx N(0, \psi_1), b_{j(i)} \approx N(0, \psi_2), \varepsilon_{ijk} \approx N(0, \sigma^2)$$

$$\text{with } b_i, b_{j(i)} \text{y } \varepsilon_{ijk} \text{ independent of each other}$$

Let y_{ijk} denote the weight of jth capybara origiating from ith litter on kth day; β_1, β_2 and β_3 represent the mean values of paramenters A, k and I; γ_1, γ_2 and γ_3 represent the fixed effects of sex (0= male) over the paramenters of the curve; b_{1i}, b_{2i} and b_{3i} represent the random effects of litter, $b_{1j(i)}$, $b_{2j(i)}$ and $b_{3j(i)}$ are the random effects of individuals nested in litters and ε_{ijk} the model error. Different functions of variance was applied to model the heteroscedasticity. In order to identify the best model the Akaike information criteria (AIC) and the Bayesian information criteria (BIC) were used. Likelihood ratio tests (LRT) was used for nested model (Pinheiro and Bates, 2000). All statistical computations were implemented in R 3.0.3 (R Development Core Team, 2014), and parameter estimation was carried out by means of the NLME library (Pinheiro et al., 2014).

3. Results

Random effects: Significant variance components were recorded both for individuals and for litter over the parameters A and k. The growth functions yield a substantial improvement of fit to data by incorporating an autoregressive process of first order CAR(1) and and variance function VarPower into the models (Table 1)

Parameter	Estimator
σ_A (kg)	5.75
σ_k (days^{-1})	1.17. 10^{-8}
Correlation structure: CAR(1)	0.997
Variance function: Power	0.392
$\sigma_{residual}$ (kg)	0.70

Table 1: Parameter estimation of nonlinear mixed model

Fixed Effects: A significant effect of sex on the mean curve parameters was registered. Males had asymptotic weight (A) and age at inflection point (I) significantly larger than females, while the growth rate constant (k) was lower (Table 2). These parameters show different growth patterns between the sexes.
Females had a higher growth rate at early ages which decreased faster than males, reaching the point of inflection at an earlier age. Meanwhile, males showed a decrease in the growth rate slower so they reached an asymptotic weight significantly higher than females (Table 2)

Parameter	Males		Females		*p*
	Estimator	EE	Estimator	EE	
A (kg)	46.78	3.33	39.88	2.41	0.039
k (days^{-1})	0.0032	0.0002	0.0039	0.0002	0.002
I (days)	190.32	14.73	151.86	8.66	0.009

Table 2: Parameter estimates for the final Lopez model

4. Discussion

This work represents the first clear evidence of sexual dimorphism capybaras. The differences observed between sexes both in age at maturity and the maximum size would be related with polygynous mating system of this species. Sexual dimorphism is associated with differential selection pressures between sexes, usually due to the competition between males to mate with females. Males are organized in stable, linear hierarchies, were the dominant male in each group is significantly heavier than any of the subordinates. Each dominant male secure significantly more matings than each subordinate (Herrera and Macdonald, 1993). This relationship between body size and reproductive success would generate a selection pressure for large males and this was reflected in the significantly higher asymptotic weight (A) of males. Due to males have chances to reproduce only when they reach a large enough size to compete with other males would be adaptive extend the period of exponential growth to an older age. Meanwhile, in females the opportunity to mate with subordinate males would reduce the levels of competition. Thus, if females reach sexual maturity at an earlier age they may extend the period in which they are sexually active. These different strategies would explain why females showed an inflection point (*I*) at a significantly younger age than males.

5. Conclusions

Nonlinear mixed models are a powerful extension of traditional regression models to analyze longitudinal growth data. These models, by including individual variability, allowed us to describe the growth of capybaras and detect, for the first time, sexual dimorphism in this specie.

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