CLIMATE-DRIVEN VARIATION IN SPACE USE
BY THE NEOTROPICAL MARSUPIAL *Metachirus nudicaudatus*

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ABSTRACT
Climatic seasonality affects marsupial space use through changes in food, mate, and nest availability. These effects can be enhanced when population size has an additive effect in the dry season. We tested if daily home range area and intensity of habitat use of the marsupial *Metachirus nudicaudatus* is affected by population size, climatic (dry and wet), and reproductive (breeding and non-breeding) seasons, and if it differs between genders. *Metachirus nudicaudatus* space use was affected by climatic seasonality, with individuals exploring larger areas in the dry season, probably in search for food. No effect of population size or differences in space use between sexes was detected. Further studies should test experimentally the effect of food availability on marsupials space use to confirm or rebut this hypothesis.
Keywords: food availability; movement; seasonality; small mammals; spool-and-line.

Many mammal species face distinct climate conditions through the year, which can affect the extent of the breeding season, the use of space, and the population dynamics (Merritt *et al.* 2001, Loretto & Vieira 2005, Cáceres *et al.* 2012). This is especially true for mammals at high latitudes, where climate varies considerably from winter to summer (Merritt *et al.* 2001). In tropical and subtropical areas, seasonality in climate also drives mammal space use, affecting both physiology and social behavior (Loretto & Vieira 2005, Cáceres *et al.* 2012). Differences in food, mate, and nest availability between dry and wet seasons have direct effects on home-range size (*i.e.*, the space used to obtain the necessary resources for survival and reproduction; Burt 1943), and intensity of habitat use (*i.e.*, the time spent per unit area; Almeida *et al.* 2010), and can have profound effects on population regulation (Loretto & Vieira 2005, Ferreira *et al.* 2016a,b).

In marsupials food and mate availability are major determinants of space use, despite differences in body size, phylogeny, and life history strategy (Cáceres *et al.* 2012). Food can vary in space with resources distributed in patches (Julien-Laferrière 1995) and in time, with differences between seasons (Loretto & Vieira 2005, Leiner & Silva 2007). Prior studies with Neotropical marsupials also stressed differences in space use between sexes and reproductive seasons (Sunquist *et al.* 1987, Loretto & Vieira 2005), which probably occur due to the sexual dimorphism in favor of males and the promiscuous mating system of several didelphid species (Ryser 1992, Cáceres *et al.* 2012).

We tested the effect of four explanatory variables (sex, population size, and climatic and reproductive seasons) on daily home range areas (DHR) and intensity of habitat use (IU) of the Neotropical marsupial *Metachirus nudicaudatus* E. Geoffroy 1803 (Didelphimorphia, Didelphidae). Hypotheses and supporting evidence were addressed as follows: (1) Movement areas differ between males and females: In general, males of didelphid marsupials have larger home ranges than females (Cáceres *et al.* 2012). (2) High population sizes increase IU and decrease DHR: Previous studies have shown a more IU (Almeida *et al.* 2015) and smaller DHR (Pires & Fernandez 1999) at high population sizes. (3) DHR are larger in the dry season: Home ranges are usually larger at periods with low resource availability (Cáceres *et al.* 2012); in the study area this period is the dry season (Ferreira *et al.* 2016b). (4) DHR are

explored less intensively in the reproductive season: Previous studies have shown a less IU by males in the reproductive season and no difference between females (Loretto & Vieira 2005).

The brown four-eyed opossum *M. nudicaudatus* is the largest Neotropical marsupial without pouch (447.8 g ± 86.5 g), with males generally heavier than females (Bergallo 1994). It is solitary, nocturnal, insectivorous-omnivorous (Freitas *et al.* 1997), and has terrestrial habits, rarely using the vertical strata (Cunha & Vieira 2002). Individuals have large home ranges (8.4 ha; Moraes Junior 2004) and are capable of large displacements (maximum of 1498 m/night; Miles *et al.* 1981). In the study area, reproduction starts in the middle of the dry season (July) and cease in the beginning of the next dry season (April; Ferreira *et al.* 2016b).

The study was conducted in the Serra dos Órgãos National Park, the largest continuous Atlantic Forest remnant in the state of Rio de Janeiro, southeastern Brazil (22°28'28"S, 42°59'86"W). The forest is part of the montane rain-forest complex, in an old-growth successional stage. The climate is mild humid-mesothermic (Nimer 1989). During the study period, monthly precipitation ranged from 0.2 to 508 mm and mean monthly temperature from 15.7 to 25ºC. Three 0.64 ha grids, each with 25 trap stations spaced 20 m apart in a 5 × 5 design, were sampled every other month from June 1999 to February 2005 (details of the study area and capture-recapture methods in Ferreira *et al.* 2016a,b). Individuals were equipped with a spool-and-line device glued to the fur between the shoulder blades using glue Super Bonder™ (cyanoacrylate ester based glue, Henkel Loctite Adesivos Ltda., Manaus, Brazil). Tracking spools consist of a bobbinless cocoon of nylon thread wrapped by a polyvinyl chloride film (Miles *et al.* 1981, Boonstra & Craine 1986). Subadult and adult individuals received spools of approximately 4.5 g (480 m). After attaching the spool, individuals were released at the point of capture and tracked on the following day. The exception was the first day of capture when individuals were followed four hours after release. After release, the researcher stood still until the animal moved away to avoid forcing it to run in any particular direction. To avoid potential adverse effects of researchers, we did not analyze the first ten meters of thread.

Animal paths, *i.e.,* the thread released by the spool-and-line device, were tracked with compass and tape measure to get polar coordinates (distance and azimuth) between points where there was a change of direction greater than 5°. Polar coordinates were transformed into Cartesian coordinates (x, y) to map individual paths. Daily home range was estimated by the Minimum Convex Polygon (MCP) enclosing Cartesian coordinates of a path in the program CALHOME (Kie *et al.* 1996). Intensity of habitat use is a dimensionless index proportional to the active time spent per unit area (Almeida *et al.* 2010). IU was estimated by dividing the amount of thread tracked of an individual by the square root of its MCP (Loretto & Vieira 2005). Data of individuals tracked less than 35 m of thread were discarded to minimize false variances.

We modeled DHR and IU as a function of the following variables: sex, current population size, and climatic and reproductive seasons. Current population size was estimated as the minimum number of animals known to be alive in the three trapping grids (Krebs 1966). Dry or wet (climatic) periods were determined by the Setzer index (Setzer 1946). This index uses data on precipitation (P) and temperature (t) of the month to estimate the effective monthly precipitation ($\pi_m = P/1.07^t$). We divided the annual effective precipitation by 12 to obtain monthly cutoff points for dry ($\pi_m \geqslant 10.8$) or wet ($\pi_m < 10.8$) periods. Reproductive/Non-reproductive seasons were defined based on the presence/absence of young and females with lactating or swollen nipples, since in males scrotum is apparent in the first months of life.

We formulated 10 general linear models (GLM) with a Gaussian distribution error and a log link function to determine the effect of the four variables on the DHR and IU, totaling 20 models. Competing models were ranked using Akaike's Information Criterion corrected for small sample size (AICc), ΔAICc (AICc$_i$ - minimum AICc)*,* and AICc weight (w_i - evidence weight that the model is the best model within the set) (Burnham & Anderson 2002). An intercept-only model composed by the intercept, the amount of thread tracked, and residual errors as parameters was also included to compare the explanatory power of

independent variable relative to other unaccounted sources of variation in data. Models were considered equally plausible with $\Delta AICc \leqslant 2$ (Richards 2005). Model selection was performed using the MuMIn package (Barton 2012) in R environment (version 2.13.0, 2011).

We tracked 61 paths of 52 individuals of *M. nudicaudatus* (22 females and 39 males): 9 females and 28 males in reproductive season, 13 females and 11 males in non-reproductive season. When grouping by climate, 9 females and 15 males were tracked during dry months, and 13 females and 24 males during wet months. DHR ranged from 0.01 to 0.85 ha (0.19 ± 0.19 ha; mean ± SD) with 0.21 ± 0.20 ha for females, and 0.18 ± 0.18 ha for males. IU ranged from 1.26 to 10.92 (4.99 ± 1.67), with 4.93 ± 1.7 for females and 4.93 ± 1.65 for males. During the study period, population size varied from 1 to 8 individuals (4.11 ± 1.73).

In total, one out of four hypotheses was supported, indicating that space use of *M. nudicaudatus* was affected mainly by climatic seasonality (Table 1). DHR varied between climatic seasons, with individuals using larger areas in the dry season (Table 2). The second-ranked model, which also included the effect of current population size, was less plausible (Table 1), and did not add extra explanation to the variation of DHR. IU was positively related only to the amount of thread tracked, and did not differ between sex and seasons (Table 1).

Table 1. Comparison of models predicting use of space by *Metachirus nudicaudatus* in Serra dos Órgãos National Park, Rio de Janeiro, Brazil. Explanatory variables: Sex, climatic season (wet and dry; Clim), reproductive season (reproductive/non-reproductive; Rep), population size (Pop), and amount of thread tracked (Thread). K = number of model parameters, AICc = Akaike Information Criteria corrected for small sample sizes, $\Delta AICc = AICc_i$ - minimum AICc, w_i = Akaike weight.

Model	K	$\Delta AICc$	w_i
Daily home range			
Clim + Thread	4	0	0.585
Clim + Pop + Thread	5	2.120	0.203
Clim + Sex + Thread	5	2.180	0.197
Thread	3	9.780	0.004
Pop + Thread	4	9.860	0.004
Rep + Thread	4	11.510	0.002
Sex + Thread	4	12.050	0.001
Rep + Pop + Thread	5	12.050	0.001
Sex + Pop + Thread	5	12.100	0.001
Sex + Rep + Thread	5	13.820	0.001
Intensity of habitat use			
Thread	3	0	0.195
Clim + Thread	4	0.150	0.181
Pop + Thread	4	0.620	0.142
Rep + Thread	4	1.100	0.112
Sex + Thread	4	2.290	0.062
Clim + Pop + Thread	5	1.480	0.093
Rep + Pop + Thread	5	1.870	0.076
Clim + Sex + Thread	5	2.520	0.055
Sex + Pop + Thread	5	2.880	0.046
Sex + Rep + Thread	5	3.290	0.038

Table 2. Standardized parameters of the top-ranked model (Clim + Thread) predicting daily home range of *Metachirus nudicaudatus* in Serra dos Órgãos National Park, Rio de Janeiro, Brazil. Explanatory variables: climatic season (wet and dry; Clim) and amount of thread tracked (Thread).

Variables		Estimate	SE
Intercept		-7.1132	0.965
Clim	wet	-0.478	0.147
Thread		1.086	0.166

Differences in DHR between climatic seasons are probably a response to changes in food availability. In the Atlantic Forest, food availability is lower in the dry season (Bergallo & Magnusson 1999, Leiner & Silva 2007), which can stimulate individuals to explore larger areas instead of exploring it more intensively. Similar results were observed in two tropical forest marsupials: females of *Didelphis aurita* had larger DHR in the dry season (Loretto & Vieira 2005) while, in *Caluromys philander*, home-range size was determined by the patterns of food availability, with individuals covering a larger area when food was patchily distributed (Julien-Laferrière 1995). In our study, differences in DHR between males and females were weak, supporting the findings of Bergallo (1994) for *M. nudicaudatus* in another Atlantic Forest area. These results differ from the accepted pattern of the group (Cáceres *et al.* 2012). The lack of difference between DHR between sexes may simply reflect similar requirements in the same period.

The lack of density dependence on *M. nudicaudatus* movements enlightens the mechanism of population regulation. Previous studies in the study area have shown that *M. nudicaudatus* is regulated by a direct negative feedback (Ferreira *et al.* 2016a), especially in the dry season (Ferreira *et al.* 2016b), and suggested intraspecific competition for food resources and/or space as the main regulatory mechanisms. Space is not a limiting factor for this population, reinforcing that most of the intraspecific competition takes place during the dry season.

Our study aimed to unravel the factors affecting the space use of a Neotropical marsupial and found support to one tested hypotheses. In short, *M. nudicaudatus* was greatly affected by climatic seasonality, probably as a consequence of the variability in food availability between seasons. No effect of population size or differences in space use between sexes was detected. These results reinforce the role of seasonality on population regulation and persistence in seasonal environments. We suggest that further studies should test experimentally, or with the natural resources available in the area, the effect of food availability on space use of marsupials in an attempt to confirm or rebut the supported hypothesis.

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