

# Scaling body mass and use of space in three species of marsupials in the Atlantic Forest of Brazil

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**Abstract** Body mass is considered a major determinant of home range size, but usually at a large scale of body mass variation. The exact scale where body size becomes more important than particular adaptations of each species is not clear, and uncertainty in the estimate of home range size is a possible cause of weak intraspecific scaling. We determine the scaling to body mass of two alternative movement measurements, daily home range (DHR) and its intensity of use (IU), in three species of didelphid marsupials, *Didelphis aurita*, *Philander frenatus*, and *Metachirus nudicaudatus* (Didelphimorphia, Didelphidae). The expected scaling exponents  $DHR \approx M^{0.5}$  and  $IU \approx M^{0.25}$  were derived from the scaling to body mass of home range and daily movement distance. Animals were tracked in Serra dos Órgãos, Rio de Janeiro, Brazil, using a spool-and-line device. Individuals of the three species were compared combining intra and interspecific variation in a single analysis, with species, body mass, and thread tracked as covariates. The model best supported included only body mass as the independent variable, with  $DHR \approx M^{0.435}$  and  $IU \approx M^{0.218}$ , close to the expected values. The second best supported model included species identity, but with a non-significant effect. It was surprising that body mass was more important than species identity in a comparison involving only three species, and considering the morphological and locomotory adaptations of the three species. Body mass may become more important than species identity when the scale of variation approaches one order of magnitude.

**Key words:** allometry, cost of transport, movement, small mammals, spool-and-line device.

## INTRODUCTION

The area used by animals during daily and routine activities, or the home range (*sensu* Burt 1943) is a central concept in the ecology of individuals, populations, and even communities (Basset 1995). One of the reasons is the scaling relationship between home range, body size, and energetic requirements of organisms in interspecific comparisons (Harestad & Bunnell 1979; Mace & Harvey 1983; Lindstedt *et al.* 1986; Basset 1995; Silva & Downing 1995; Kelt & Van Vuren 2001). Such scaling relationships are less frequently studied intraspecifically (Kjellander *et al.* 2004), but in carnivores the intraspecific scaling exponent of home range with body mass is quite variable (Nilsen & Linnell 2006). One of the possible causes of the variable intraspecific association between home range and body mass is the very estimate of home range size, which is highly dependent on the number of captures or fixes, grid size, and the sampling interval (Bergallo 1990; Cameron 1995; Gautestad & Mysterud 1995). An asymptotic home range size is

usually sought, but rarely reached, and may never be found if home range size is an ever-increasing function of the number of captures (Gautestad & Mysterud 1995). Analysis and comparison of other movement measures may be useful, but rarely considered in studies of animal movement.

Daily home range (Spencer *et al.* 1990; Cameron 1995) is such an alternative movement measure that rarely has been used in studies of animal movement. A related and more explored measure is daily movement distance, the linear distance between initial and final locations of the animal (Garland 1983; ‘day range’ in Carbone *et al.* 2005; Schradin 2006). However, daily movement distance may not reflect the actual movement involved in a 24-h period of activity. The linear distance between the initial and last position of the animal is the end result of daily movements, which are spread over an area for terrestrial animals, or volume for arboreal, flying and aquatic animals. Different shapes of areas or volumes may result in similar daily movement distances. Thus, daily home range (DHR) – the area traversed during a 24-h period – would give a more accurate inference of total movement spent per unit of area than daily movement distance.

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Another rarely considered measure directly related to movement areas is 'intensity of use' (IU) (Loretto & Vieira 2005). Intensity of use can be defined as the amount of individual movement per unit of area or volume. It is indirectly related to time to independence (Swihart *et al.* 1988), the ratio of area to the square of path length (Hailey & Coulson 1996), and directly related to measures of tortuosity such as the fractal dimension  $D$  (Benhamou 2004). Individuals could have movement areas of similar size, but use them with different intensities.

Two animals that differ only in size of DHR and the movement path within, but whose shape is identical – one is simply an enlarged picture of the other – should have identical IU (but see Benhamou 2004). This would not happen if IU were estimated as the amount of movement (a linear measurement) divided by daily home range; an area measurement. The larger animal would always have a lower IU because area measurements increase with the square of linear measurements. One solution is to bring the two measurements to a common scale, taking square root of the area measurement (Loretto & Vieira 2005). Thus,

$$IU = \frac{\text{movement}}{\text{area}^{0.5}} \Rightarrow \frac{\text{movement}}{DHR^{0.5}} = \text{movement} \cdot DHR^{-0.5}$$

Daily home range and IU should scale with body mass, but not necessarily with the same scaling exponent of home range. Energetic requirements scale as  $M^{0.75}$  (reviewed in Marquet *et al.* 2005; but see Kozłowski & Konarzewski 2005) but for mammals larger than 100 g home range scales as  $M^{1.0}$  (Harestad & Bunnell 1979; Lindstedt *et al.* 1986; Kelt & Van Vuren 1999, 2001). Thus, home range size increases more than expected based on energetic requirements. Based on simple transformation to linear units of the scaling of home range with body mass, daily movement distance should scale as  $M^{0.5}$ , but actually scales as  $M^{0.25}$  (Garland 1983; Carbone *et al.* 2005). Consequently, the increase in daily movement distance with body mass is not sufficient to cover the increase in home range area, and large mammals take longer to travel through their home ranges than small mammals (Garland 1983). Swihart *et al.* (1988) reached the same conclusion based on the scaling of time to independence, the time necessary for two locations along the path of an animal to become statistically independent of each other. In this regard, IU provides a critical evaluation of how animals change their use of either home range, or DHR, with body mass. The scaling exponent of IU will indicate how intensively large individuals use their movement areas compared to small individuals: more intensively (a positive exponent), less intensively (a negative exponent), or similarly (an exponent close to zero).

As a measurement of area, and assuming a circular shape, DHR would be proportional to the square of its linear distance, hence proportional to the square

of daily movement distance. If daily movement distance  $\approx M^{0.25}$  (Carbone *et al.* 2005), then

$$DHR \approx (M^{0.25})^2 \approx M^{0.5}$$

If the amount of movement is standardized and made constant, then

$$\text{and} \quad IU \approx DHR^{-0.5}$$

$$IU \approx (M^{0.5})^{-0.5} \\ IU \approx M^{-0.25}$$

Thus, IU would decrease with body mass, whereas daily movement distance would increase. The  $-0.25$  scaling coefficient of IU to body mass also was observed for costs of locomotion in terrestrial animals, the cost of moving a unit body mass over a unit of area (Schmidt-Nielsen 1984; Full & Tu 1991), and for the specific metabolic rate (reviewed in Marquet *et al.* 2005).

We compare daily home ranges and their intensity of use between individuals of three species of didelphid marsupials. Our objectives were to determine the importance of body mass relative to species-specific effects on the scaling of DHR and IU, and to compare their scaling exponents with the values predicted based on daily movement distance ( $DHR \approx M^{0.5}$  and  $IU \approx M^{-0.25}$ ).

## METHODS

### Study area

We conducted fieldwork in the Coastal Forest of the Serra do Mar, a subdivision of the Atlantic Forest Biome (Dinerstein *et al.* 1995), located in the mountain range of Serra dos Órgãos, in the Parque Nacional da Serra dos Órgãos (PARNA/SO), municipality of Guapimirim, state of Rio de Janeiro, Brazil, locally known as Garrafão (22°28'28'S, 42°59'86'W). The forest is part of one of the largest continuous stretches of Atlantic Forest remaining (SOS Mata Atlântica/INPE/ISA). The canopy height reaches 20–25 m, with tree-trunk diameter varying from 40 to 60 cm, sometimes reaching 1 m. A sub canopy and understory are present, but generally it is not possible to distinguish them clearly. Lianas, palm trees, epiphytes, ferns, and bromeliads are common. Common tree species belong to the genera *Sloanea*, *Ficus*, *Cedrela*, *Carimiana*, *Vochysia*, and *Cecropia*. Common species of the sub canopy and understory include tree ferns of the genera *Alsophila*, *Cyathea*, and *Hemitelia*, and the palm tree *Euterpe edulis* (Rizzini 1979). Currently the area is surrounded by holiday houses that could have some influence on the structure and composition of the forest (Freitas 1998).

## Species

The three species of study, *Didelphis aurita* Wied-Neuwied (1826), *Philander frenatus* (Olfers 1818), and *Metachirus nudicaudatus* (Desmarest 1817) (Didelphimorphia, Didelphidae) occur throughout the Atlantic Forest of Brazil (Emmons 1990). We tracked 37 *Didelphis aurita* (20 males and 17 females), 14 *Philander frenatus* (nine males and five females), and 19 *Metachirus nudicaudatus* (nine males and 10 females). They were among the more abundant didelphid marsupials in the study area. For more information on their population ecology, see Gentile *et al.* (2004).

Body mass of the majority of didelphid marsupials varies from 50 to 600 g excluding species of *Didelphis*, whose adult body mass varies from 500 to 2300 g (Emmons 1990). Individuals of the three species studied varied from 85 to 1885 g (range: 1800 g). However, body mass variation of *D. aurita* alone was approximately in the same range, from 135 to 1885 g ( $\bar{x}$  = 928 g, SD = 462). Range of body mass was 85–565 g in *P. frenatus* ( $\bar{x}$  = 292 g, SD = 155), and 120–590 g in *M. nudicaudatus* ( $\bar{x}$  = 391 g, SD = 123). Didelphids are considered mostly omnivorous with varying degrees of subtle feeding specializations (Astúa de Moraes *et al.* 2003). Species of *Philander* are described as carnivorous-omnivorous, *Metachirus* as insectivorous-omnivorous, and *Didelphis* spp. may be considered the most omnivorous didelphids (Astúa de Moraes *et al.* 2003). Differences between didelphids in the use of the forest strata are more clear-cut in general (Vieira & Monteiro-Filho 2003), but the three species studied are terrestrial or semiterrestrial, climbing above the forest floor only occasionally (Cunha & Vieira 2002). The more terrestrial species, *Metachirus nudicaudatus*, rarely leaves the forest floor. It is considered the only truly cursorial species of the group, with morphological specialization to develop speed on the forest floor (Szalay 1994). Information on home range and daily movements of didelphid marsupials is scant, but it suggests that *Didelphis* move over a larger area than *Philander* and *Metachirus*, which are more similar in their daily movement distance (Miles *et al.* 1981; Charles-Dominique 1983; Sunquist *et al.* 1987).

## Trapping and handling of animals

Animals were captured in bimonthly trapping sessions of five consecutive nights each, from January 1998 to June 2000, as part of a mark-recapture study of small mammal populations of the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro. Three grids of 0.64 ha, named A, B, and C, were established in the area at different altitudes (748 m, 652 m, and 522 m, respectively). The distance between grids A and B was 853 m, and 573 m between grids B and

C. Each grid had 25 trapping stations 20 m apart, with two traps per station; one Tomahawk (41 × 14 × 14 cm) and one Sherman (30.5 × 9.8 × 8.0 cm) both on the ground. After identification, marking with ear-tags if necessary, and body mass measuring, animals were equipped with a spool-and-line device based on Miles *et al.* (1981), and Boonstra and Craine (1986). Anaesthetics were not necessary because animals were handled quickly and without harm. Quilting cocoons no. 5 or no. 10 of nylon thread were used (Cansew Inc., Montreal, Canada) weighing about 1.7 g (175 m of thread) and 4.7 g (480 m of thread), respectively. The small cocoon was used for young *Philander frenatus* and *Metachirus nudicaudatus*, representing never more than 1.7% of a young body mass. The large cocoon was used for adults of these species and all individuals of *Didelphis aurita*, weighing never more than 3.5% of body mass. Cocoons of five colours were used to facilitate the identification of threads of different individuals in the field. Colors also helped in case of thread breakage to find the other end of the thread. The cocoon was covered with heat-shrinking plastic, and wrapped with masking tape to form the spool. The spool was attached to the fur between the shoulders with an ester-cianocrilate based glue. Any marks of cocoon or glue disappeared in animals recaptured one or two trapping sessions later.

Animals were tracked and thread collected the day after release. Animals released on the first day of the trapping session also were tracked on the same day, but at least 4 h after the release. On the first day there were no other threads to track, which allowed us to track first-day animals twice, 4 h after release, and the next day. First-day paths allowed us to determine nest location with certainty, and to evaluate possible differences in movement patterns immediately after release. Thread was collected and mapped until the nest was found, where the thread was cut off and tied next to the entrance of a nest to continue tracking on the next day. We never found any individual snagged along its path, but on one occasion we found an individual captured in a Sherman trap tangled with the thread. It was recaptured with thread left in the spool, and got tangled inside the trap. After disentangling the thread, it was released without any apparent harm.

Differences between movement patterns before and after the nest were not detected. Behaviour of animals after release also did not suggest any major stress from trapping and handling. Animals were gently put on the ground, and immediately moved away from the observers at a fast pace, but only up to 5 m. Thereafter some animals took a slow pace, others stopped for up to 5 min of grooming, others started to forage litter arthropods, and others stopped to drink water accumulated on leaves or trunk cavities. All of these behaviours were observed less than 5 m from the observers,

suggesting that animals quickly return to routine behaviours after release.

Animal paths were mapped using compass and tape-line to take polar coordinates (distance and azimuth) between points where the animal clearly changed movement direction. These points were defined as any change of more than  $5^\circ$  in the animal path. To calculate total movement of an individual, we multiplied total weight of collected thread by the ratio between total cocoon length and weight. Polar coordinates were transformed to Cartesian coordinates (x, y), and area of the 100% minimum convex polygon (MCP) was calculated with the program CALHOME (Kie *et al.* 1996).

These movement areas were used as estimates of DHR (Spencer *et al.* 1990; Mendel & Vieira 2003). They provide a direct measurement of the area used relative to a certain amount of thread tracked. The MCP was used instead of other area estimators for two reasons: (i) it allowed comparison with DHR estimated by radiotracking and capture-recapture studies, which frequently use MCP even when also using another area estimator (White & Garrott 1990); and (ii) because the spool-and-line technique allows a precise and accurate description (not an estimate) of the actual path of the animal. Statistical methods such as those based on Kernel distributions are not appropriate because the path obtained with the spool-and-line technique is not an estimate, but the actual path taken by an animal. To minimize spurious variance, data for individuals tracked less than 35 m were discarded. Average thread tracked for an individual was 147 m in *D. aurita* (range 40–440 m), 175 m in *M. nudicaudatus* (range 38–418 m), and 149 m in *P. frenatus* (range 42–402 m).

### Statistical analyses

Frequency distributions of DHR and IU followed a log-normal distribution. Initially, frequency distributions were analysed separately for each species, mostly using probability plots of observed against expected values from normal, log-normal, exponential, and gamma distributions. The hypothesis of normality of DHR and IU was rejected in most species with Lilliefors' test ( $P < 0.05$  in all species). In agreement with the results of the pooled data, in most species the log-normal was the frequency distribution of best fit to DHR and IU values. Therefore, variables were log-transformed in the following analysis to normalize the data, and to enhance homogeneity of variances.

We used a model selection approach (reviewed in Hobbs & Hilborn 2006) based on ANCOVA design and maximum likelihood to estimate the effects of body mass on DHR and IU. The full model included the amount of thread tracked for each individual and body

mass as covariates, a variable coding for the effect of species membership, and interaction terms between the covariates and the species factor. Thread tracked was included as a covariate because DHR and IU are a direct function of the amount of thread tracked, which varies between individuals. Interaction terms were included to test the assumption of homogeneity of slopes in the ANCOVA (Statsoft 2001). A significant interaction implies that slopes between the covariate and the dependent variable differ between factors, in effect, when scaling coefficients differ between species (when variables are log-transformed, the slopes are the scaling coefficients).

Subsets of these variables formed 16 different models, whose performance was compared using statistics derived from the corrected Akaike Information Criterion (AICc), appropriate when the ratio of sample size to number of parameters is less than 40 (Burnham & Anderson 2002). The smaller the value of AICc, the better the fit to the data taking into consideration the number or parameters of the model. However, the value of AICc is relative to the other models in the set. Thus, the first derived statistic was the AICc difference,  $\Delta_i$ , the difference between a given model and the most likely model of the set. Models with  $\Delta_i > 4$  are considered to have considerably less empirical support from the data than models with  $\Delta_i < 4$ , and empirical support for models with  $\Delta_i > 10$  is essentially none (Burnham & Anderson 2002). The second statistic was Akaike weight,  $w_i$ , which estimates the relative likelihood of a model given the data and the set of models analysed, namely, the weight of evidence in favour of a model (Burnham & Anderson 2002). The sum of  $w_i$  over the models adds to 1.

For the selected models, significance of regression coefficients were evaluated by the Wald test, which is similar to a *t*-test, except that variance is estimated by maximum likelihood, *n* is used in the denominator instead of *n*-1, and is tested against a  $\chi^2$  distribution (Dobson 1990). For models that include thread length as a covariate, Wald statistics for DHR and IU are the same. Daily home range and IU are not necessarily correlated when thread length varies between individuals (Pearson *r* varied from  $-0.382$ – $0.003$  in the four marsupials, with probabilities of 0.145 and 0.988, respectively). However, if the amount of movement is standardized and made constant, IU is proportional to  $\text{DHR}^{-0.5}$  (see Introduction). This is exactly what happens in an ANCOVA with thread length (= movement) as a covariate. In this situation, the relationship parameter estimates and their asymptotic variances are the same for DHR and IU, resulting in the same Wald statistic.

We did not consider phylogenetic relationships between these species, which represent groups with different degrees of dependence between each other. Nevertheless, in the three species studied most

**Table 1.** Performance of models predicting daily home range (DHR) and its intensity of use (IU) of individuals of three species of didelphid marsupials

	Model	Variables	d.f.	<i>K</i>	AICc	$\Delta_i$	$w_i$
DHR	1	Thread + body mass	2	4	185.229	0.000	0.501
	2	Thread + body mass + species	4	5	186.544	1.315	0.260
	3	Thread + species	3	4	188.290	3.061	0.109
	4	Thread + body mass + species + 2*3	6	6	190.686	5.457	0.033
	5	Thread + body mass + species + 1*3	6	6	190.858	5.629	0.030
	6	Thread + body mass + species + 1*2*3	6	6	190.899	5.670	0.029
	7	Thread	1	3	192.517	7.288	0.013
IU	1	Thread + body mass	2	4	82.643	0.000	0.501
	2	Thread + body mass + species	4	5	83.958	1.315	0.260
	3	Thread + species	3	4	85.704	3.061	0.109
	4	Thread + body mass + species + 2*3	6	6	88.100	5.457	0.033
	5	Thread + body mass + species + 1*3	6	6	88.272	5.629	0.030
	6	Thread + body mass + species + 1*2*3	6	6	88.313	5.670	0.029
	7	Thread	1	3	89.931	7.288	0.013

$\Delta_i$ , difference in AICc between the given model and the best model; AICc, Akaike Information Criteria corrected for small samples; *K*, number of parameters of the model;  $w_i$ , Akaike weight, the relative likelihood of a model given the data and the set of models analysed. Asterisks indicate interactions between variables, coded by numbers (thread = 1, body mass = 2, species = 3).

variation in body mass occurs between individuals, which are considered independent data points.

All analyses were carried out with the Generalized Linear Models module of STATISTICA (Statsoft 2001).

## RESULTS

Three models stood out from the rest. None of these models included interaction terms between 'species' and the two covariates (Table 1). The remaining models, from Model 4 on, had  $\Delta_i > 4$ , and models that did not include thread length had the worst likelihood, with  $\Delta_i > 10$ . Models with only body mass or species had essentially no support from the data (Models 13–16). In these models, thread length was not included as a covariate; hence the effects of body mass and species membership were not standardized for thread length. Accordingly,  $\Delta_i$  and  $w_i$  have different values for DHR and IU in Models 13–16. Akaike weights further emphasize the larger likelihood of the first three models. Model 4 had  $w_i$  dropping approximately 15 times relative to Model 1. Therefore, we considered only the three best models in the analysis of regression coefficients.

The three selected models included thread length as a covariate, but Model 1 included only body mass, without a species effect. Model 2 included species and two covariates, and Model 3 included only thread length and species (Table 2). Model 1 did not include a species effect, but the coefficients of thread length and body mass were highly significant (Table 2). In Model 2, species were added as a factor, but it was not significant. In Models 2 and 3, *P. frenatus* is the refer-

ence species to which the categorical variables coding for the other two species are compared.

The coefficients of body mass in Model 1 were close to the expected values for DHR (0.5) and IU (−0.25). In Model 2, however, the inclusion of species as a factor caused the coefficient for DHR and IU to become 0.359 and −0.179, respectively (Table 2). Nevertheless, 95% confidence limits of DHR and IU still included the expected values of 0.5 and −0.25, respectively (Table 2).

When body mass was not considered (Model 3), species membership was a significant factor (Table 2). However, only *D. aurita* differed significantly from *P. frenatus* in the intercepts of DHR and IU. Significance of pairwise comparisons between species can be further analysed by non-overlapping confidence intervals of their means standardized to a common thread length (Table 3). For comparison with other studies, DHR and confidence intervals were also estimated in square meters using a standard thread length of 400 m, close to the longest thread length tracked (Table 3).

## DISCUSSION

Scaling relationships of metabolism with body mass usually appear only in comparisons between species, involving a large range of variation in body mass (reviewed in Marquet *et al.* 2005). Thus, it was surprising that a comparison between only three species revealed body mass as more important than species-specific factors in the scaling of DHR and IU. Part of the reason may be in the range of body mass considering the three species, from 85 to 1885 g, more than

**Table 2.** Parameters of the best models predicting daily home range (DHR) and its intensity of use (IU) of individuals of three species of didelphid marsupials

Model	Variables	DHR			IU			d.f.	Wald statistic	P
		Estimate	SE	CL	Estimate	SE	CL			
1	Intercept	-3.257	1.104	2.164	1.629	0.552	1.082	1	8.7	0.003
	Thread length	1.474	0.116	0.228	0.263	0.058	0.114	1	161.0	<0.001
	Body mass	0.435	0.136	0.267	-0.218	0.068	0.123	1	10.2	0.001
	Scale	0.809	0.067	0.130	0.405	0.033	0.065	1	148.0	<0.001
2	Intercept	-2.696	1.293	2.533	1.348	0.646	1.267	1	4.4	0.037
	Thread length	1.450	0.115	0.225	0.275	0.057	0.112	1	160.0	<0.001
	Body mass	0.359	0.176	0.345	-0.179	0.088	0.172	1	4.2	0.041
	Species							2	3.0	0.218
	<i>Didelphis aurita</i>	0.070	0.161	0.316	-0.035	0.081	0.158	1	0.2	0.665
	<i>Metachirus nudicaudatus</i>	0.198	0.145	0.283	-0.099	0.072	0.142	1	1.9	0.171
	Scale	0.793	0.065	0.128	0.396	0.033	0.064	1	148.0	<0.001
3	Intercept	-0.308	0.564	1.105	0.154	0.282	0.552	1	0.3	0.585
	Thread length	1.406	0.116	0.227	0.297	0.058	0.113	1	147.6	<0.001
	Species							2	9.0	0.011
	<i>D. aurita</i>	0.281	0.127	0.249	-0.141	0.064	0.125	1	4.9	0.027
	<i>M. nudicaudatus</i>	0.145	0.146	0.287	-0.073	0.073	0.143	1	1.0	0.320
Scale	0.815	0.067	0.131	0.407	0.033	0.066	1	148.0	<0.001	

Wald statistic and associated probability (*P*) estimate the significance of regression coefficients. For models that include thread length as a covariate, Wald statistic for DHR and IU is the same. In Models 2 and 3, *Philander frenatus* is the reference species to which the other two are compared.

**Table 3.** Estimates of daily home range (DHR) and its intensity of use (IU) standardized to 400 m of thread tracked (= total movement) for the three species of didelphid marsupials

	<i>Didelphis aurita</i>	<i>Metachirus nudicaudatus</i>	<i>Philander frenatus</i>
<i>n</i>	37	20	17
Log standardized DHR (m <sup>2</sup> )	8.66	8.34	7.87
95% CI	8.45–8.87	8.16–8.52	7.63–8.12
Standardized DHR (m <sup>2</sup> )	5769	4183	2626
95% CI	4672–7125	3494–5009	2049–3367
Log standardized IU	1.66	1.82	2.05
95% CI	1.61–1.71	1.78–1.87	1.99–2.12
Standardized IU	5.27	6.18	7.81
95% CI	5.00–5.55	5.91–6.47	7.34–8.31

Estimates of 95% confidence intervals (CI) were based on log-transformed values, which were transformed back to the original scale.

one order of magnitude. Thus, when the difference in body mass approached one order of magnitude it became more important than species-specific effects. However, body mass variation of *D. aurita* was approximately the same range, from 135 to 1885 g, but no significant effect of body mass was detected. Another part of the reason may be the combined analysis of intra and interspecific variation. This analysis provided a more powerful test than separate analyses for each species, or use of the mean value of each species as is usually done in comparative studies.

Based on model selection statistics it was not possible to choose between Models 1 and 2; however,

Model 1 was more parsimonious and reached the highest rank. The addition of species membership as a factor did not improve the likelihood of Model 2, hence body mass and thread length alone were the only variables that matter for DHR and IU.

Selecting Model 1 as the best model implies that the scaling of DHR and IU with body mass has a good agreement with the expected values of 0.5 and -0.25. It also supports the assumptions that DHR increases with the square of daily movement distance in the three marsupials studied, that DHR is generally circular (Garland 1983), and that daily movement distance scales as  $M^{0.25}$  (Carbone *et al.* 2005). Circular DHR,

however, are not necessarily a general pattern. Daily home ranges of hispid cotton rats (*Sigmodon hispidus*), for example, are more linear and elongated than multiday home ranges (Spencer *et al.* 1990).

If the exponent of DHR was indeed smaller than 0.5, say the observed value of 0.435, it would be possible to speculate on the relationship between observed exponents of DHR and daily movement distance. The observed scaling exponent of DHR was approximately

$$\text{DHR} \approx M^{0.435}$$

which would be obtained from daily movement distance  $\approx M^{0.25}$  only if

$$\text{DHR} \approx (M^{0.25})^{1.74} \approx M^{0.435}$$

An exponent of 1.74 would mean that DHR is more elliptical than circular. The smaller the scaling exponent of DHR to body mass, the more elongated would be the shape of DHR. In the limit, DHR would be a single line, when both DHR and daily movement distance would be proportional to  $M^{0.25}$ .

For IU, it is surprising that body mass was more important than species membership considering the cursorial specializations of *Metachirus nudicaudatus*. Among terrestrial or semiterrestrial didelphid marsupials, *M. nudicaudatus* is considered the only species with morphological specializations to develop speed on the ground (Miles *et al.* 1981; Szalay 1994). The other two species, *Didelphis aurita* and *Philander frenatus*, are semiterrestrial, using the understory and the canopy occasionally (Cunha & Vieira 2002), but their morphology is basically scansorial (Szalay 1994; Vieira 1997). In spite of these specializations, their IU decreased with body mass.

The decrease in IU with body mass could be related to its association with costs of locomotion, which also scales as  $M^{-0.25}$  across species of animals (Schmidt-Nielsen 1984; Full & Tu 1991). It is reasonable to assume that (i) the amount of thread released is directly proportional to the tortuosity of the path; and (ii) the more tortuous the path, the more expensive it is for the animal to cross a certain distance, or to cover a unit of area. Consequently, Intensity of Use (the amount of thread released per unit of area) is directly related to the amount of energy spent to cover a unit of area, the definition of cost of locomotion (Schmidt-Nielsen 1984).

The use of thread length as a covariate (standardizing movement of individuals to a common thread length) allowed intra and interspecific comparisons of DHR and IU. Estimates of DHR may vary simply because animals are captured and released with a tracking device at varying distances from its nest or refuge (regardless of the tracking device used, a radiotransmitter or a spool-and-line cocoon). This source of noise may be disregarded if the same animal is tracked for many days, but it should be important if

the animal is tracked for one or a few days. Standardization to a common thread length reduces this source of noise.

Body mass was the main determinant of differences between individuals and species in daily home ranges and its intensity of use. Thus, regardless of morphological and locomotory adaptations of these species, daily movements are determined mostly by body mass when it spanned one order of magnitude. The scaling exponents of daily home range and its intensity of use agreed with the expected based on the scaling of daily movement distance and cost of transport. Scaling to body mass was close to 0.5 for daily home range, and  $-0.25$  for its intensity of use. These results were only possible by the combination of intra and interspecific variation in a single analysis, by the standardization of area measurements to unit of movement, and by a model selection approach to hypothesis testing. Studies of the same species at different sites, and of other species of small mammals are necessary to test the generality of these scaling relationships.

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