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NATURAL HISTORY OF THE WATER OPOSSUM *CHIRONECTES MINIMUS*: A REVIEW

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ABSTRACT
We reviewed information about the natural history of the water opossum *Chironectes minimus* and brought new data on a population studied in Atlantic Forest streams of Rio de Janeiro State, Brazil. The study was carried out from October 2004 to February 2011 using capture-mark-recapture and radiotelemetry techniques. We obtained 127 captures of 43 individuals, and 439 nocturnal locations of 13 individuals. Between July 2006 and October 2007 the population density varied between 0.11 e 0.73 ind./km of river. The overall sex ratio of captured individuals was biased towards males by 3.5:1. Adult males had a mean weight 24% greater than adult females. Young individuals were captured throughout the year, except in August, September and November. Water opossum presented a unimodal activity pattern, with activity increasing after sunset and decreasing thereafter along the night. Their activity patterns were influenced by sex and season. Home lengths varied from 870 to 5,860 m. We observed a high home length overlap between individuals, except among females. Water opossum abundance was higher in wide rivers with high tree density in the riverbank. Their resting sites were placed in river banks with well preserved and forested vegetation, evenly located in rocky substrate, in root systems within terricolous soil or in a mixture of the three different types of substrate (i.e. rocks, roots and soil). Although water opossum is a semi-aquatic species, it presents a lot of similarities with the terrestrial opossums, like sexual dimorphism, poliginic/promiscuous mating system, and nocturnal habits. Like other opossums, habitat loss and transformation are major issues for the conservation of this species.
Keywords: activity patterns; demography; habitat selection; resting sites; spatial patterns.

INTRODUCTION

Rui Cerqueira, to whom this special issue pays homage, has inspired hundreds of scientific studies and careers in Brazilian mastozoology and mammal ecology. In this case, however, he probably has never realized that he had such a role. The first time one of us (FASF) ever heard of a strange animal called the water opossum *Chironectes minimus* (Zimmermann 1780) (Figure 1), was from Rui. The fascination was so great that FASF went to the mammal collection at Museu Nacional, in Rio de Janeiro, moved only by the curiosity to

Figure 1. Water opossum *Chironectes minimus* with radiocollar from our 7-year project in southeast Brazil.

see an animal that should be fantastic even as preserved skins – and it was. At the time, to study the water opossum's ecology looked like a distant dream. But distant dreams sometimes come true as well, and this is why this paper is here.

By the time of that first contact, in the early eighties, the water opossum or yapok was an utterly unknown species, and its short, speculative account in *Mammalian Species* (Marshall 1978) reflected this situation. What was known on its anatomy revealed a truly extraordinary animal. Water opossum is the world's only semi-aquatic marsupial (Nowak 1999), and morphological studies had shown that it had a striking collection of unique adaptations. These include a sixth finger in the forepaws, derived from the wrist bone, which served as an opposable thumb; fully webbed hind paws; a slightly flattened tail that could help swimming; and a marsupial pouch in the female with the entrance directed backwards and with a muscular sphincter to keep it watertight. The female can actually swim underwater with the young in her pouch, just as in a submarine. Even more extraordinary, the male also has a pouch, which protects the scrotum from low water temperatures. Nevertheless, little was known about the water opossum's natural history, and next to nothing about its population ecology (Marshall 1978, Nowak 1999).

Water opossums occur in water bodies from southern Mexico to northern Argentina (Nowak 1999, Ardente *et al.* 2013). Most studies that mention the water opossum to date merely record its presence in faunistic surveys, with a few morpho-physiological and genetic studies, and a few on its behavior in captivity (Nowak 1999). There had not been a single study purposefully designed to study water opossum's demography, spatial patterns or habitat selection, because of methodological limitations. Water opossums are not usually captured in common small mammal live traps, therefore available knowledge was based on occasional information on individuals accidentally captured during studies with other purposes. This situation started to change in 2003, when Vinícius Bressiani and Maurício Graipel developed an effective method for capturing water opossums (see Bressiani and Graipel 2008). With the development of this method, the opportunity appeared to make true FASF's old dream. In 2004, we started a study on the population ecology of the water opossum in Atlantic Forest streams at Northern Rio de Janeiro, Brazil. This study lasted until early 2011, and resulted in the first detailed information published on the water opossum spatial patterns, reproduction, activity patterns, habitat selection and conservation (Galliez *et al.* 2009, Galliez and Fernandez 2012, Galliez *et al.* 2012, Leite *et al.* 2013).

The objective of this article is to review what is presently known on population ecology of water opossum. As there have been so far few other studies on the water opossum's ecology, we review mostly the data from our own project. We provide a synthesis of all the results of our 7-years study on population ecology in Atlantic Forest streams. We update published information and present previously unpublished data, in order to provide for the first time a comprehensive account of the population ecology of the water opossum. Besides, we present additional information from other studies when available and discuss the improvement in knowledge on water opossum population ecology along the last decade.

Demography

The only study on water opossum demography was carried out in streams of northern Rio de Janeiro state (Galliez *et al.* 2009, Queiroz 2011). The main rivers studied were Águas Claras and Gaviões Rivers, two tributaries of the São João River, one of the most important watercourses in Rio de Janeiro State, south-eastern Brazil (Figure 2). A capture-mark-recapture study was carried out with 60 monthly trapping sessions (except when high water levels prevented us using the capture method, see below) in streams of Águas Claras and Gaviões Basins, within the period from October 2004 to January 2011. Each trapping sessions comprised five consecutive nights. Trap stations were placed in favorable river sites where the animals could be directed through dams to pass through the traps, following the method of Bressiani and Graipel (2008). For more detailed sampling and trapping methods, see Galliez *et al.* (2009) and Queiroz (2011).

In the whole study (Galliez *et al.* 2009, Queiroz 2011, plus unpublished data), 135 captures of 49 individuals of water opossum were obtained, including 38 males (101 captures) and 11 females (34 captures), with a total sampling

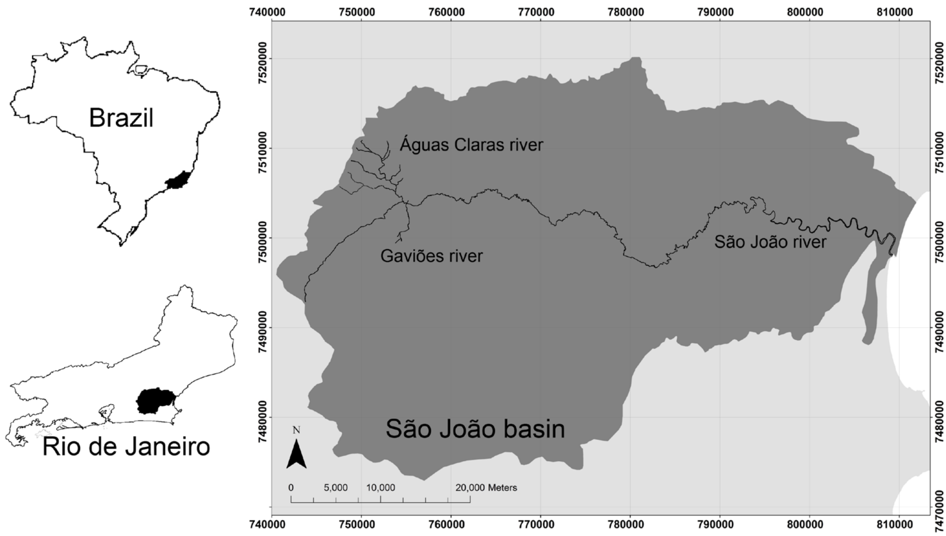

Figure 2. Location of study area in Brazil and in Rio de Janeiro State (left); São João Basin, with the studied rivers and tributaries (right). Values are Universal Transverse Mercator (UTM) coordinates.

effort of 5,926 trapnights. The sex ratio of individuals was strongly biased toward males in Águas Claras Basin (37:9). However, there was no evidence of a similar pattern in the Gaviões Basin (1:2). Adult males had a mean weight of 470g (355-620 g, n = 20) and they weighed 24% more than adult females (mean weight = 379 g, 250-425 g, n = 6; Linear models selection: "Sex effects model": number of model parameters k = 3, AICc = 303.7, Akaike weigth w_i = 0.921; "Null model": number of model parameters k = 2, AICc = 308.6, Akaike weigth w_i = 0.079; Figure 3). Females with pouch young or swollen mammae were captured in January, March and from August to November. The number of pouch young varied between one and four (mean = 3.1, n = 9). Juveniles (individuals with deciduous premolars, based on Rocha 2000) were captured in all months except August, September and November.

Due to a low capture rate, we could only model water opossum's demography in Águas Claras Basin between July 2006 and October 2007, when capture success was about 5%. We obtained 54 captures of 17 individuals (Queiroz 2011; Leite unpublished data). With these data, we performed a model selection in MARK (White and Burnham 1999), using Robust Design (Pollock 1982). Model parameters were estimated by maximum likelihood and models were compared by Akaike Information Criteria corrected for small samples (AICc; Burnham and Anderson 2002). In the best model, water opossum's survival was negatively influenced by variation in monthly rainfall (Leite unpublished data; Table 1), and capture rate was bigger

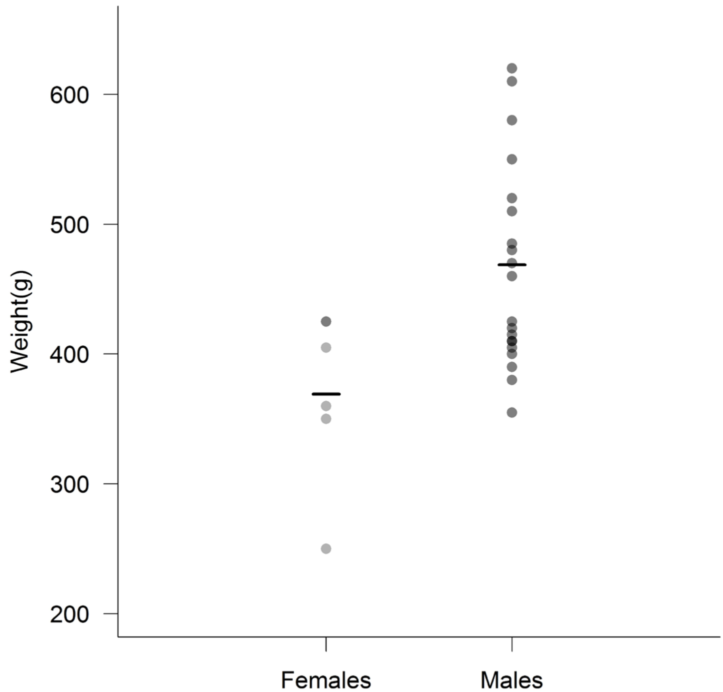

Figure 3. Sexual dimorphism in body weights for *Chironectes minimus*. The horizontal lines indicate the average values. Results of linear models selection: "Sex effects model": number of model parameters k = 3, AICc = 303.7, Akaike weight w_i = 0.921; "Null model": number of model parameters k = 2, AICc = 308.6, Akaike weight w_i = 0.079.

than recapture rate. This model (Table 2) had an accumulated evidence weight of 0.67. Population density varied from 0.11 to 0.73 ind./Km (Figure 4), which corresponds to an individual every 8,300 to 1,300 meters of river length, respectively (Queiroz 2011, Leite unpublished data).

Spatial patterns

In Águas Claras Basin, adult water opossums captured weighing > 350g were fitted with radio-collars with activity sensors (SOM-2380A, Wildlife Materials, Murphysboro, USA; or TXE-207C, Telenax, Playa del Carmen, Mexico). Animals were monitored using the homing-in on the animal technique (White & Garrot 1990). For more detailed methods see Galliez *et al.* (2009) and Leite (2009).

The most extensive analysis on water opossum spatial patterns was achieved by Leite (2009), using all the results published by Galliez *et al.* (2009) plus additional data. Although 18 individuals were monitored, only six males and three females were considered in this analysis (Leite 2009). The number of fixes obtained for each animal varied from 16 to 65 (Table 3). There was no correlation

Table 1. Selection of candidate models for estimating population parameters water opossum *Chironectes minimus* by the Akaike information criterion for small samples (AICc). The models considered the survival (S), the parameters of temporary emigration (g' and g''), and the capture (p) and recapture (c) probability. The survival could be constant (.), vary on time (t), or vary according to monthly variation of daily rains. The other parameters were maintained to be constant. K, number of model parameters; ΔAICc, difference between the AICc of the considered model and the best model; wi, Akaike weight.

Model	K	AICc	ΔAICc	wi
S(var_ppt) g'(.)=g''(.) p(.) c(.)	**5**	**199.84**	**0**	**0.67**
S(.) g'(.)=g''(.) p(.) c(.)	4	202.02	2.18	0.22
S(.) g'(.) g''(.) p(.) c(.)	5	230.9	4.05	0.08
S(var_ppt) g'(.)=g''(.) p(.)=c(.)	4	210.03	10.19	0
S(var_ppt) g'(.) g''(.) p(.)=c(.)	5	210.16	10.62	0
S(var_ppt) g'(.) g''(.) p(.) c(.)	6	210.89	11.04	0
S(.) g'(.)=g''(.) p(.)=c(.)	6	212.47	12.63	0
S(.) g'(.) g''(.) p(.)=c(.)	4	214.69	14.85	0
S(t) g'(.)=g''(.) p(.) c(.)	15	229.28	29.44	0
S(t) g'(.) g''(.) p(.) c(.)	16	234.62	34.78	0
S(t) g'(.)=g''(.) p(.)=c(.)	14	237.4	37.56	0
S(t) g'(.) g''(.) p(.)=c(.)	15	242.77	42.93	0

between the numbers of fixes and the estimated home lengths (Spearman's rank correlation: r_s = 0.02, n = 9, p = 0.95), neither between body mass and home length (Spearman's rank correlation: r_s = 0.15, n = 9, p = 0.70). Home lengths varied from 870 to 5,860 m (Table 3). Males showed home lengths about three times larger than females (medians and extremes: males: 3,530, 2,580–5,860; females: 1,250, 870-2,330 m; Mann–Whitney test: U' = 18, n1 = n2 = 3, p = 0.02). There was a high overlap between home lengths of individuals monitored at the same period. Between 26% and 100% of the home length of each male was included within the home length of another male (median = 56%), and between 12% and 26% was included within the home length of one female (median = 20%). Females had between 54% and 78% (median 76%) of their home lengths overlapped with males. There were no female-female home length overlaps, due to absence of females monitored at the same period (Leite 2009).

Habitat selection

In Águas Claras Basin, a habitat selection analysis was carried out by Galliez and Fernandez (2012). For methods see Galliez and Fernandez (2012) and Galliez (2012). Water

Table 2. Demographic parameters estimation of the most plausible model (see Table 1). S, survival; Gamma' and Gamma", the parameters of temporary emigration (g' and g''); p, capture probability; c, recapture probability.

Parameter	Estimation	Standard error	Inferior CI	Superior CI
S1	0.900	0.103	0.487	0.989
S2	0.681	0.107	0.449	0.848
S3	0.816	0.114	0.499	0.952
S4	0.721	0.108	0.475	0.881
S5	0.545	0.131	0.299	0.771
S6	0.103	0.165	0.003	0.792
S7	0.670	0.107	0.440	0.839
S8	0.721	0.108	0.474	0.881
S9	0.891	0.106	0.490	0.986
S10	0.717	0.108	0.473	0.878
S11	0.916	0.097	0.480	0.992
S12	0.909	0.100	0.483	0.991
Gamma´´	0.470	0.156	0.206	0.752
Gamma´	0.470	0.156	0.206	0.752
p	0.485	0.086	0.324	0.649
c	0.100	0.032	0.053	0.181

Table 3. Home lengths of nine water opossum *Chironectes minimus* estimated from trapping data (number of captures) and radiotracking data (number of locations) in the Águas Claras Basin, southeastern Brazil. According to Leite (2009).

Individual	Sex	Mass (g)	Tracking period	Locations	Home length (m)
Godofredo	male	380	July-November 2005	60	3,370
Margarida	female	310	August-September 2005	16	870
Robin	male	321	August 2005-February 2006 and August-November 2007	34	4,140
Paçoca	female	235	May-October 2006	28	1,250
Panqueca	male	390	April-October 2006 and January-July 2007	54	2,390
Tonico	male	340	January-March 2007	17	3,440
Malandro	male	330	April-July 2007	19	3,620
Florzinha	female	350	April 2007-April 2008	65	2,330
Rivaldo	male	335	April-July 2008	28	5,860

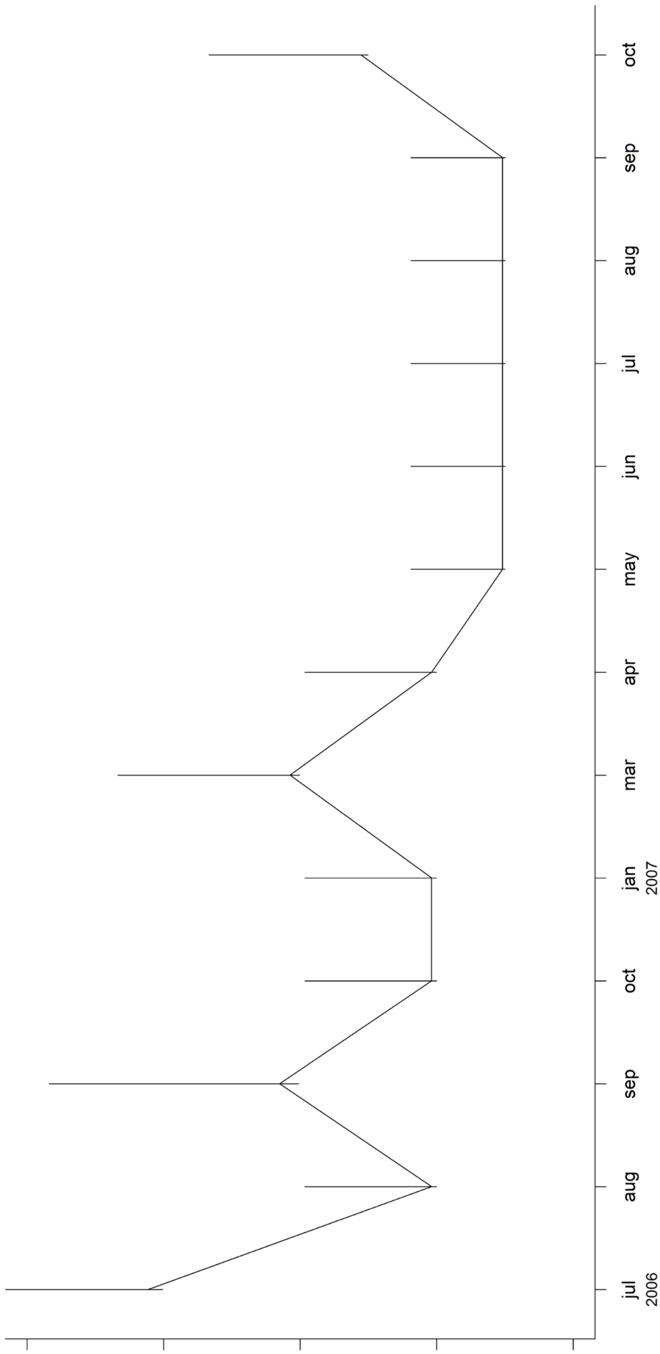

Figure 4. Population size estimates of the water opossum *Chironectes minimus* in the Águas Claras Basin. The upper and lower vertical bars show the confidence intervals (95%).

opossums were captured in 10 of 12 river stretches sampled. We recorded six physical and vegetational habitat variables for each river stretch. These variables were chosen because they were thought to be biologically relevant for semiaquatic small mammals. Water opossums seem to select river stretches with high density of trees and large river channels (Table 4). The best of the candidate models explained 52.4% of the variation in water opossum abundance (multiple regression, model Tre(+), Cha(+): K = 3, AICc = 11.923, wi = 0.363, $R^2 = 0.524$). The variables proportion of forest at 5 or 50 m away from the river appeared in four of the selected models ($\Delta AICc \leq 2$; Table 4), indicating that water opossum abundance was also associated with habitat variables related to the degree of conservation of the surrounding landscape.

Resting sites

In the Águas Claras Basin, Palmeirim *et al.* (2014) observed 25 different resting sites used by 14 radio-tracked water opossums. The numbers of resting sites used by males (median = 4, minimum = 2 and maximum = 5) and females (3, 3-8) did not differ (data from three males and three females that had more than six radio locations, Mann–Whitney test: U = 4, $n_{male} = 3$, $n_{females} = 3$, p = 0.83). Most resting sites were in river banks in forested areas (92.3%); the remaining ones were in areas with shrubby vegetation (7.7%). The resting sites were in holes among stones (50%), in bare soil (38%) or in tree roots (12%). The distance of the den's entrance to water varied from zero to 2.5 m (median = 0.6 m, n = 20) and the height from water varied from zero to 1.8 m (median = 0.3 m, n = 20). Water opossums seem

Table 4. Multiple regression models selected to explain water opossum *Chironectes minimus* in Águas Claras Basin, southeast Brazil. K, number of model parameters; AICc, Akaike information criterion for small samples; ΔAICc, difference between the AICc of the considered model and the best model; wi, Akaike weight; (+), positive relationship; and (−), negative relationship. Variable abbreviations: Cha, river channel size (m^2); Sub, river substrate size index; Veg, riparian vegetation index; Tre, tree density (n/10 m); F5, proportion of forest at 5 m away from the river; and F50, proportion of forest at 50 m away from the river. According to Galliez and Fernandez (2012).

Model	K	AICc	DAICc	wi
Tre(+), Cha(+)	**3**	**11.92**	**0.00**	**0.36**
Tre(+)	2	12.85	0.93	0.23
Tre(+), Cha(+), F50(+)	4	13.19	1.27	0.19
Tre(+), Cha(+), F5(+)	4	13.86	1.93	0.14
Tre(+), Cha(+), F50(+), Sub(−), F5(−), Veg(−)	6	15.21	3.29	0.07
Null	1	19.23	7.31	0.01

to select forested river stretches with small width and depth to establish their dens in river banks (Palmeirim *et al.* 2014).

Activity patterns

The activity patterns of water opossums in Águas Claras Basin were studied by Galliez *et al.* (2009) and Leite *et al.* (2013), by radio-tracking water opossums with activity sensor collars. For more detailed methods, see Galliez *et al.* (2009) and Leite *et al.* (2013). A total of 439 fixes were obtained for 15 water opossums (11 males and four females), of which 228 (52%) were active fixes and 211 (48%) inactive ones (Leite *et al.* 2013).

Water opossums are mostly nocturnal animals, with little crepuscular activity. Out of 53 diurnal fixes, 46 individuals were found inactive in their dens and seven were active fixes in crepuscular periods (about 30 minutes before or after sunset or sunrise). Females were more active in the first period of the night (Figure 5). Both sexes decreased their activity along the night (Figure 5). Males increased their activity length in the dry season, and for females the pattern was the opposite (Leite *et al.* 2013).

Ecological interactions

During our project, we did not detect any interaction between water opossum

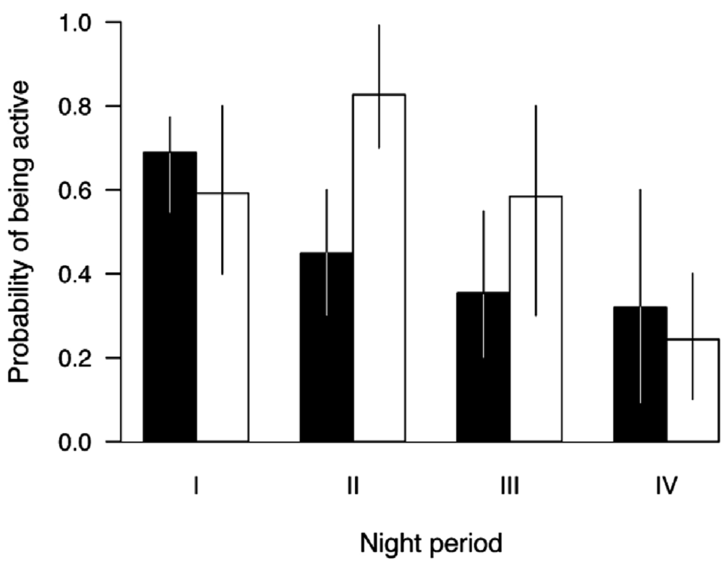

Figure 5. Probability of being active in the night periods for females (black bars) and males (white bars) of the water opossum *Chironectes minimus* in the Águas Claras Basin, south-eastern Brazil. For each night, the four periods had equal length independent of night length. Vertical error lines are 95% confidence intervals. According to Leite *et al.* (2013).

and other animals. In the study site, there are other two semiaquatic mammals, the Neotropical otter *Lontra longicaudis* and the water rat *Nectomys squamipes,* that could interact at least indirectly with the water opossum. However, Galliez and Fernandez (2012) did not find any evidence of competition in the spatial segregation between water opossums and water rats. They concluded that water opossums and water rats had quite different habitat preferences, the former preferring more well preserved river stretches with denser riverine forests than the latter.

The only predation on the water opossum was reported by Tortato (2009). It is based on an anecdotal observation of a single hawk (*Rupastor magnirostris*) eating an individual water opossum in Santa Catarina, South Brazil, in 2004. As the water opossum was already dead at the beginning of the observation, the hypothesis of this event representing scavenging rather than actual predation cannot be discarded.

Breviglieri and Pedro (2010), on the other hand, reported an opportunistic predation by water opossum on bats *Carollia perspicillata* and *Sturnira lilium* at São Paulo, Southeast Brazil, during a riparian's fauna sampling. Water opossum climbed up the mist net and ate two bats trapped in the net's lower region. Despite this report, the water opossum is a piscivorous-cancrivorous species (Zetek 1930, Mondolfi & Padilla 1958, Marshall 1978, Galliez *et al.* 2009), and the predation on bats seems to be an occasional event. Studies about opossum's diet are commonly based on feces collected during the handling procedure of captured individuals (ex. Macedo *et al.* 2010). However through our 7-years study no water opossum captured defecated during the handling procedure. Information about water opossum's diet was based only on stomach contents (Mondolfi and Padilha 1958), contents found inside dens (Zetek 1930) and cranial morphology (Monteiro-Filho *et al.* 2006). Though, a gap still remains on its interactions with the riverine fauna.

DISCUSSION

The improvement in knowledge about the water opossum ecology can be evaluated just by comparing the situation in the early eighties with the present one. At the time of that first inspiring talk on the water opossum, nearly all aspects of water opossum's ecology were utterly unknown. Now, we can have at least some understanding on how this strangest of mammals relates with its environment.

Regarding demography, the 7-year study in the northern Rio de Janeiro streams was the first to estimate demographic parameters for a water opossum population. This can serve as an inspiration for further studies that will investigate the influences of different endogenous and environmental factors shaping the population dynamics of this species, and other semiaquatic or furtive species. The sex ratio of captured individuals, strongly biased towards males, was a striking pattern, but it happened only in Águas Claras Basin (with better samples); it could not be reproduced in Gaviões Basin.

An interesting pattern was that water opossum survival was lower in the months with higher rainfall. This may reflect in part a methodological artifact, as Bressiani and Graipel's (2008) method does not work so well when water levels are too high. Although, it may also happen due to biological causes, such as increased difficulty to capture prey in fast flowing streams and/or destruction of the resting sites, which are quite low on the water (Palmeirim *et al.* 2014). In conjunction with this, the months with higher rainfall coincide with the weaning period (Queiroz 2010), the critical period for survival for many species (ex. Kajin *et al.* 2008).

After this 7-year study we can observe that the water opossum presents seasonal reproduction, similar to that observed for most of Neotropical marsupial species. Previous studies by Mondolfi and Padilla (1958) and Galliez *et al.* (2009) have failed to detect seasonality, but the first study was carried out at a much lower latitude where the breeding period of marsupials is expected to be longer (Rademaker and Cerqueira 2006), and both were based in much smaller data bases than the present study. The breeding season in the study area probably begins between the months of June and July and should extend to the months of January and February (Queiroz 2011). The several captures of water opossum females with pouch young or swollen mammae in different months in other studies corroborate this conclusion (Mondolfi and Padilha, 1958, Nowak 1999, Monteiro-Filho *et al*. 2006). More than one reproductive event can occur in the same breeding season (Queiroz 2011).

For the first time, an estimate of water opossum's population density could be obtained by Queiroz (2011) and Leite (unpublished data), varying from 0.11 and 0.73 ind./km of river. The abundance of water opossum along its distribution has been a controversial point, always based on anecdotal observations. Emmons and Feer (1997) regarded it as scarce throughout its distribution, including Argentina (Ojeda *et al.* 2002), Mexico (Ceballos and Navarros 1991; Medellín 1994), Peru (Terborgh *et al.* 1984), and Uruguay (Baes *et al.* 2002). However, in Panama (Handley 1966), French Guiana (Voss *et al.* 2001) and Guyana (Engstrom and Lim 2002), water opossums were regarded as common. The density estimate obtained in the northern Rio de Janeiro streams tends to agree with the latter group of authors, showing that where it occurs, water opossum can be at least a locally abundant animal.

Zetek (1930) and Mondolfi and Padilla (1958) had already observed that water opossum is nocturnal, but that was all that was known about it at the time. Now we know that water opossums present a unimodal activity pattern along the night, with activity increasing after sunset and decreasing thereafter (Galliez *et al.* 2009, Leite *et al.* 2013). Leite *et al.* (2013) found that males and females behave differently in respect of the probability of being active during the night and the activity length during dry and wet season, which can be attributed to different sex and breeding conditions in species with sexual dimorphism

(Marcelli *et al.* 2003). The distribution of the activity along the night was similar to most other Neotropical marsupials studied (ex. Oliveira-Santos *et al.* 2008, Streilein 1982), suggesting that this feature was determined more strongly by phylogenetic constraints than by the unique ecology of this only aquatic marsupial.

By the time of Marshall's (1978) and Nowak's (1999) accounts, how far a water opossum ranged along a river was completely unknown, but Galliez *et al.* (2009) and Leite (2009) point to individuals of water opossum using river extensions from about 1 to 6 Km as their home lengths. The unidimensional approach adopted in these studies - using home lengths instead of home ranges - was suitable for the water opossum because it, in this case confirming expectations, seldom gets far from the watercourses. Galliez *et al.* (2009) and Leite *et al.* (2009) also showed that home length overlaps were extensive among individual water opossums, except among females. These patterns, together with the sexual dimorphism found, are consistent with a poliginic or with a promiscuous mating system (Ostfeld 1990). These results again are similar to patterns found for several other Neotropical marsupials (ex. Pires and Fernandez 1999), suggesting that the water opossum's radically different ecology have not obscured phylogenetic constraints in determining its spatial patterns and mating system.

The controversy about abundances of the water opossum along its geographical distribution may also reflect its preference, in smaller spatial scales, for well conserved river stretches. This factor, together with the animal's nocturnal habits and avoidance of usual traps, should explain why water opossums are often regarded as rare. However, its habitat preferences are likely to make water opossum vulnerable in the long term, as human population growth and development have made preserved rivers an ever scarcer commodity. Habitat selection results (Galliez and Fernandez 2012) show that water opossum is dependent on riverine forest, and should be particularly affected by its degradation. Besides, its position in the trophic chain suggests that it should be highly vulnerable to water pollution as well. Thus, we think that water opossum status as "least concern" in the IUCN and national lists of endangered species is likely an underestimate; its status as "vulnerable" in most state lists in Brazil probably informs better the species' situation (Galliez *et al.* 2012).

Much remains to be understood about the fascinating water opossum, but the progress achieved in the last decade is one more example of the impressive flourishing in the Brazilian mammal ecology that Rui Cerqueira in many ways helped to foster.

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MATERIAL AND METHODS

We provide a synthesis of all the results of our 7-years study on population ecology in Atlantic Forest streams. We update published information and present previously unpublished data, in order to provide for the first time a comprehensive account of the population ecology of the water opossum. Besides, we present additional information from other studies when available and discuss the improvement in knowledge on water opossum population ecology along the last decade.

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