Growth and home range size of the gracile mouse opossum *Gracilinanus microtarsus* (Marsupialia: Didelphidae) in Brazilian cerrado

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(*Accepted 8 October 2009*)

Abstract: Differences in growth patterns between the sexes of the gracile mouse opossum *Gracilinanus microtarsus* and the consequences for home range size were investigated in a savanna habitat (cerrado) of south-eastern Brazil. A total of 51 juvenile individuals of *Gracilinanus microtarsus* was monitored using capture–mark–recapture from November 2005 to August 2006. The increase in body mass of gracile mouse opossums was described using the Gompertz growth model. Male gracile mouse opossums grew faster than females (dimorphic ratio of 1.5). Home range size, estimated with the minimum convex polygon method, was positively related to body mass. Model selection using Akaike's Information Criterion (AIC$_c$) and incorporating body mass, sex and season as independent variables showed that the best-supported model describing variance in home range sizes included only body mass. Our data suggest that a greater body mass gain in juvenile males is probably the proximate cause of sexual dimorphism in adult gracile mouse opossums and that energetic needs required for growth have a greater influence in home range size.

Key Words: body mass, cerrado, growth, home range, marsupial, population ecology

INTRODUCTION

Sexual size dimorphism (SSD) is widespread and variable among animals and the ultimate causes of SSD are associated with three major processes: sexual selection, fecundity selection and ecological causation (Blanckenhorn 2005, Shine 1989). From a proximate perspective, the SSD of a given species is caused by sex-biased maternal investment (before birth or during food provisioning/suckling) or differences between the sexes in development time and growth rate (the larger sex has to develop faster or for a longer period of time) (Foster & Taggart 2008, Koskela *et al.* 2004).

Mammals are generally dimorphic in size with a bias toward males, with males being at least 10% larger than females in over 45% of species (Lindenfors *et al.* 2007). Male-biased SSD may evolve through sexual selection on male body size: larger males can be more successful at acquiring mating opportunities through male-male combat, leading to the evolution of larger male body size (Cox *et al.* 2003, Weckerly 1998).

SSD is common in didelphids (Cáceres *et al.* 2007, Isaac 2006, Loretto & Vieira 2008) with males being larger than females in most species. Didelphids are considered polygynous, and in this promiscuous mating system males compete for access to breeding females, which favours phenotypic adaptations that enhance the ability of a male to prevail in male-male contests; e.g. a rapid growth rate and large body mass (Moore 1990, Schulte-Hostedde *et al.* 2001).

Dimorphism in body mass can contribute to differences in the behaviour, demography, life history, physiology, ecology and evolution of males and females within a population (Cox *et al.* 2003). Variability in growth parameters between the sexes may have consequences in

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space-use patterns (Dahle *et al.* 2006, Kelt & Van Vuren 1999). In polygynous mating systems females tend to have more stable home ranges whereas males tend to be more vagile, resulting in differences in use of space between the sexes (Loretto & Vieira 2005).

Home range is the area traversed by the individual in its normal activities of food gathering, mating and caring for young (Burt 1943). McNab (1963) suggested that mammal home range area reflects metabolic needs. Many studies have employed allometric relationships to demonstrate the relationship between home range size and body mass (Kelt & Van Vuren 2001, Linstedt *et al.* 1986). Besides body mass, others factors like sex, diet, population density, resource seasonality and habitat heterogeneity can cause variation in home range size (Dahle & Swenson 2003, Harestad & Bunnel 1979).

Home range size can differ between the sexes because males and females are dimorphic in size and have differences in metabolic need (Cederlund & Source 1994), use resources differently (Safi *et al.* 2007) or have different reproductive strategies (Dahle & Swenson 2003).

Seasonal differences in home range size can result from differences in the availability of resources at different times of the year, so at times when food is scarce or when there is the need to find mates (during the breeding season), individuals travel greater distances compared to periods in which food is abundant or during times outside the breeding season (Getz & McGuire 2008, Lesmeister *et al.* 2009).

In this study, we gathered data on a cohort of *Gracilinanus microtarsus*, a species of south-eastern Brazil with SSD to test the following hypotheses: (1) that the proximate cause of sexual size dimorphism in *G. microtarsus* is the difference in growth velocity (growth constant) between the sexes, and (2) that the home range size is positively related to body mass and consequently the home range size is larger in males than in females.

METHODS

Study species

Gracilinanus microtarsus Wagner 1842 is a small, solitary, arboreal and nocturnal didelphid marsupial that inhabits cerrado (savanna) and the Atlantic forest of south-eastern Brazil (Costa *et al.* 2003, Martins *et al.* 2006a). This species shows sexual size dimorphism, with adult males (30–45 g) being larger than adult females (20–30 g) (Martins *et al.* 2006a) and occurs at high densities in the cerrado (Martins *et al.* 2006a). Mating in this species is concentrated in a short period between August and September (the end of the cool-dry season) and individuals reproduce for the first time when they are approximately 1 y old, so females rear their offspring during the first half

of the warm-wet season (October–December) (Martins *et al.* 2006a).

Study area

Our study was carried out in savanna habitat at the Reserva Biológica de Mogi Guaçu (RBMG) located in the district of Martinho Prado, Mogi Guaçu, São Paulo ($22°15'–22°18'$S; $47°08'–47°13'$W). Vegetation at the RBMG consists of cerrado, which is a neotropical savanna formation comprising different vegetation physiognomies that differ in the density and composition of woody and ground-layer plants, forming a continuum from open and dry grassland to dense forest (Goodland 1971). The RBMG is a remnant of the physiognomy known locally as 'cerrado *sensu stricto*' which is woodland with scattered trees 5−8 m tall and closed scrub (Oliveira-Filho & Ratter 2002). The climate of the region has two well-defined seasons: the warm-wet season occurs from October to March whereas the cool-dry season occurs from April to September. The mean annual rainfall and the mean annual temperature are, respectively, 1430 mm and $21°C$ (data from the meteorological station of RBMG).

Data collection

Fieldwork was conducted from November 2005 to August 2006. In November 2005, a cohort of *G. microtarsus* was captured and then monitored until they reached the sub-adult stage. The marsupials were captured monthly within the 4 mo of the warm-wet season (November 2005, December 2005, January 2006 and March 2006) and within the 4 mo of the cool-dry season (May 2006, June 2006, July 2006 and August 2006). The data location points were obtained on 10 consecutive days in each mo. An $11 × 11$ trapping grid ($22\,500\,m^2$) with 121 trapping stations located 15 m apart was used. A single Sherman live-trap ($7.5 × 9.0 × 23.5$ cm) was set on trees at each trapping-station *c.* 1.75 m above ground and baited with banana and peanut butter. The individuals captured were marked with a numbered leg-band and their sex and weight were recorded with a Pesola® balance (precision = 1 g) (Costa *et al.* 2003). Location points of the captures was recorded and defined as *x* and *y* co-ordinates in the space of trapping-stations.

Live specimens are more prone to measurement error than are dead specimens (Blackwell *et al.* 2006), however it was necessary to monitor live individuals for a certain period of time to obtain growth and home range data. Weight record error was minimised because all individuals (males and females) were weighed by the same observer in all samples, using the same balance and procedure.

Data analysis

Body mass data from females and males were fitted using the non-linear Gompertz growth model $W = Ae^{-e^{-K(t-I)}}$ where W represents body mass at time t, A the asymptotic body mass, I the inflection point and K a growth constant (Begall 1997). The day of first capture of juveniles was designated as day 0 for modelling procedures and we fixed the asymptotic mass at mean values of adult females and males captured early in the study area ($A_{\female} = 29 \pm 2$ g, n = 10 and $A_{\male} = 38 \pm 2$ g, n = 6). The parameters K and I were estimated by least squares using the Gauss–Newton algorithm, and the adequacy of the model was determined from a determination coefficient (R^2 of the correlation between observed and predicted body mass values) (Souza 1998). The growth constant K can be regarded as a measure of growth; i.e. the higher the K, the faster the growth; and because of its independence of adult weight, intraspecific comparisons are possible (Begall 1997). Thus, differences in model parameters between females and males were evaluated using a t-test with $\alpha = 0.05$. The analyses were conducted using SAS.

Data location points were used to estimate home range sizes of individuals of *G. microtarsus* through the minimum convex polygon (MCP) method (Mohr 1947) using the program CALHOME (Kie *et al.* 1996). In the MPC method the outer data points obtained for an individual animal are connected by a connection rule in which no internal angle of the polygon exceeds 180° (Mohr 1947). The area of the polygon is then calculated and taken as an estimate of the home range size. As minimum convex polygon estimates are dependent on the number of captures per individual, all estimates of home range sizes were based on individuals with at least five location points, for which estimates were more reliable (Cáceres & Monteiro-Filho 2001). In the CALHOME program we chose 90% MCPs, so that the program excluded 10% of the outer data points to generate home range areas. Therefore, a 90% convex polygon is the smallest area derived by connecting location points such that the resultant polygon encloses 90% of all observations. The 90% MCPs are less dependent on the sample size, because as new positions are added, more outlying positions are excluded (Dahle & Swenson 2003).

We applied a linear regression by plotting the distribution of the logarithm of home range size (m^2) against $\log_{10}$ body mass (g) to determine if there was a significant relationship between home range size and body mass. We only used data from individuals that had home range areas located totally inside the trapping grid away from the boundaries for the linear regression because sometimes the home range areas can be underestimated if they are located on the trapping-grid boundaries.

We used home range estimates obtained from the MPC method to model variation in home range size as function of body mass, sex and season. Generalized linear models were used with the response variable (home range size) distributed according to a Gamma distribution and with the inverse link function (Dobson 2002, McCullagh & Nelder 1989). We fitted models including the following effects (notation): (1) mass (mass); (2) sex (sex); (3) season (season); (4) additive effect of mass and season (mass + season); (5) additive effect of mass and sex (mass + sex); (6) additive effect of sex and season (sex + season); (7) additive effect of mass, sex and season (mass + sex + season); (8) additive effect of sex and season and interaction between sex and season (sex + season + sex × season); (9) additive effect of mass, sex and season and interaction between sex and season (mass + sex + season + sex × season).

The adequacy of the general model to data was tested using a Pearson chi-squared test (Sokal & Rohlf 1995). The selection of most parsimonious model to describe the data was based on Akaike's Information Criterion, AIC, using the corrected version for small sample size, AIC_c (Burnham & Anderson 1998). AIC_c was calculated as $AIC_c = -2 \ln L(\hat{\theta}|m) + 2K \left(\frac{n}{n-K-1}\right)$, where $\ln L(\hat{\theta}|m)$ is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates of a given model (m), K is the number of parameters in the model and n is the sample size. According to this criterion, the model with the lowest AIC_c value is the most parsimonious model. Differences of AIC_c values between m model and the most parsimonious model, Δ_m, were used to compare the support of different models in the set of candidate models. As suggested by Burnham & Anderson (1998), models with $0 \leq \Delta_m \leq 2$ were considered high support models. Statistics analyses were conducted using the GLM procedure in SAS.

RESULTS

Body mass

A total of 51 juvenile individuals of *Gracilinanus microtarsus* were captured from November 2005 to August 2006. During the initial fieldwork in November, individuals captured had body masses that ranged from 6 g to 11 g. The mean body mass for both sexes in each month is shown in Table 1.

The Gompertz model described the body mass growth for both females and males ($R^2_{\female} = 0.646$ and $R^2_{\male} = 0.789$) (Table 2, Figure 1). After the age of 180 d, body mass of males and females did not overlap (Figure 1). The K and I parameters differed between females and males in the Gompertz model with males showing the growth constant (K) larger than females (t = 3.15; df = 103; P = 0.003) and the inflection point (I) later than females (t = 2.12; df = 103; P = 0.04) (Table 2). The dimorphic

Table 1. Mean ± SD body mass of males and females of *Gracilinanus microtarsus* captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil.

Months	Season	Body mass (g)	
		Female (n)	Male (n)
November	Warm-wet	8 ± 2 (7)	11 (1)
December	Warm-wet	10 ± 2 (15)	13 ± 2 (10)
January	Warm-wet	13 ± 2 (15)	14 ± 1 (7)
March	Warm-wet	14 ± 3 (9)	18 ± 2 (9)
May	Cool-dry	15 ± 1 (6)	18 ± 2 (6)
June	Cool-dry	16 ± 1 (5)	23 ± 3 (5)
July	Cool-dry	17 ± 2 (4)	26 ± 2 (5)
August	Cool-dry	18 ± 1 (2)	29 ± 4 (7)

Table 2. Gompertz growth model parameters of *Gracilinanus microtarsus* (♀ = female, ♂ = male) captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006. ($\widehat{K}$ = the growth constant, $\widehat{I}$ = the inflection point).

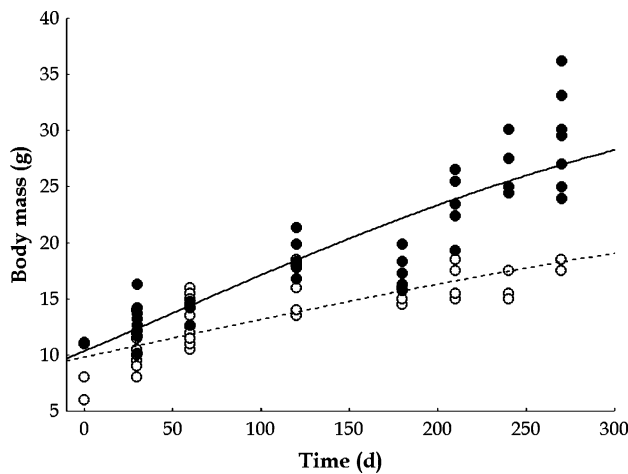| Parameter	Estimate	Asymptotic SE	$\dfrac{\text{Estimate}}{\text{Asymptotic SE}}$	95% Confidence Interval
$\widehat{K}_{♀}$	0.00316	0.000325	9.72	0.0029–0.0046
$\widehat{K}_{♂}$	0.00483	0.000403	11.98	0.0048–0.0068
$\widehat{I}_{♀}$	26	10	2.6	6–47
$\widehat{I}_{♂}$	55	9	6.1	37–73

Figure 1. Body growth of the females (observed values = open circles; Gompertz curve = dotted line) and males (observed values = closed circles; Gompertz curve = solid line) of *Gracilinanus microtarsus* captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006. $R^2_{♀} = 0.646$ and $R^2_{♂} = 0.789$.

ratio ($\widehat{K}_{♂} / \widehat{K}_{♀}$) was 1.5, indicating that males grew faster than females.

Home range

We used data location points from 26 individuals (12 females and 14 males) to estimate home range size due to requirements of the MPC method. These data were used

Table 3. Home range area of *Gracilinanus microtarsus* (♀ = female, ♂ = male) captured in both seasons in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006, as estimated by the MPC method.

Individuals	Sex	Body mass (g)	Home range size (m²)	Season
B89	♀	14	1463	warm-wet
		17	1688	cool-dry
B92	♀	11	2587	warm-wet
		15	900	cool-dry
B120	♀	12	2363	warm-wet
		16	2700	cool-dry
B123	♀	14	563	warm-wet
		15	675	cool-dry
B131	♂	16	1800	warm-wet
		22	6300	cool-dry
B152	♂	21	1350	warm-wet
		21	1350	cool-dry

for the analysis of models that best explained the variance in home range size.

Analysing only the individuals for which a home range area was estimated in both seasons, we noted that home range size increased proportionally to the body mass gain. Table 3 shows that females B89 and B120 increased 3 g and 4 g, respectively, in their body mass and increased 225 m² and 337 m² in their home range, respectively, from the warm-wet season to the cool-dry season. The female B123 increased 1 g in its body mass and 112 m² in its home range from the warm-wet season to the cool-dry season. Whereas male B131 increased 6 g in its body mass and 4500 m² in its home range from the warm-wet season to the cool-dry season, male B152 remained with the same weight and the same home range size from the warm-wet season to the cool-dry season.

Although female B92 had a body mass gain of 4 g, there was a reduction in the size of her home range from the warm-wet season to the cool-dry season.

Plotting home range size against body mass of individuals with home range areas located totally inside the trapping grid, we observed that the linear regression has a significantly positive slope ($y = 0.88 + 1.84x$; $R^2 = 0.39$; $F = 5.84$; $df = 1.9$; $P = 0.04$; $n = 10$; Figure 2).

The general model (mass + sex + season + sex × season) fit the data well ($\chi^2 = 23.1$; $df = 31$; $P = 0.85$). The model selection using Akaike's Information Criterion (AIC$_c$) showed that the most parsimonious model to describe variance in home range sizes included only body mass as the independent variable. The summary of the statistics of model selection and parameter estimates of the best model is shown in Tables 4 and 5, respectively.

DISCUSSION

The juveniles of *Gracilinanus microtarsus* grew throughout the study to reach adult body size. No female individual

Table 4. Selection of the most parsimonious model based on Akaike's information criterion (AIC_c) for the description of home range data of *Gracilinanus microtarsus* captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006. AIC_c = Akaike's Information Criterion corrected for small samples, Δ_m = differences of AIC_c values between a given model m and the most parsimonious model, w_i = the proportional likelihood of the models, K = the number of parameters in the model.

Model	AIC_c	Δ_m	w_i	K
mass*	0.94*	0.00*	0.49*	2*
mass + season	3.21	2.27	0.16	3
mass + sex	3.32	2.38	0.15	3
season	4.86	3.92	0.07	2
mass + sex + season	5.74	4.80	0.04	4
sex + season	6.49	5.55	0.03	3
sex	6.62	5.67	0.03	2
sex + season + sex × season	8.34	7.39	0.01	4
mass + sex + season + sex × season	8.40	7.45	0.01	5

Table 5. Parameter estimates of the best model for the description of home range data of *Gracilinanus microtarsus* captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006.

Model	Estimates	SE	Wald statistic	P
Intercept	0.00133	0.000249	28.3	< 0.00001
Mass	–0.000029	0.000010	8.61	0.003336

had reached adult body mass by the end of the fieldwork and only a few male individuals had already reached adult body mass in July and August. Adult males of the gracile mouse opossum weigh 30–45 g and adult females weigh 20–30 g (Martins *et al.* 2006a).

Differences in growth patterns between the sexes, with males having a faster body mass gain, resulted in sexual size dimorphism in this marsupial. This proximate
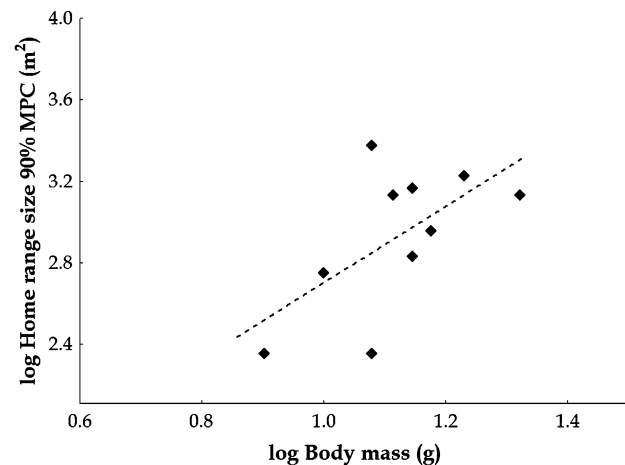

Figure 2. Plot of the distribution of home range size against body mass of juveniles of *Gracilinanus microtarsus* captured in RBMG, Martinho Prado, São Paulo, south-eastern Brazil, from November 2005 to August 2006. $R^2 = 0.39$; $F = 5.84$; df = 1.9; $P = 0.04$; regression line = dotted line.

mechanism probably occurs after birth (during suckling or after they begin to forage by themselves), because marsupial offspring born after a very short gestation period at an early stage of development weigh less than 1 g at birth (Isaac 2006). Many marsupials and other mammals present differences in post-weaning growth rates and juvenile males often grow faster than juvenile females (Badyaev 2002, Isaac 2006, Lee & Cockburn 1985).

The majority of mammals have a predominantly polygynous mating system, with males competing for access to breeding females (Krebs & Davies 1981) and it can therefore be predicted that selection will favour phenotypic adaptations that enhance the ability of a male to grow rapidly and have a large body size. However, the mating success of females is commonly less dependent on body size and therefore females are expected to invest resources into reproduction rather than body growth (Isaac 2006, Schulte-Hostedde *et al.* 2001).

Gracilinanus microtarsus has a polygynous mating system and mating is concentrated in a short period between August and September (the end of cool-dry season) allowing females to rear their offspring during the first half of the warm-wet season (October to December) (Martins *et al.* 2006a) when insects, the main food resource for this species (Martins & Bonato 2004, Martins *et al.* 2006b), are highly abundant in the cerrado (Pinheiro *et al.* 2002). Therefore, weaning probably occurs at the beginning of the warm-wet season.

Martins *et al.* (2006c) demonstrated that males of *G. microtarsus* are partially semelparous (a condition in which mortality after the first mating is high but not complete, with a small fraction of males surviving to a second breeding season). One of the forces that drives semelparity (a single reproductive episode followed by death) in males is inter-male competition (Holleley *et al.* 2006). Intense male–male competition during a short mating period and low probability of male survival to the next breeding season due to severe physiological stress results in selection for males to expend maximum effort in a single breeding season (Boonstra 2005, Oakwood *et al.* 2001). A larger body size can intensify reproductive effort since it increases mating access and maintains intromission despite aggression from other males (Holleley *et al.* 2006, Schulte-Hostedde *et al.* 2001, Weckerly 1998), but the stress leads to reduced survival (Martins *et al.* 2006c, Oakwood *et al.* 2001).

Home range size was positively related to body mass, so heavier individuals had larger home ranges. Larger species have higher energy demands and necessitate larger areas for food gathering (Harestad & Bunnel 1979, Kelt & Van Vuren 1999, 2001; McNab 1963), unless food exists in superabundance. At the intraspecific level, larger individuals have larger home ranges because they probably have larger energy demands and need to cover larger distances to find the amount of food that supplies

their requirements. However, home range sizes can be underestimated because the MPC method describes only a 2-dimensional area, and, since *G. microtarsus* is an arboreal species, individuals can utilise both the vertical and horizontal dimensions of the habitat, perhaps using one dimension to a greater extent than the other.

Since *G. microtarsus* is sexually dimorphic in size, sex should be an important factor influencing home range size. Differences between male and female home range sizes as a consequence of size dimorphism are observed in some marsupials, like *Burramys parvus* (Broome 2001), *Dasyurus maculatus* (Belcher & Darrant 2004), *Didelphis aurita* (Cáceres & Monteiro-Filho 2001), *Micoureus demerarae* (Moraes-Júnior & Chiarello 2005) and *Phascogale tapoatafa* (Soderquist 1995). However, because almost no individual had reached adult body mass at the end of data collection, sexual dimorphism was not as pronounced and was unlikely to cause a great effect on home range size.

Reproductive season is another factor that probably causes variation in home range size. However, this factor could not be investigated because we did not observe a reproductive season during the data sampling period. In some species that have a promiscuous mating system, reproductive season can cause great variation in male home range size. In this season, males increase their home range sizes while searching for breeding females to mate (Loretto & Vieira 2005, Moraes-Júnior & Chiarello 2005).

Habitat quality and structure can also influence home range size. In habitats with abundant food resources, the resource quality alone might dictate smaller home range sizes than in habitats where these factors are scarce (Ims 1987, Stradiotto *et al.* 2009). Therefore, stability in habitat quality may be reflected in stability of home range sizes. In addition to habitat quality, habitat structure may influence the size and spatial distribution of the home range (Lambert *et al.* 2008, Lucherini & Lovari 1996). The female B92 may have found a microhabitat of better quality and therefore not expanded the size of her home range despite having increased her body mass from the warm-wet season to the cold-dry season.

In the present study, body mass was the most important factor influencing home range size, probably because energetic needs required for growth can be an important factor in juveniles that are growing to reach adult body size.

ACKNOWLEDGEMENTS

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