Spatial patterns of the semi-aquatic rodent *Nectomys squamipes* in Atlantic forest streams

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ABSTRACT

Nectomys squamipes is a semi-aquatic rodent with a wide geographic range in Brazilian forests and savannas. This species is a host for several parasites associated with aquatic environments, especially *Schistosoma mansoni*, and thus its spatial pattern may influence some diseases' patterns. Here we present important aspects of water rat spatial behaviour, including technical and ecological aspects. Water rats were studied by live trapping in rivers and in gallery forests between January 2005 and August 2008, with a total sampling effort of 9511 trap-nights. We also studied some animals through radio tracking and the spool-and-line technique. Water rat movement was distributed evenly between the terrestrial and aquatic environments. *Nectomys squamipes* occurrence in small tributaries was higher than in larger and lotic rivers. Both home range, the conventional two-dimensional approach, and home length, a one-dimensional approach, proved to be useful to study *N. squamipes*, depending on the shape of the water body used by the individual. Although *Nectomys squamipes*' home length was positively correlated with body weight, sex was also important to explain home length variation; at similar body weights, males have larger home lengths than females. Males explored larger areas during the rainy season, likely in search of females, as this is the water rat reproductive season in Atlantic forest. In contrast, females explored larger areas during the dry season, likely looking for additional food supplies as a result of deficient water rat food supplies during the Atlantic forest dry season. Females overlapped home lengths with more than one male, and males with more than one female, suggesting a promiscuous mating system for this species.

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Introduction

The water rat, *Nectomys squamipes*, is a Neotropical semi-aquatic rodent with a wide geographic range in Atlantic Forest and Cerrado (Bonvicino et al. 2008). The water rat has morphological adaptations to semi-aquatic life, such as water-resistant hair (Santori et al. 2008) and inter-digital membranes on the hind feet (Ernest 1986). Santori et al. (2008) observed in *Nectomys* a superior hydrodynamic posture and swimming speed when compared to oryzomyines species of the genus *Cerradomys*, which is a terrestrial

genus. According to Ernest and Mares (1986), the proximity and abundance of water bodies have a strong influence on *N. squamipes* occurrence. Corroborating this, nests and shelters are only found close to streams (Briani et al. 2001). *Nectomys squamipes* is omnivorous, the diet composed mainly of plant matter, insects, tadpoles and small fishes (Ernest and Mares 1986). This species reproduces throughout the year, although there is a reproductive peak during the rainy season (Ernest and Mares 1986; Bergallo 1994; Bergallo and Magnusson 1999; Gentile et al. 2000; D'Andrea et al. 2007). *Nectomys squamipes* is a host for several parasites associated with aquatic environments and it is considered an important vector for *Schistosoma mansoni* (Ernest 1986; Ernest and Mares 1986; Picot 1992; Gentile et al. 2000). Considering the role of this rodent for these parasites, the spatial behaviour of the water rat is likely to influence the parasites' population dynamics and reproductive cycle.

For an animal that uses both terrestrial and aquatic environments, the shape of the home range tends to follow the shape of the water bodies (Blundell et al. 2001). In linear habitats, such as rivers, home ranges tend to be one-dimensional and are called home length or home range length (Ribic 1982; Serena 1994; Galliez et al. 2009). In contrast, in two-dimensional aquatic habitats, such as marshes, the conventional two-dimensional home range is observed (Schooley and Branch 2006). The two-dimensional home range is also observed for semi-aquatic species that explore large terrestrial areas adjacent to water bodies (e.g. some otter species; Reid et al. 1994; Johnson and Berkley 1999; Gorman et al. 2006). Although this pattern in home range shapes in respect to water body shape has been confirmed by several studies for semi-aquatic species (e.g. Serena 1994; Blundell et al. 2000; Benstead et al. 2001; Moorhouse and Macdonald 2005; Sepúlveda et al. 2007; Galliez et al. 2009), the use of space by *N. squamipes* has been analysed only using the two-dimensional home range approach (Ernest and Mares 1986; Bergallo and Magnusson 2004), regardless of the shape of the water body concerned. Ernest and Mares (1986) reported rectangular home ranges parallel to rivers for *N. squamipes*, reinforcing that home range length is probably more appropriate to quantify and describe the use of space by this species in linear water bodies. In addition, the method applied to estimate home ranges was only capture–mark–recapture (CMR), which tends to underestimate home range sizes (Sunquist et al. 1987; Bergstrom 1988; Ribble et al. 2002; Lira and Fernandez 2009). Moreover, the relationship of *N. squamipes* with different water bodies, the relative use of the terrestrial environment and movement variation during seasons and between sexes have not been studied in detail.

To improve the understanding of the use of space by *N. squamipes* and obtain insights about its natural history, our objectives were to analyse: (a) how the locations of this water rat are distributed between the aquatic and terrestrial environments; (b) the use of rivers of varying widths; (c) the best approach (one- or two-dimensional home range) to study water rat spatial patterns; and (d) sexual and seasonal differences in spatial patterns.

Material and methods

Study area

This study was carried out in the Águas Claras River subbasin (22.30° S, 42.30° W), Rio de Janeiro state, southeastern Brazil (Figure 1). The study area includes rivers and small

Figure 1. Study area, in Rio de Janeiro state, Brazil. Tg 1 and Tg 2 are tributaries of Águas Claras River; Tf 1 and Tf 2 are tributaries of Floresta River.

tributaries running through remnants of primary and secondary Atlantic Forest. We carried out the study in three rivers – Águas Claras, Floresta and Dona Rosa rivers – and four tributaries – two of the Águas Claras River (Tg 1 and Tg2) and two of the Floresta River (Tf1 and Tf2). All the rivers and tributaries studied vary from 1 to 10 m in width and from 10 to 100 cm in depth.

The weather of the region is warm and humid. The mean temperature is 19°C during winter and 25°C during summer (Mantovani 1997). The annual rainfall varied from 1500 to 3500 mm between 1986 and 2007 (average of 2230 mm; ANA 2010). Rainfall is not evenly distributed during the year; the months between May and October are dry (monthly rainfall between 65 and 145 mm between 1986 and 2007; ANA 2010) and the rainy season occurs between November and April (monthly rainfall between 190 and 365 mm from 1986 to 2007; ANA 2010).

Data collection

We used three methods to study water rat spatial behaviour: CMR, generating data comparable to prior studies; radio tracking, providing accurate home range size and shape estimates; and a spool-and-line technique, which enabled measurements of small-scale movements. These three methods were complementary, generating detailed and precise information about the relation of *N. squamipes* with different water bodies, home range layouts and seasonal/sexual differences in space use.

Capture-mark-recapture

Forty-one monthly CMR sessions were carried out between January 2005 and August 2008. Each session lasted five consecutive nights, and traps were checked the following

morning. The Floresta and Dona Rosa Rivers and the four tributaries were sampled using double-entrance traps (Tomahawk Live Trap Co., $97 \times 15 \times 15$ cm or $81 \times 23 \times 23$ cm; Gabrisa Ltd, $90 \times 21 \times 21$ cm) set on platforms inside riverbeds. Traps were placed in the middle of small barriers, leading the water flow and swimming animals to our traps. This method was proposed by Bressiani and Graipel (2008) and used by Galliez et al. (2009) to capture the water opossum *Chironectes minimus*. Trap locations were selected according to the facilities to build the barriers; the distance between adjacent traps varied between 55 and 260 m (125 ± 60 m; mean $\pm$ standard deviation).

The Águas Claras River, whose flow was too intense to use Bressiani and Graipel's method, was sampled only on riverside and on gallery forest with Sherman and Tomahawk traps (Sherman Live Trap Co., $38 \times 10 \times 12$ cm; Tomahawk Live Trap Co., $48.4 \times 15.2 \times 15.2$ cm). On the left margin we sampled with three transects (one riverside, one at 30 m from the river side and another at 60 m from the river side). On the right margin we restricted our sampling to two transects due to human activities (one riverside and one at 30 m from the river side). All transects were parallel to each other (following the river shape) and the ones at 30 and 60 m from the river side were inserted in a gallery forest. Each transect was sampled with 15 traps 20 m apart from each other.

The sampling effort was 1461 trap-nights in the Floresta River, 827 trap-nights in its tributaries (Tf1 and Tf2), 1291 trap-nights in the Dona Rosa River, 3660 trap-nights along the Águas Claras riverside, 1170 trap-nights in gallery forest adjacent to the Águas Claras and 1102 in tributaries of Águas Claras (Tg1 and Tg2). The total sampling effort was 9511 trap-nights.

Traps inside riverbeds were baited with frozen shrimp or fish (*Anchoviella lepidontostole*), depending on the availability in the local market. Traps in riverine and gallery forest were baited with shrimp/fish or with a mixture of banana, bacon, oats and peanut candy. We tested the trap efficiency of the banana/bacon/oats/peanut bait against the shrimp/fish bait on riverside and on gallery forest traps and found no difference in their efficiency to capture *N. squamipes* (chi-square: $\chi^2 = 2.00$; gl = 1; $p = 0.29$).

Captured animals were marked with numbered ear tags (model 1005-1, National Band and Tag Co., Newport, USA) and released at the same capture location. For each capture the following data were recorded: date, capture location, individual tag number, body weight and sex.

Spool-and-line technique

The spool-and-line technique was used between November 2007 and August 2008. Nine adult individuals of *N. squamipes* were equipped with a 170-m spool-and-line device (Cansew, Montreal, Canada; Miles et al. 1981; Boonstra and Craine 1986). This cocoon was glued between the shoulder blades of the studied animals with ester of cyanoacrylate glue. The animals equipped with the spool-and-line device were released at the same capture location. We only applied the spool-and-line device on animals captured on small tributaries, where the smooth water flow did not interfere in the line path and where there were enough rocks and vegetation to mark the paths even within the stream channel. The movement paths were mapped the day following capture. The first

10 m of line were not considered, because they are likely to reflect the animal's escape movements. To evaluate the habitat preferences, the line was separated into two types: terrestrial environment – mainly gallery forest – and aquatic environment – river and swamps. Due to the nodes caused by the frequent attachment of the line to plants and rocks, we used the line dry weight (and not the distance) as a measure of individuals' habitat use instead of line length.

Radio tracking

From January to August 2008, adult animals received radio-tracking collars (TXE0207C, Telenax, Playa del Carmen, Mexico). As the collars weighed 14 g, we selected only animals with more than 280 g of body weight, to assure that the collar would correspond to a maximum of 5% of the animals' body weight, as recommended by Jacob and Rudran (2003) and Gannon and Sikes (2007). The collars had movement sensors: the signal oscillated from 30 to 60 beats per second, indicating if the animal was active or not. To capture the signal, we used a TR-4 receiver set at the frequency of 150 MHz, and a hand-held antenna (Ra-14K, Telonics, Mesa, USA). Records were geographically fixed with a global positioning system (GPS) device (Garmin, Olathe, USA), using the Universal Transverse Mercator coordinate system. The GPS location inaccuracy on study area was 8.2 m (standard deviation = 2.2 m, $N = 2.113$).

The individuals were monitored at night, with occasional daytime locations. We followed individuals using the 'homing in on the animal' technique (White and Garrott 1990). This technique consists of following the collar signal until sighting the animal. However, as *N. squamipes* is often difficult to see, due to its nocturnal habits and small size, and also due to the dense rainforest on study area, we followed the methodology of Lira et al. (2007) and recorded a location point when the signal could be captured only with the receptor, without the antenna. The inaccuracy derived by the adapted 'homing in on the animal' technique was 6.8 m (standard deviation = 5.3 m, $N = 12$) and was measured as the distance between the estimated and the real collar location, which had been previously hidden by another person. To avoid spatial autocorrelation, the interval between successive locations was at least 1 hour (Harris et al. 1990; Linders et al. 2004; Endries and Adler 2005; Lira et al. 2007; Galliez et al. 2009).

Data analysis

A regression with a curve adjustment (Motulsky and Christopoulos 2004) between the river/tributary width (explanatory variable) and the trapping success (dependent variable) was calculated to detect a preference of *N. squamipes* for larger or smaller water bodies. River/tributary width was measured as the distance between the left and right river banks.

We carried out a habitat selection analysis with spool-and-line technique data. We compared aquatic and terrestrial use with a paired t test (Zar 1999). In this test we compared the dry weight of lines that came from movements performed in aquatic environments with the dry weight of lines that came from movements performed in terrestrial environments.

Individuals equipped with radio collars had their home lengths (HL) and home ranges (HR) estimated using occurrence points achieved with radio tracking and CMR data. We used only individuals with more than 30 locations + captures (mean 45; maximum 60). For each individual that fulfilled this criterion, we used 95% of the locations + captures in the analysis. The exclusion of the farthest 5% of the locations/captures was made due to the possibility of these movements representing random activities, and thus not representing daily activities. The HL was calculated as the distance between the two farthest locations following the river path (Galliez et al. 2009) and the HR was calculated through the minimum convex polygon method (Mohr 1947).

We also estimated HL for individuals assessed only through CMR method. In this estimate, we use only individuals captured in the study area for at least 2 months and with at least three captures (mean 5; maximum 13). We did not estimate HR for individual assessed only through the CMR method because traps with a high enough number of captures were those inside riverbeds or on the river side, so that two-dimensional spatial use could not be accurately represented. We examined the relation between the HL size and the number of captures through a simple linear regression. The influence of body weight and sex on HL estimated by CMR was investigated through an analysis of covariance (ANCOVA; Zar 1999). We also examined the spatial overlap between individuals studied by CMR and radio tracking; this was calculated as a percentage of the HL/HR of each animal inside the HL/HR of adjacent animals.

We calculated the distance between successive captures (DSC) through the CMR method for individuals with at least two captures in the same month. DSC was calculated as the distance between two successive capture locations following the river path. The DSCs were analysed regarding differences related to sexes and seasons with a generalised linear model using the Poisson distribution. We used model selection based on Akaike information criterion to obtain the most parsimonious model (Burnham and Anderson 2002).

Results

We obtained 340 captures of 124 individuals, with a trapping success of 3.6%. Traps within gallery forest presented the lowest capture success, obtaining only 10 captures in 1170 trap nights – a trapping success of 0.9%. Rivers and tributaries had a trapping success varying between 2.2 and 13.6%; smaller tributaries presented the highest trapping successes (Figure 2). The relationship between trapping success and river width was best described by a geometric regression ($r^2 = 0.95$; $p < 0.001$; Figure 2), showing that trapping success changed rapidly between 1 and 4 m of river width.

Nine animals were equipped with a spool-and-line device. For eight of them (five males and three females) the line could be located, with a total of 617 m of tracked line. Animals concentrated similar portions of their movements in aquatic and terrestrial environments ($t = 0.45$; $p = 0.67$, $n = 8$; proportions of line in aquatic and terrestrial environments: 0.46 ± 0.23 and 0.54 ± 0.23 , respectively). Nevertheless, when animals explored the terrestrial environment, they were never located far away from the water bodies; the maximum distance recorded was 7 m with spool-and-line and radio-tracking data.

Figure 2. Geometric regression curve between river/tributary width (m) and *Nectomys squamipes* trapping success (%). The regression equation is presented on the figure. TS = trapping success.

Table 1. Home length and home range of four individuals of the water rat *Nectomys squamipes* studied with radio tracking and capture–mark–recapture. Individuals (R-M for males and R-F for the female), body weight (g), period of capture, period of radio tracking, number of captures, number of tracking nights, number of locations, home length (HL; 95%, in m) and home range (HR; MCP 95%, in ha) are shown.

Individual	Body weight (g)	Period of capture	Period of radio tracking	Number of captures	Number of nights	Number of locations	HL (m)	HR (ha)
R-M 2	430	June 2007–March 2008	February 2008–March 2008	8	4	28	960	3.87
R-F 1	280	December 2007–February 2008	February 2008–March 2008	2	3	29	305	0.81
R-M 3	280	April 2008–June 2008	April 2008–July 2008	7	6	44	500	0.72
R-M 4	340	June 2008–July 2008	June 2008–August 2008	4	7	56	1085	3.93

Four males and one female captured at Floresta River and its tributaries were equipped with radio-tracking collars. They were tracked for 21 nights, with a total of 166 locations (Table 1). Male R-M 1 removed its collar after one tracking night and was excluded from the analysis with only nine locations. The end of tracking for R-M 2 occurred because of collar failure; R-F 1 was preyed upon by the Brazilian Rainbow Boa *Epicrates cenchria* (Pinho et al. 2009); R-M 3 removed its collar, and thus R-M 4 was the only individual tracked until the end of the study.

Figure 3. Home length and home range (MCP) for four males (R-M) and one female (R-F) of *Nectomys squamipes* monitored through radio tracking and capture–mark–recapture.

The HLs estimated by radio tracking varied between 305 and 1055 m (Table 1). Although the small sample size does not allow statistical testing, the HL of the tracked female (R-F 1) was smaller than the minimum value found for male HLs. Home ranges varied from 0.72 to 3.93 ha (Table 1). The home range of three individuals (R-M 2, R-F 1 and R-M 4) included almost their entire HL and large portions of land far from water bodies, where the animals were never observed (Figure 3). In contrast, the HL of the individual R-M 3 – the only one using a marshy area – included river stretches where the individual was never observed, and its HR did not include any underused terrestrial areas (Figure 3). This suggests that HL was more accurate to describe R-M 2, R-F 1 and R-M 4's location points, while HR was more accurate to describe R-M 3's location points.

For 21 males and 10 females, we could estimate their HLs using CMR data (Table 2). Two of them, one male (C-M 11) and one female (C-F 4), had very high HL estimates – 1700 and 1675 m, respectively – and were excluded from the analysis. These movements possibly represented dispersal events. Considering the remaining 29 individuals, the mean HL size was 165 ± 116 m (standard deviation). The number of captures did not influence the HL ($r^2 = 0.04$; $F = 1.0$; $p = 0.32$). Otherwise, the individuals' sex and body weight were important variables explaining the difference among HLs: heavier animals

Table 2. Home lengths and home length overlaps of 31 individuals of *Nectomys squamipes* studied with the capture-mark-recapture method. Individuals (C-M for males and C-F for females), body weight (g), period of captures, number of captures, home length (HL, in m), percentage of HL overlapped with individuals from the same sex (same sex overlap; %) and percentage of HL overlapped with individuals from the opposite sex (opposite sex overlap; %) are shown. Multiple values in 'same sex overlap' or 'opposite sex overlap' columns are the result of an individual's HL overlapped with more than one other *N. squamipes*. The grey shading indicates individuals that possibly dispersed during the study. We did not analyse the HL overlap for these individuals.

Individual	Body weight (g)	Period of capture	Number of captures	HL (m)	Same sex overlap (%)	Opposite sex overlap (%)
C-F 1	190	April 2006–June 2006	6	65		100 /62
C-F 2	165	April 2006–May 2006	4	20		
C-F 3	235	April 2006–July 2006	3	50		100
C-F 4	205	May 2006–June 2006	3	1675		
C-F 5	220	July 2006–May 2007	6	70		100/ 100
C-F 6	190	August 2006–September 2006	3	30		100
C-F 7	240	February 2007–September 2007	3	180		64
C-F 8	155	July 2007–September 2007	6	120		100/ 72
C-F 9	220	August 2007–September 2007	7	0		
C-F 10	200	November 2007–December 2007	3	0		
C-M 1	305	October 2005–April 2006	3	340	72	
C-M 2	345	October 2005–January 2006	3	295		
C-M 3	280	May 2006–June 2006	5	75		
C-M 4	260	April 2006–October 2006	13	215		33
C-M 5	305	February 2006–May 2006	4	255	96	20
C-M 6	230	April 2006–August 2006	4	125	80	52/ 24
C-M 7	270	May 2006–July 2006	3	250		
C-M 8	210	June 2006–August 2006	4	100	100	40
C-M 9	325	August 2006–January 2007	4	245		
C-M 10	255	February 2007–April 2007	3	180		
C-M 11	245	February 2007–May 2007	3	1700		
C-M 12	225	August 2007–November 2007	7	110	36	
C-M 13	155	April 2007–May 2007	5	85		
C-M 14	295	March 2007–July 2007	3	70		100
C-M 15	290	May 2007–September 2007	5	200	65	33
C-M 16	390	June 2007–March 2008	8	180	100	
C-M 17	330	July 2007–September 2007	11	360	50	32
C-M 18	245	July 2007–October 2007	4	160		
C-M 19	110	August 2007–October 2007	5	220	18 /60	39
C-M 20	310	April 2008–June 2008	7	415	87	
C-M 21	345	June 2008–July 2008	4	360	100	

Table 3. Model selection among generalised linear models of distance between successive captures of *Nectomys squamipes*. Explanatory variables were sex (female vs male) and season (rainy vs dry). K = number of model parameters; AIC = Akaike information criterion; Δ AIC = AIC – minimum AIC. * indicates interaction between variables.

Model	K	AIC	Δ AIC
Sex * season	4	4898	0
Sex + Season	3	5070	172
Sex	2	5211	313
Season	2	5608	710

Figure 4. Linear regressions between body weight (g) and home length (m) for 29 individuals of *Nectomys squamipes* analysed through capture–mark–recapture (CMR). Black circles represent males and grey circles represent females. The top line represents the linear regression for males, while the bottom and dotted line represents the linear regression for females. The regression equations are presented on the figure. HL = home length; BWeight = body weight.

had larger HLs, and males had even larger HLs than females with the same body weight (body weight: $F = 6.6$, $p = 0.016$; sex: $F = 6.5$, $p = 0.017$; $r^2 = 0.51$; Table 3; Figure 4).

We detected 15 cases of HL overlap among 29 animals analysed by CMR (Table 2). Nine overlap cases were between opposite sexes, and six between males. Females did not overlap HLs. Three females had their HL overlapped by two males; one male overlapped HLs of two females and the other male overlapped HLs of two males. Regarding the animals studied through radio telemetry, R-M 2 and R-F 1 presented an overlap of 190 m on HL (representing 62% of R-F 1 HL and 20% of R-M 2 HL) and of 0.25 ha on HR (representing 31.5% of R-F 1 HR and 6.5% of R-M 2 HR); R-M 3 and R-M 4 presented an overlap of 380 m on HL (representing 76% of R-M 3 HL and 35% of R-M 4 HL) and of 0.23 ha on HR (representing 32% of R-M 3 HR and 6% of R-M 4 HR).

DSC was calculated for 65 individuals (46 males and 19 females), although a male was excluded from the analysis; its DSCs (625 m) was 3.9 times higher than the 90% percentile. The DSC median value estimated from the remaining 64 individuals was 34 m (quartiles 97–0 m). Using model selection, we found that there is an interaction between sexes and seasons that explains DSC variations (Table 3). Males had higher DSC than females (male: median 51, quartiles 112–0 m; female: median 15, quartiles 37–0 m; Figure 5), but concerning seasonal variation, DSC varied in a different way for males and females. Males had higher DSCs during the rainy season (rainy season: median 116, quartiles 168–93 m; dry season: median 40, quartiles 96–0 m; Figure 5), while females had higher DSCs during the dry season (rainy season: median 0, quartiles 20–0 m; dry season: median 19, quartiles 35–0 m; Figure 5).

Figure 5. Box plots of distance between successive captures (DSC) for 64 individuals of *Nectomys squamipes* studied using capture–mark–recapture (CMR). (a) Males' DSC between seasons; (b) females' DSCs between seasons. The middle line on boxes represents the median; the bottom and top of the boxes represent the first and the third quartiles; the whiskers extend to no more than 1.5 times the interquartile range from the boxes or to the extreme data point. Numbers in parentheses are the sample sizes for each sample group.

Discussion

Based on the trapping success results, *N. squamipes* does not use rivers of different widths equally, favouring smaller rivers. A hypothesis for the observed preference is the larger proportion of lentic regions in small streams. These regions, in general, are more productive than lotic areas and thus may attract more individuals – as observed for other semi-aquatic species (Foster-Turley 1992). The home ranges tend to be smaller in highly productive environments because resources are easier to find, thus allowing higher population densities. Blundell et al. (2000) and Schooley and Branch (2006) found smaller home ranges for the Canadian otter (*Lutra canadensis*) and the muskrat (*Neofiber alleni*), respectively, in high productivity areas (i.e. high fish density/marshy areas). In our study, male R-M 3 had its home length and home range equivalent to less than half of the values found for other males studied by radio tracking. This male was located almost exclusively in a lentic and marshy region on a small tributary, which suggests that *N. squamipes* may favour smaller home ranges on lentic regions. Additionally, *N. squamipes* may be limited in movement by larger and lotic rivers. *Nectomys squamipes* is highly adapted to a semi-aquatic life (Ernest 1986; Santori et al. 2008); however, its small size may hamper locomotion in larger/turbulent rivers, which are used easily by large-sized semi-aquatic species.

In the present study, *N. squamipes*' movements were equally distributed between aquatic and terrestrial environments. This result can reflect the time spent in each environment, during the individuals' daily activities: foraging, searching for mates and resting. Our results also indicate that *N. squamipes* restrict their movements to a narrow strip along the river bank; when animals were on land they were never located more than 7 m from water bodies. This corroborates previous studies (Ernest 1986; Ernest and Mares 1986; Briani et al. 2001) highlighting *N. squamipes*' dependence on water bodies. However, the water rat seems to be capable of travelling by land; in small remnants of the Atlantic Forest, a male moved 520 m between forest fragments during the dry season when there was no water body available (Pires et al. 2002).

In respect to the individuals' HR shapes estimated by radio tracking, our analyses suggest that the two-dimensional approach to measure *N. squamipes* movements in linear environments is not accurate. This conclusion can be particularly observed for the individuals R-M 2, R-F 1 and R-M 4, as their HRs included vast unused areas. In contrast, HL was not always accurate, as observed for individual R-M 3. This male intensely used a marshy region (a non-linear water body), and therefore the linear approach failed to include areas where it was located and included unused river stretches. We recommend that future studies with *N. squamipes*, and with other semi-aquatic species, take into account the shape of the water body where the animals are found when selecting the most appropriate method for estimating home ranges; a similar recommendation was given by Serena (1994) and Otley et al. (2000).

We found a positive relation between individual's body weight and HL. A similar pattern was also documented for the HRs of several mammals (Harestad and Bunnell 1979; Mace and Harvey 1983; Fernandes et al. 2010; Oliveira et al. 2012). As bigger animals demand more resources, they need to explore larger areas to find them (Harestad and Bunnell 1979). Nevertheless, while for some species the body weight alone accounts for the differences between sexes (Harestad and Bunnell 1979), we found that sex itself was also an important factor in HL. Considering the same body weight, we still found longer HLs for males than for females. Both the sexual difference in the HL and the overlap patterns for *N. squamipes* are consistent with results from previous studies, suggesting polygamy as the mating system for this species (Bergallo and Magnusson 2004). This is the most likely mating system for *N. squamipes* as males have larger HRs and HLs than females do; males overlap their HL with those of more than one female and females also overlap their HL with those of more than one male. These characteristics have been described for promiscuous mating systems (Ostfeld 1990). The lack of overlap between females suggests territorial behaviour, which also can be related to their shorter HLs, as smaller territories would be easier to protect (Ostfeld 1990).

We found that males explored larger areas during the rainy season, probably in search of females. Even though *N. squamipes* reproduces throughout the year, most of its breeding activity was found to occur during the rainy season (Ernest and Mares 1986; Bergallo 1994; Bergallo and Magnusson 1999; Gentile et al. 2000; D'Andrea et al. 2007). Females explored larger areas during the dry season. As females in general do not look for mates, their movement rates are probably related to food supply, as in Atlantic forest the dry season represents a time of food shortage for this species (Bergallo and Magnusson 1999). The observed pattern is congruent with the theory that male fitness is determined mainly by the number of inseminated females, while female fitness is determined mainly by the quantity of resources ensured for herself and her offspring during the less favourable seasons.

In conclusion, both one- and two-dimensional approaches were useful to describe the use of space by *N. squamipes*. However, analytical approaches should consider the shape of the water body where individuals live. In respect to our ecological assessment of *N. squamipes*, we found that individuals used terrestrial and aquatic environments in equal proportions, but they were never located far away from the water bodies. We recorded a higher abundance in small tributaries than in larger rivers, which can be explained by smaller HR/HL in lentic and more productive areas, or by a deficient adaptation to explore large and lotic environments. Also, both body weight and sex influenced HL. Regarding the seasonal variation, males explored larger areas during the rainy season, which coincides with the reproductive period for this species, while females explore

larger areas during the dry season, when food supply is scarcer. We observed a possible display of territorial behaviour as we did not find an overlap of HL between females. Females did overlap with more than one male, and one male overlapped with more than one female, suggesting a promiscuous mating system for *N. squamipes*.

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