Original investigation

Spatial ecology of the water opossum *Chironectes minimus* in Atlantic Forest streams

Melina de Souza Leite [*,1], Maron Galliez [2], Thiago Lopes Queiroz, Fernando A.S. Fernandez

Laboratório de Ecologia e Conservação de Populações, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CxP 68020, 21941-590 RJ, Brazil

ABSTRACT

The water opossum *Chironectes minimus* is the world's only semi-aquatic marsupial. It is considered rare, and it is reported on several regional conservation lists of species as either endangered or data deficient. Given its uniqueness and the poor knowledge of its ecology, we aimed to investigate home range size and overlap and habitat selection of the water opossum in Atlantic Forest streams in southeastern Brazil. We radio tracked water opossums and collected information about their habitats and behaviour from October 2004 to April 2010. We combined common home range estimators for animals living in linear habitats with the synoptic model of home range and habitat selection. For the 10 individuals monitored, the home ranges varied between 0.80 and 9.66 km of watercourses; none of them had exclusive home ranges. The home range size for males was, on average, three times larger than for females. The overlap data showed that, on average, one male could encompass the home ranges of up to five females simultaneously, but more than one male could have access to the same female. For habitat selection at the individual level, we could not find any strong influence of habitat features on water opossum preferences because individuals selected different sets of habitat variables. However, at the population level, we found a negative relationship between home range size and river size. The water opossum seems to prefer shallow and narrow watercourses to establish its home ranges. Here, we present valuable information to advance our knowledge of the water opossum and its ecology, which is urgent for conservation purposes.

© 2016 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Spatial ecology of animal species has been one of the main concerns of ecology, evolutionary biology and, more currently, conservation biology. It describes the way individuals of a population use the space, including the maintenance of home ranges and territories. This organization may be strongly influenced by a combination of physiological, ecological, and social factors. Physiological factors, such as body size and metabolic requirements (Tucker et al., 2014), usually regulate home ranges and movement patterns of individuals. Among ecological factors, spatial distribution and configuration of habitats and resources play important roles in shaping the movement patterns and space use of an animal (McClintic et al., 2014). In addition, social interactions within a pop-

ulation can also shape home ranges (Mattisson et al., 2013), even in solitary animals (Quaglietta et al., 2014). Therefore, the spatial organization of individuals is often used to infer the mating and social system of a population (Ostfeld, 1990; Adler, 2011). In particular, sex-specific differences in home-range use can yield insights into the mating system and can improve understanding of the behaviour of scarcely studied (Clutton-Brock, 1989; Ostfeld, 1990) and cryptic species (Adler, 2011).

Animals must address their physiological needs for survival and reproduction through the use of resources that are often heterogeneously distributed in habitats. Resource and habitat selection by animals is a hierarchical process of behavioural responses to particular environmental features (Horne et al., 2008). The main purpose of habitat selection studies is to understand which habitat features are more used according to its availability and how they shape animals' movements and home ranges. Better understanding of the processes that lead to patterns of space use is of major importance for animal management and conservation (Mattisson et al., 2013). Unfortunately, information scarcity is common for important yet threatened species and habitats through much of the developing world (e.g. Vanak and Gompper, 2010).

* Corresponding author.
  E-mail address: melina.leite@ib.usp.br (M.d.S. Leite).
  [1] Present address: Departamento de Ecologia, Universidade de São Paulo, 05508-090 SP, Brazil.
  [2] Present address: Departamento de Biologia e Biotecnologia, Instituto Federal do Rio de Janeiro, 20270-021 RJ, Brazil.
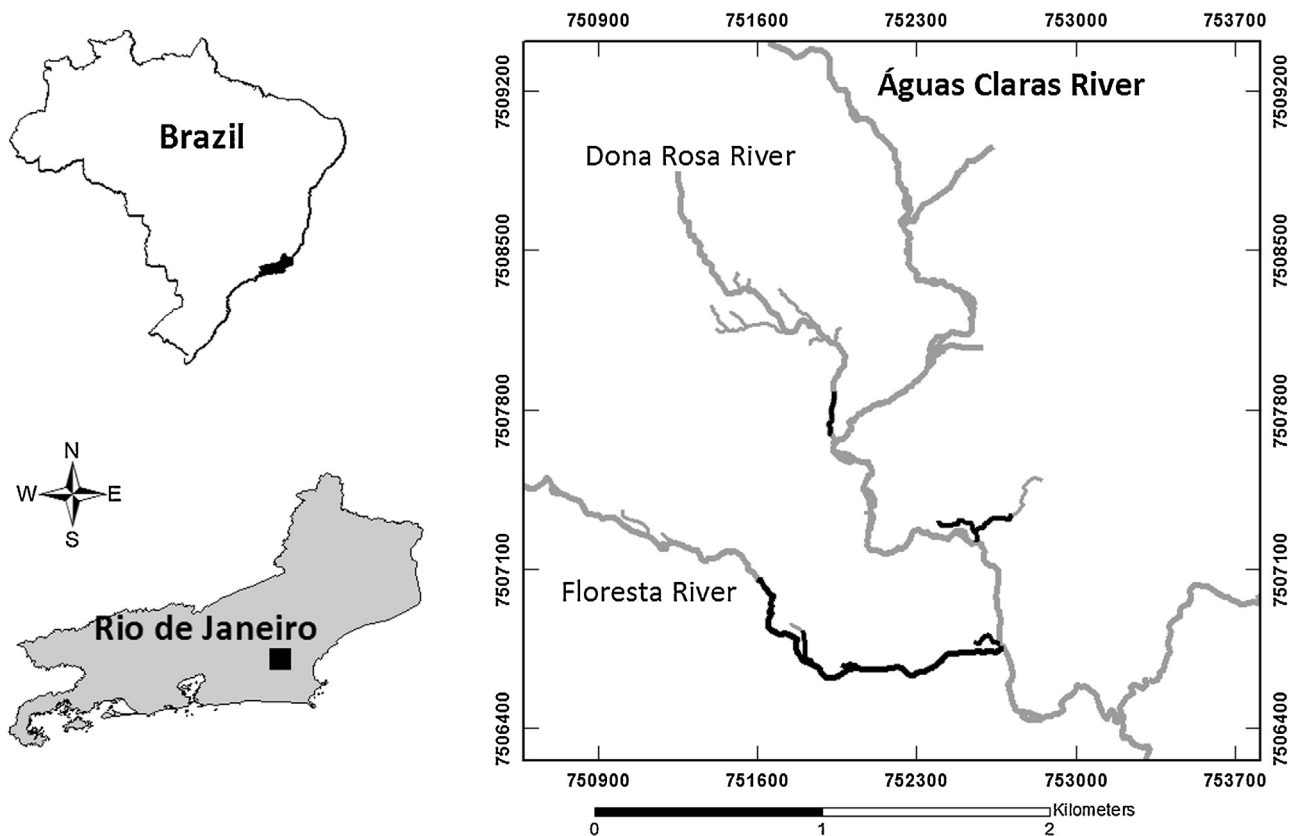
Fig. 1. Study area in the state of Rio de Janeiro, southeastern Brazil. Enlarged, part of ÁguasClaras River basin showing the main tributaries and watercourses used by the radio-tracked water opossums, *Chironectes minimus*. The stretches of trapped area are in bold. Coordinates in UTM (Universal Transverse Mercator).

The water opossum *Chironectes minimus* is the world's only semi-aquatic marsupial (Marshall, 1978), and it inhabits rivers from northern Argentina to southern Mexico. It is a cryptic nocturnal species with a relatively low rate of trap success (Bressiani and Graipel, 2008). The water opossum is considered rare along its distribution (Marshall, 1978; Fernandez et al., 2015), and it appears on several regional lists of endangered species in Brazil, either as data deficient, vulnerable, endangered or critically endangered (Chiarello et al., 2008). Populations of the water opossum in the Atlantic rainforest biodiversity hotspot can be even more threatened due to habitat loss and fragmentation. Today, less than 11% of the original area of this biome persists, and the remaining area is patchily distributed in very small fragments (Ribeiro et al., 2009). Given the rarity and conservation status of the water opossum and the poor knowledge of its ecology, we aimed to investigate the spatial patterns of organization of this organism in Atlantic Forest streams.

We were particularly interested in assessing home range and habitat selection by males and females of the water opossum to infer what type of mating system this population presents and what type of habitat features the species prefers. Based on spatial organization models for small mammals (e.g., Ostfeld, 1990) and knowledge about American marsupials (see Appendix S1 in Supplementary material for references), we expected that males and females would show different patterns of home range and habitat selection. As specific goals, we aimed to (1) calculate and compare home range sizes using various methods to select the best linear home range estimator for the water opossum; (2) simultaneously analyse the home range and habitat selection of the water opossum using the synoptic model of space use; (3) evaluate the habitat features selected by the water opossum to understand the habitat requirements of the species; (4) assess and compare the home range overlap among pairs of individuals to understand the spatial arrangement of the population; and (5) compare the home range size and overlap between the sexes.

Material and methods

Study area

The study was carried out in the basin of the Águas Claras River (22°30′S, 42°30′W) in Rio de Janeiro State, southeastern Brazil. The climate is tropical, wet and warm, with monthly precipitation (mean ± SD) between 105.6 ± 50.8 mm in the dry season (April–September) and 278.1 ± 75.4 mm in the wet season (October–March) (2010, Agência Nacional de Águas, www.ana.gov. br). Mean monthly temperatures vary from 19 °C to 25 °C. The vegetation is submontane rain forest with a mixture of secondary forest.

The sampled area encompasses the final stretch of the higher course, the middle course and the beginning of the lower course of the Águas Claras River (Fig. 1). We classified the river stretches in different types of habitat according to environmental features. In the higher and middle courses, the Águas Claras River has clear water, stony substrate and runs, riffles and occasional deep pools; this stretch presented a continuous riparian forest. The lower course flows through agricultural fields and pastures; the channel has a sandy substrate, slow and shallow water, and long stretches without riparian forest. The Dona Rosa and Floresta rivers are the main tributaries of the Águas Claras River and present well-preserved conditions similar to those in the upper part of the
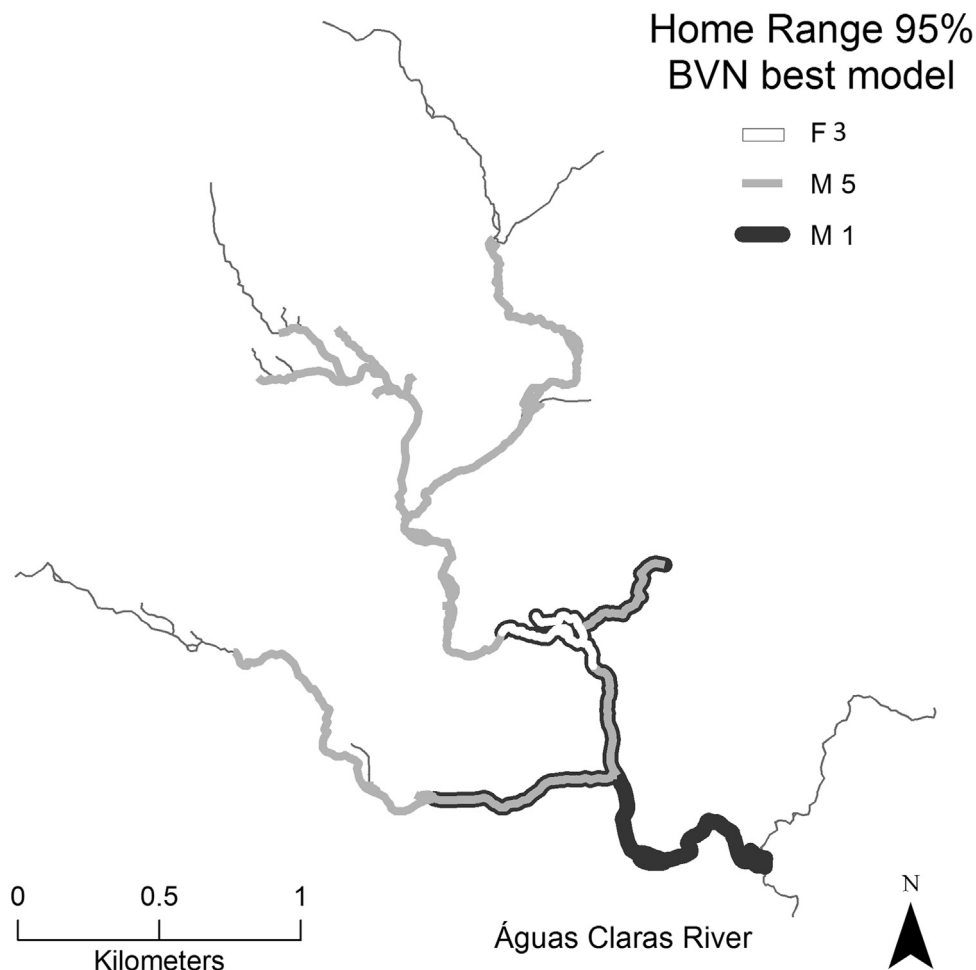
Fig. 2. Home ranges of three water opossums monitored at the same period in Águas Claras River basin. We used the best bivariate normal estimator (BVN-best) with 95% of volume contour. For details of the method and animals see Table 1 and Appendix S4 in Supplementary material.

basin. The other tributaries are smaller and narrower, with sandy or stony substrate and different degrees of riparian forest cover. The entire sampled area was georeferenced using the program ArcGIS 10 (ESRI, Redlands, California).

Trapping and tracking methods

We performed 55 five-night trapping sessions monthly from October 2004 to April 2010, except for 12 non-consecutive months not trapped for logistical reasons. We placed double-door traps into the river between barriers built with stones and branches, following Bressiani and Graipel (2008). We baited the traps with shrimp or fish. For details on the trapping methods, see Galliez et al. (2009).

We fitted adult water opossums with radio collars equipped with activity sensors (SOM-2380A, Wildlife Materials Inc., Murphysboro, USA; or TXE-207C, Telenax, Playa del Carmen, Mexico). The collars weight (between 9.0 and 13.5 g) corresponded to up to 5% of animals' weight. We observed no adverse effects of the radio collars on the animals. During the night, we monitored the animals by homing in on each animal (White and Garrot, 1990) with a TR-4 receiver and a RA-14k antenna (Telonics, Mesa, USA). We obtained the consecutive locations of each individual with intervals of at least one hour, sufficient time for an individual to traverse the entire extent of its home range. Each radio-tracking session started when an animal left the den and finished at the following sunrise. The entire dataset of the radio-tracked animals and georeferenced habitat variables is available on Movebank (movebank.org, study

name "Spatial ecology of the water opossum (data from Leite et al., 2016)") and are published in the Movebank Data Repository with DOI 10.5441/001/1.4rr97k10. All procedures for capture, handling and tracking of individuals were approved by the Brazilian environmental agency (IBAMA-SISBIO, process numbers 12425-1 and 20643-2).

Measurement of habitat variables

We chose habitat variables based on our knowledge about the species and study site and on the literature about semi-aquatic mammals (Appendix S2 in Supplementary material). Moreover, these variables can be considered as important features of the different types of habitat available in Águas Claras basin. The variables were measured at georeferenced points spaced 50 m apart, along all watercourses in the sampled area. Because our location data on individuals were collected over six years, we included four general classes of variables that should not change over time but vary widely within the study site. All habitat variables were measured in August 2010.

We used river channel (CHA, the product of the river width and depth) to assess if there are preferences for watercourses within a certain size. Because of the large difference in the types of river substrates within the study area, we calculated an index of substrate type (SUB) based on the proportions of soil, gravels, rocks and boulders. To understand the structure of the riverbank and the surrounding vegetation of the watercourses, we estimated tree
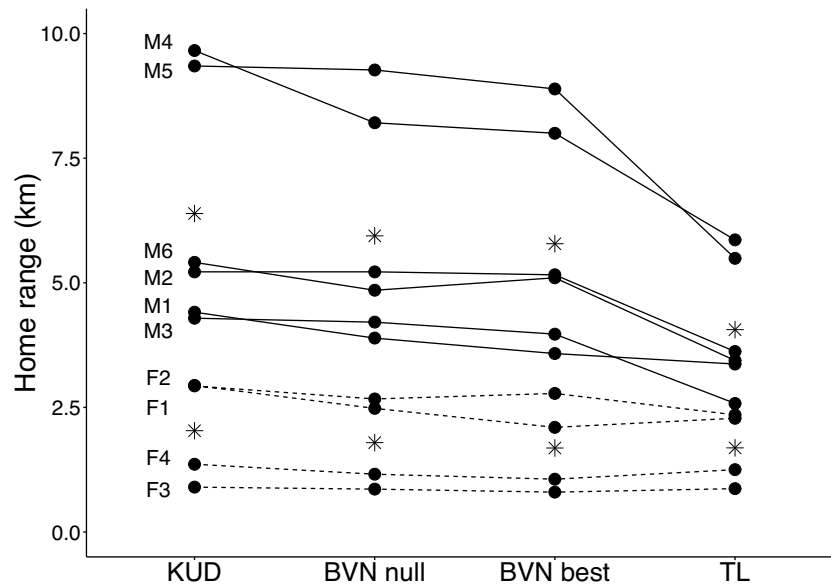
Fig. 3. Estimates of home range size for 10 water opossums, six males M1–M6 (continuous lines) and four females F1–F4 (discontinuous lines). Lines connecting dots indicate the same individual. Asteriscs indicate mean values for each sex. See Table 1 for the names of the home range estimators and animals information.

density (TRE; diameter at breast height >10 cm) in a section of 10 m of both riverbanks and recorded the presence/absence of canopy cover above the river channel (CAN). We reported 50% or more canopy cover as present and less than 50% canopy cover as absent (for details of the variables and calculations, see Appendix S2 in Supplementary material). We checked the variables for collinearity using variance inflation factors, of which the values were less than 1.2, and we found very low correlation coefficients among them (r < 0.3). Continuous covariates were standardized to range between 0 and 1 to simplify the likelihood estimation within the synoptic model (Horne et al., 2008).

Home range estimators

Home range analysis was performed only for radio-tracked animals with sufficient data. We analysed sampling sufficiency as the relationship between the number of locations and the home range size using an asymptotic approach to create cumulative home range sizes (Mattisson et al., 2013). We estimated that a minimum of 16 locations was required to adequately represent a home range of our radio-tracked animals (Appendix S3 in Supplementary material).

Most home range estimators overestimate home range size for animals constrained to linear habitats because they include large unused areas (Sauer et al., 1999; Blundell et al., 2001; Slaght et al., 2013). Therefore, we modelled and estimated the home range size for the water opossum in three different ways. The first method used the distance (km) along the river courses between the farthest locations (TL), a widely used estimator for semi-aquatic mammals. The second method was the fixed kernel density estimator (KUD), using the package 'adehabitatHR' (version 0.4.14, Calenge, 2006) in R (R Core Team, 2015). We used the fixed kernel with reference smoothing parameter to estimate the KUD inside 95% of the volume of the home range (Blundell et al., 2001). Sometimes kernel density estimators can overestimate home range sizes for animals constrained by linear habitats (Slaght et al., 2013). The third choice was the synoptic model of space use (Horne et al., 2008), the methods of which are detailed in the next section. For comparison, we used the null bivariate normal distribution (BVN-null) and the best

bivariate normal distribution (BVN-best) based on habitat selection for each animal in the synoptic model selection, using 95% of volume contour. Comparing the null model with the best model based on habitat selection can tell us how habitat features influenced the water opossum's home range. For the BVN and KUD models, we calculated the length (km) of the watercourses inside the area estimated by the model.

We compared home range sizes among the estimators and sex using a model-selection approach based on Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002). We built linear mixed effects models using individuals as the random factor and home range size as the dependent variable. We used all combinations of independent variables (estimator and sex), including interaction, to build the model selection. We used the package 'lme4' in R (version 1.1-6, Bates et al., 2015) to perform the analysis.

Modelling home range and habitat selection simultaneously

We estimated home range size and second-order habitat selection (*sensu* Johnson, 1980) within the same modelling process using the synoptic model of space use for each animal (Horne et al., 2008). The synoptic model structure is based on a weighted distribution used to predict a species' probability of use of a given area based on an individual's space use (i.e., home range) and the habitat features that influence their space use (Horne et al., 2014).

First, we compared two null distributions of space use to model the probability of use in the absence of habitat selection: a bivariate normal distribution (BVN) and an exponential distribution. The BVN characterizes the space use of an animal that biases movements towards a central place, and the exponential model allows for a more uniform distribution of space use (Slaght et al., 2013). We compared null models of both distributions for each individual using AICc. As the BVN performed much better for all animals (i.e., differences in AICc > 3), we used only the BVN for the subsequent analysis. We used maximum likelihood (via numerical optimization) to estimate the parameters governing the null model of the

Table 1
Linear home range estimates in kilometres of watercourse for 10 water opossums (F—females; M—males). TL—distance along the river courses between the farthest locations; BVN best—the best bivariate normal distribution estimator in the synoptic model selection for each animal; BVN null—the bivariate normal distribution estimator without the influence of habitat covariates; KUD—fixed kernel density estimator.

Individual	Body mass (g)	Monitoring period	# of fixes	TL	BVN best	BVN null	KUD
F1	440	Feb–May 2010	35	2.28	2.10	2.48	2.94
F2	350	Apr 07–Apr 2008	65	2.35	2.78	2.67	2.93
F3	310	Aug–Sep 2005	16	0.87	0.80	0.86	0.90
F4	235	May–Oct 2006	28	1.25	1.06	1.16	1.36
M1	380	Jul–Nov 2005	60	3.37	3.58	3.89	4.41
M2	330	Apr–Jul 2007	19	3.62	5.16	5.22	5.22
M3	390	Apr–Oct 2006 Jan–Jul 2007	54	2.58	3.97	4.21	4.29
M4	335	Apr–Jul 2008	28	5.86	8.00	8.21	9.66
M5	320	Aug 05–Feb 2006 Aug–Nov 2007	34	5.49	8.89	9.27	9.35
M6	340	Jan–Mar 2007	17	3.44	5.10	4.85	5.41
Average Female	334	6.25 months	36	1.69	1.69	1.79	2.03
SD Female	85		21	0.74	0.92	0.92	1.06
Average Male	349	6.83 months	35	4.06	5.78	5.94	6.39
SD Male	29		18	1.31	2.17	2.24	2.45

home range and the selection coefficients in R (code in Slaght et al., 2013).

To assess home range and habitat selection by the water opossum, we developed 16 models using all additive combinations of the four habitat covariates described in the previous section, plus the null model. We selected the best synoptic model from the candidate set based on AICc. Competitive models were those with AICc values that differed from that of the best model by not more than two (Burnham and Anderson, 2002). Furthermore, we averaged selection coefficients across all candidate models for each animal based on Akaike's weights. As our primary goal of modelling was to evaluate the relative importance of habitat variables, we drew inferences from averaged models based on the strength of parameter estimates (85% confidence intervals CI) following Arnold (2010). We also used the relative importance index of the variables (RI; Burnham and Anderson, 2002) to infer which covariates are more important to habitat selection by individuals.

We tested for overall differences in individual selection coefficients between males and females with multivariate analysis of variance (MANOVA) using the Pillai-Bartlett statistic (Horne et al., 2014). If there were no significant differences ($P < 0.05$) in selection coefficients between sexes, we averaged the selection coefficients across individuals to generate population-level estimates.

Home range overlap

We analysed the static interaction (White and Garrot, 1990) between two individuals tracked at the same period to measure the degree of home range overlap. Overlaps were estimated using the proportion of the home range (BVN best model) of individual A overlapped by that of individual B and the proportion of the home range of individual B overlapped by that of individual A. We calculated overlaps in male-male, male-female and female-male home ranges. As no two females were tracked simultaneously, female-female overlaps could not be analysed.

Results

We equipped 18 individuals with radio collars. We obtained 475 locations between July 2005 and May 2010, with a great variation in number of locations (2–65) and monitoring period (2–14 months) per individual. Only 10 individuals (four females and six males) were considered to have sufficient data (>16 locations) for the analysis of home range and habitat selection. The body mass of the radio-tracked individuals varied between 235 and 440 g (Table 1). On average, both sexes presented similar

monitoring periods (approximately six months) and number of locations (36 ± 18; mean ± standard deviation). We did not detect any relationship between body mass and home range size for any estimator: TL: $r = 0.11$, $P = 0.76$; KUD: $r = 0.08$, $P = 0.83$; BVNbest: $r = 0.03$, $P = 0.92$; BVNnull: $r = 0.06$, $P = 0.86$. We also did not find correlation between sample size (number of locations) and home range size: TL: $r = -0.02$, $P = 0.94$; KUD: $r = -0.07$, $P = 0.85$; BVNbest: $r = -0.09$, $P = 0.81$; BVNnull: $r = -0.07$, $P = 0.85$.

Home range size

The estimated home range sizes varied between 0.80 and 9.66 km of watercourses (Table 1 and Fig. 2). The most plausible model to explain home range size was the interaction model between sex and home range estimator. This model was responsible for all the evidence weight, and the AICc difference to the second-best model was 50.6. The home range size for males was, on average, three times larger than for females (Fig. 3). Females presented low variance among estimates: the highest estimate (KUD) was, on average, 1.2 times larger than the lowest estimates (BVN-best and TL), a difference of 0.3 km in home range size. Additionally, for females, the BVN-null model estimate was 1.06 times larger than that of the BVN-best model. For males, the TL estimates were much lower than the other estimates (Fig. 3). The KUD estimates in males were, on average, 1.6 times larger than the TL estimates, a difference of approximately 2.3 km in home range size. In males, the estimates from the BVN-best and BVN-null models were quite similar.

Home range overlap

We simultaneously monitored five male-male and five male-female/female-male pairs. No individual had an exclusive home range. Substantial overlap occurred both between and within sexes. Female-male overlaps, i.e., the proportion by which the home range of a female overlapped with the home range of a male, were higher (median: 1.00, min 0.74; max 1.00) than male-female overlaps (median 0.20; min 0.09; max 0.31). For male-male overlaps, almost 50% of the home length of a male overlapped with another male (median 0.49; min 0.27; max 1.00).

Spatial overlaps between males were also evident through the capture of different males at the same trapping station (three males on one occasion) and adjacent trapping stations (12 occasions). Male-female overlaps were also common at adjacent trapping stations (nine occasions). Nevertheless, female-female overlaps or proximity were not observed at the trapping stations.

Table 2
Parameter estimates (β), associated standard error (SE) and relative importance (RI) of the averaged model of habitat selection for each individual water opossum and for the population. Significant parameters (85% confidence interval) appear in bold.

Individual	River channel (CHA)			Substrate index (SUB)			Trees in riverbank (TREE)			Canopy cover (CAN)		
	β	SE	RI	β	SE	RI	β	SE	RI	β	SE	RI
F1	−7.26	5.42	0.51	−0.11	0.97	0.27	−0.13	1.07	0.28	−0.13	0.37	0.28
F2	−5.07	3.58	0.60	−0.75	0.67	0.41	0.02	0.72	0.29	−0.23	0.27	0.35
F3	**−3.22**	**1.93**	**0.21**	**−6.09**	**2.19**	**1.00**	−1.70	2.67	0.31	**5.17**	**3.00**	**0.84**
F4	−5.11	8.01	0.32	1.13	1.17	0.37	**3.40**	**1.76**	**0.70**	−0.65	0.56	0.41
M1	0.46	1.31	0.28	**−2.26**	**0.60**	**1.00**	**−2.10**	**1.00**	**0.81**	**−2.79**	**1.03**	**1.00**
M2	−2.33	2.81	0.34	−0.12	1.02	0.27	**−3.53**	**1.86**	**0.76**	**−1.58**	**1.06**	**0.66**
M3	**−5.48**	**2.35**	**0.90**	**−1.03**	**0.71**	**0.48**	**2.20**	**0.61**	**0.99**	**0.81**	**0.38**	**0.79**
M4	2.94	2.14	0.46	1.44	0.94	0.58	0.13	0.99	0.26	0.63	0.44	0.49
M5	−2.26	2.40	0.36	0.23	0.84	0.27	**1.86**	**0.80**	**0.81**	**1.44**	**0.43**	**0.99**
M6	−6.98	5.04	0.77	0.07	1.23	0.27	−2.17	2.18	0.38	−0.32	0.53	0.30
Population-level	**−3.43**	**1.03**	**0.48**	−0.75	0.68	0.49	−0.20	0.70	0.56	0.26	0.67	0.61

Habitat selection

No single model was clearly the best for explaining habitat selection (Appendix S4 in Supplementary material). Each individual's model selection had more than one competing best model (i.e., ΔAICc $\leq$ 2) and a different set of top models. The model averaging results for each animal (Table 2) suggested that three individuals (F1, F2 and M6) did not select any habitat variable, i.e., all the parameter estimates overlapped 0 (85% CI). Two individuals presented a negative relationship with river channel (CHA). For substrate index (SUB), three individuals presented a negative response, while one individual had a positive response. In general, we found two groups of males: one group selected positively trees in riverbank (TRE) and canopy cover (CAN), and the other group selected the same parameters negatively. The model selection results and model averaging did not show any indication of difference between males and females. This result is confirmed by MANOVA analysis showing no difference in selection coefficients between sexes ($F_{4,5}$ = 0.87, P = 0.54). At the population level, only the confidence interval for the parameter of CHA did not overlap 0 (Table 2), showing a negative relationship despite its low relative importance in relation to the other variables (0.47).

Discussion

Our results represent the most complete information to date about spatial ecology of the water opossum. We found marked sexual differences in home range sizes and overlaps, which is very important in the determination of the mating system of the population. Nevertheless, habitat selection analysis did not show any strong water opossum preferences. Although we must be cautious when drawing conclusions due to the small sample size, we found valuable information that should be used for conservation of the water opossum in the endangered Atlantic Forest biome.

Home range size

Home range estimators must be constrained where animal movements are constrained by their environment (Powell and Mitchell, 2012). However, obtaining constrained home range estimates remains difficult (e.g., Slaght et al., 2013). We found that the movements of the water opossum are constrained to river channels and banks. In six years of research at the study site, we have never located animals away from the watercourses. To address this, we compared four linear home range estimators, two of which are commonly used for semi-aquatic mammals (TL and KUD) and two derived from a synoptic model of home range and habitat selec-

tion (BVN). The synoptic model was recently developed (Horne et al., 2008) and also used with an animal constrained to riparian habitats (Slaght et al., 2013). The total length of the watercourses between the farthest locations (TL) tended to underestimate the home ranges (Sauer et al., 1999; Blundell et al., 2001), although kernel density estimators (KUD) seemed to overestimate the home range sizes. We believe that the BVN estimators were reliable in estimating the home range sizes for the water opossum. Additionally, the small difference between the best BVN model and the null BVN model for both sexes indicates a weak selection of habitat features by these animals.

Spatial organization and mating system

We interpreted the absence of a relationship between body mass and home range size in our results as an indication that the mating system is the major cause of the differences found in home range size between the sexes (Fisher and Owens, 2000). According to predictive models about social organization of small mammals (Ostfeld, 1990; Adler, 2011), female home range size is influenced by resource abundance and distribution, while male home ranges are determined by the spacing patterns of the females. In a polygynous or promiscuous mating system, males should have larger home ranges, overlapping with other males and females (Adler, 2011). Male water opossums presented home ranges averaging three times the size of females' home ranges, and they overlapped home ranges with many other individuals. Female opossums' home ranges highly overlapped with those of the males, but in the six years of study, we could not detect any interaction between females, nor was overlap observed in the capture data. The overlap data showed that on average, one male could encompass the home ranges of up to five females simultaneously, a pattern consistent with polygyny. However, more than one male could have access to the same female, which enables promiscuity in the population. Data on social interactions between females and/or genetic patterns of paternity are still needed to infer polygyny or promiscuity for the water opossum.

Emlen and Oring (1977) stated that two factors determine the mating system in a population: environment and phylogeny. As seen above, environmental factors shape the population potential for polygamy according to resource distribution. Phylogenetic factors are related to species' ability to adapt their potential to polygamy in the environment (Emlen and Oring, 1977). In Australian marsupials, almost all the species present a promiscuous mating system with overlapping home ranges and marked sexual dimorphism (Fisher and Owens, 2000). Although genetic or experimental methods must be confirmed, this pattern seems to also

be true for American marsupials. The social organization of the water opossum is similar to those of many other marsupials that have been studied (Appendix S1 in Supplementary material). These results reinforce the statement that marsupials are very similar in morphology, physiology and behaviour (Fisher et al., 2001), even though they have very distinct ecological specializations.

Habitat selection

The only population-level habitat feature selected was river channel (CHA). Water opossums seem to prefer shallow and narrow watercourses to establish their home ranges. Similar results were found for resting site selection by the water opossum at the same study site (Palmeirim et al., 2014). Small watercourses can be considered safe and sheltered places due to their shallow and calm waters. They also provide a rich and easy source of prey. In the study site, the abundance of shrimp was much greater in the small watercourses year-round, while small fish were equally abundant in the large and small watercourses during the rainy season (Leite et al., 2009). Water opossums' use of first-order tributaries can also prevent agonistic interactions with otters, a potential competitor or predator widely present in the study site. Otters commonly select the main rivers as their habitat (Somers and Nel, 2004).

Intraspecific variation in the use of resources is a common behaviour in a population (Pulliam and Danielson, 1991). Some animals can select specific resources or habitat features, while others go in the opposite direction. The substrate index (SUB) was selected by four individuals, three of them showing a negative selection. A negative selection means that the animals preferred watercourses with sandy/clay substrate, which is a characteristic of the small tributaries of the Águas Claras River. Males that positively selected the density of trees in the riverbank also positively selected canopy cover. Consequently, we can separate the males into two groups. The first is formed by animals that use the upper part of the Águas Claras basin, with a high density of trees in the riparian forest and a small river width, irrespective of river depth. This enables a closed canopy above the watercourses. The second group includes animals with home ranges established in the middle and lower part of the basin, with open canopy and less riparian forest. Even in the latter group, the animals still tended to select resting sites in well-preserved areas (Palmeirim et al., 2014). The selection of the habitat variables corresponding to a highly preserved riparian forest is an indicator of the water opossums' sensitivity to human disturbance (Galliez and Fernandez, 2012).

The aquatic habitat is one of those worldwide most endangered by anthropogenic actions, suffering from habitat loss, fragmentation and pollution. Summing up all these threats with the differences in sexual behaviour (this study), large area requirements (this study) and low population density (Fernandez et al., 2015), we argue that is extremely urgent to review water opossum conservation status in the highly fragmented Atlantic rainforest.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.05.003.

References

Adler, G.H., 2011. Spacing patterns and social mating systems of echimyid rodents. J. Mammal. 92, 31–38.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manage. 74, 1175–1178.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. J. Stat. Softw. 67, 1–48.

Blundell, G.M., Maier, J.A.K., Debevec, E.M., 2001. Linear home hanges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecol. Monogr. 71, 469–489.

Bressiani, V.B., Graipel, M.E., 2008. Comparação de metodos para captura da cuíca d'água *Chironectes minimus* (Zimmerman, 1780) (Mammalia, Didelphidae), no sul do Brasil. Mastozool. Neotrop. 15, 33–39.

Burnham, K., Anderson, D., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2nd edn. Springer-Verlag, New York.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Modell. 7, 516–519.

Chiarello, A.G., Aguilar, L.M.D.S., Cerqueira, R., de Melo, F.R., Rodrigues, F.H.G., da Silva, V.M.F., 2008. Mamíferos Ameaçados de Extinção no Brasil. In: Machado, A.B.M., Drummond, G.M., Paglia, A.P. (Eds.), Livro Vermelho da Fauna Brasileira Ameaçada de Extinção, vol. II. MMA—Ministério do Meio Ambiente, Brasília.

Clutton-Brock, T.H., 1989. Mammalian mating systems. Proc. R. Soc. 236, 339–372.

Leite, M.S., Galliez, M., Queiroz, T.L., Fernandez, F.A.S., 2016. Data from: spatial ecology of the water opossum *Chironectes minimus* in Atlantic forest streams. Movebank Data Repos., http://dx.doi.org/10.5441/001/1.4rr97k10.

Emlen, S.T., Oring, L.W., 1977. Ecology sexual selection, and the evolution of mating systems. Science 197, 215–223.

Fernandez, F.A.S., Galliez, M., Leite, M.S., Queiroz, T.L., Palmeirim, A.F., 2015. Natural history of the water opossum *Chironectes minimus*: a review. Oecol. Aust. 19, 47–62.

Fisher, D.O., Owens, I.P.F., 2000. Female home range size and the evolution of social organization in macropod marsupials. J. Anim. Ecol. 69, 1083–1098.

Fisher, D.O., Owens, I.P.F., Johnson, C.N., 2001. The ecological basis of life history variation in marsupials. Ecology 82, 3531–3540.

Galliez, M., Fernandez, F.A.S., 2012. Spatial segregation between the water opossum *Chironectes minimus* and the water rat *Nectomys squamipes*: just competition avoidance or a conservation problem as well? Mamm. Biol. 77, 447–450.

Galliez, M., Leite, M.S., Queiroz, T.L., Fernandez, F.A.S., 2009. Ecology of the water opossum *Chironectes minimus* in Atlantic forest streams of southeastern Brazil. J. Mammal. 90, 93–103.

Horne, J., Craig, T., Joly, K., Stout, G., Cebrian, M., Garton, E., 2014. Population characteristics, space use and habitat selection of two non-migratory caribou herds in central Alaska, 1994–2009. Rangifer 34, 1–20.

Horne, J.S., Garton, E.O., Rachlow, J.L., 2008. A synoptic model of animal space use: simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. Ecol. Modell. 214, 338–348.

Johnson, D., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 71, 65–71.

Leite, M.S., Galliez, M., Queiroz, T.L., Lima, D.O., Cid, B., Pinho, G., Fernandez, F., Caramaschi, E., 2009. O gambá d'água como espécie guarda-chuva para a conservação da fauna associada a rios de Mata Atlântica/RJ Technical Report., Available at: http://www.fundacaogrupoboticario.org.br/pt/o-que-fazemos/editais/pages/apoio-projetos-detalhes.aspx?identificador=0750_20071.

Marshall, L., 1978. Chironectes minimus. Mamm. Species 109, 1–6.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R., Pedersen, H.C., 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173, 813–825.

McClintic, L.F., Taylor, J.D., Jones, J.C., Singleton, R.D., Wang, G., 2014. Effects of spatiotemporal resource heterogeneity on home range size of American beaver. J. Zool. 293, 134–141.

Ostfeld, R.S., 1990. The ecology of territoriality in small mammals. Trends Ecol. Evol. 5, 411–415.

Palmeirim, A.F., Leite, M.S., Santos-Reis, M., Fernandez, F.A.S., 2014. Habitat selection for resting sites by the water opossum (*Chironectes minimus*) in the Brazilian Atlantic Forest. Stud. Neotrop. Fauna Environ. 49, 231–238.

Powell, R.A., Mitchell, M.S., 2012. What is a home range? J. Mammal. 93, 948–958.

Pulliam, H.R., Danielson, B.J., 1991. Sources, sinks, and habitat selection—a landscape perspective on population-dynamics. Am. Nat. 137, S50–S66.

Quaglietta, L., Fonseca, V.C., Mira, A., Boitani, L., 2014. Sociospatial organization of a solitary carnivore, the Eurasian otter (*Lutra lutra*). J. Mammal. 95, 140–150.

R Core Team, 2015. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153.

Sauer, T.M., Ben-David, M., Bowyer, R., 1999. A new application of the adaptive-kernel method. Estimating linear home ranges of river otters, *Lutra canadensis*. Can. Field-Nat. 113, 419–424.

Slaght, J.C., Horne, J.S., Surmach, S.G., Gutiérrez, R.J., 2013. Home range and resource selection by animals constrained by linear habitat features: an example of Blakiston's fish owl. J. Appl. Ecol. 50, 1350–1357.

Somers, M.J., Nel, J.A.J., 2004. Movement patterns and home range of Cape clawless otters (*Aonyx capensis*), affected by high food density patches. J. Zool. 262, 91–98.

Tucker, M.A., Ord, T.J., Rogers, T.L., 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. Glob. Ecol. Biogeogr. 23, 1105–1114.

Vanak, A.T., Gompper, M.E., 2010. Multi-scale resource selection and spatial ecology of the Indian fox in a human-dominated dry grassland ecosystem. J. Zool. 281, 140–148.

White, G., Garrot, R., 1990. Analysis of Wildlife Radiotracking Data. Academic Press, San Diego.