

Ecology of the Water Opossum *Chironectes minimus* in Atlantic Forest Streams of Southeastern Brazil

Authors: Galliez, Maron, de Souza Leite, Melina, Queiroz, Thiago Lopes, and dos Santos Fernandez, Fernando Antonio

Source: Journal of Mammalogy, 90(1) : 93-103

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/07-MAMM-A-397.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

ECOLOGY OF THE WATER OPOSSUM *CHIRONECTES MINIMUS* IN ATLANTIC FOREST STREAMS OF SOUTHEASTERN BRAZIL

MARON GALLIEZ, MELINA DE SOUZA LEITE, THIAGO LOPES QUEIROZ, AND
FERNANDO ANTONIO DOS SANTOS FERNANDEZ*

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

We studied the population structure, spatial patterns, and activity patterns of the water opossum (*Chironectes minimus*) via capture–mark–recapture and radiotelemetry from October 2004 to October 2006 in Atlantic Forest streams in southeastern Brazil. We tested the hypothesis of reproductive seasonality, the usual pattern in neotropical marsupials, by examining recruitment of juveniles. The hypothesis was rejected, supporting the alternative hypothesis that breeding by water opossums was better explained by its habitat characteristics and prey availability than by its phylogenetic ancestry. The observed sex ratio was significantly biased toward males. The home lengths of individual water opossums varied from 844 to 3,724 m. Males had larger home lengths than females, and there were male–male and male–female overlaps. The longer home lengths for males may explain the observed sex ratio bias, because males are more exposed to capture. All individuals used stream stretches with preserved riparian forest, fast-flowing water, and stony substrate. The hypothesis that activity was homogeneously distributed throughout the night was rejected; activity began right after sunset and ended before sunrise, but with higher levels of activity in the first 6 h of the night. Because of anthropogenic alterations of hydrographic basins, water opossums may be threatened by reduction of their main habitat, streams with fast-flowing water and stony substrate.

Key words: activity period, conservation, marsupials, population structure, spatial patterns

The water opossum (*Chironectes minimus*) is the only semiaquatic marsupial (Marshall 1978; Mondolfi and Padilla 1958; Nowak 1991). Water opossums have many morphological convergences with otters, plus several unique features (Marshall 1978; Nowak 1991). Like otters, they have a streamlined body shape, large webbed hind feet, dense, nonwetable fur, and supernumerary facial bristles (Marshall 1978; Nowak 1991). Water opossums are unique among neotropical marsupials in their opposable 6th “finger” in the front feet, derived from a wrist bone, and also in that both sexes have a well-developed waterproof marsupium. This last feature allows a female to swim with young in her pouch and protects a male’s scrotum from low water temperatures (Marshall 1978; Nowak 1991).

Water opossums occur in water bodies from southern Mexico to northern Argentina (Nowak 1991). Despite their

wide distribution, there is little and inconclusive information about their ecology (Mondolfi and Padilla 1958; Zetek 1930). Most studies that mention the water opossum to date merely record its presence in faunistic surveys, with a few morphophysiological and genetic studies, and a few on its behavior in captivity (Nowak 1991). Its abundance in nature is controversial. In Peru (Terborgh et al. 1984), México (Ceballos and Navarro 1991; Medellín 1994), Uruguay (Baes et al. 2002), and Argentina (Ojeda et al. 2002), it has been reported as rare and vulnerable. Emmons and Feer (1997) regarded it as rare throughout its distribution. However, in Panama (Handley 1966), French Guiana (Voss et al. 2001), and Guyana (Engstrom and Lim 2002), water opossums were regarded as common. In most studies, captures or sightings occurred mainly in forested streams with clear, fast-flowing waters. Regarding its diet, Zetek (1930) and Medellín (1991) found that water opossums feed mainly on crustaceans, whereas Mondolfi and Padilla (1958), analyzing stomach contents, found that its diet is essentially piscivorous. As for the breeding season, females with offspring were captured in January, July, and November in Venezuela (Mondolfi and Padilla 1958); in Brazil, females with offspring were captured between

* Correspondent: rodentia@biologia.ufrj.br

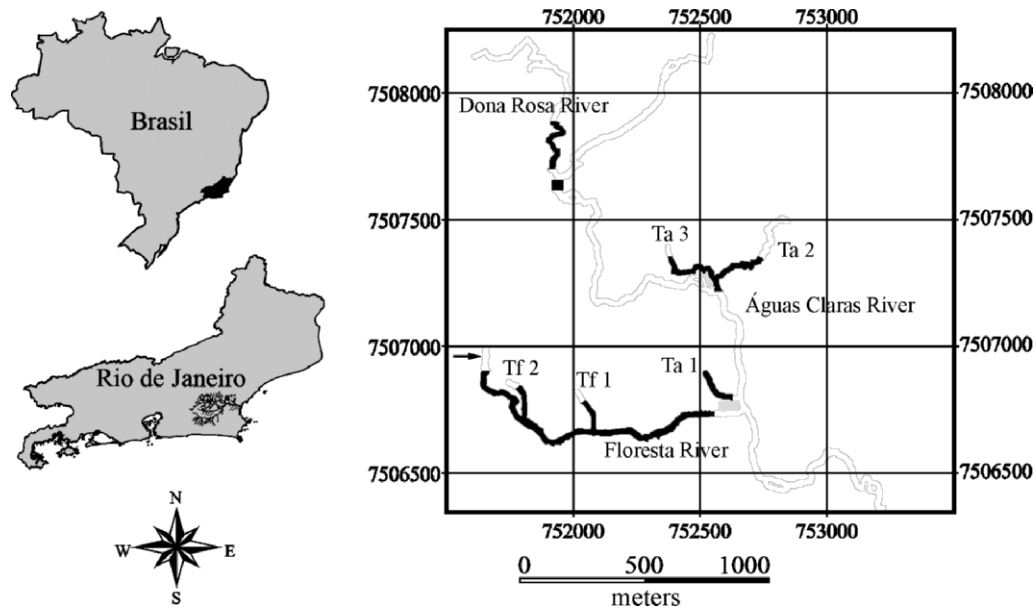


FIG. 1.—Location of study area in Brazil and in Rio de Janeiro State (left); middle course of the Águas Claras River subbasin, with the studied rivers and tributaries (right). Ta 1, Ta 2, and Ta 3 are Águas Claras River tributaries; Tf 1 and Tf 2 are Floresta River tributaries. The black square indicates a dam in Águas Claras River; the arrow indicates a waterfall sequence in Floresta River. Values are Universal Transverse Mercator (UTM) coordinates.

December and February (Nowak 1991); and in northern Argentina, the presence of offspring was recorded in August (Monteiro-Filho et al. 2006).

Nothing is known, among other subjects, about population structure, reproduction in the wild, spatial patterns (home lengths and overlaps and habitat selection), and activity patterns of water opossums. In all these aspects, there are open questions as to whether the patterns shown by water opossums are similar to those found in other neotropical marsupials, due to phylogenetic constraints, or if they are similar to those shown by other semiaquatic mammals, indicating that ecology had a preponderant role in shaping these characteristics.

Because of their semiaquatic and nocturnal habits, water opossums have seldom been captured by the traditional methods used for other small mammal species (Mondolfi and Padilla 1958). An efficient method for trapping the water opossum was only developed in 2003 (Bressiani and Graipel 2008), enabling more thorough studies of their ecology.

The present study focused on the ecology of water opossums in Atlantic Forest streams in southeastern Brazil, attempting to fill some of the many gaps in the knowledge of this species and to test some hypotheses on its reproductive seasonality, spatial patterns, and activity patterns. Regarding reproduction, we tested the hypothesis that water opossums show reproductive seasonality, as usual among neotropical marsupials (Fleming 1972; Fonseca and Kierulff 1989; O'Connell 1989; Tyndale-Biscoe and Mackenzie 1976). Alternatively, reproduction by water opossums could reflect the absence of a well-defined seasonality in its river habitat. Regarding spatial patterns, we estimated the home lengths—the distance along the river course between the most widely separated locations of each

individual—and analyzed home-length overlaps. We compared the patterns found for water opossums to those of terrestrial didelphids, which in most cases show territorial females with smaller ranges and nonterritorial males with larger ranges (Cáceres 2003; Lira et al. 2007; Moraes Junior and Chiarello 2005; Sunquist et al. 1987). The alternative hypothesis in this case is that water opossums show different spatial patterns reflecting its peculiar habitat for a didelphid. We also described the activity pattern of water opossums to determine whether activity is homogeneously distributed throughout the night or if there are well-defined peaks of activity.

MATERIALS AND METHODS

Study area.—The study was carried out in Águas Claras River, Floresta River, and Dona Rosa River, 3 streams of the Águas Claras River subbasin (22°30'S, 42°30'W), in Rio de Janeiro State, southeastern Brazil (Fig. 1). The region is greatly influenced by the surrounding mountain ranges, which reach elevations around 1,000 m above sea level (Mantovani 1997). The climate has been classified as tropical wet and warm and, from 1968 to 1988, the mean monthly precipitation (\pm SD) varied between 78.2 ± 30.1 mm in the dry season (April–September) and 262.8 ± 54.6 mm in the wet season (October–March—Mantovani 1997). The vegetation of the region has been classified as submontane rain forest, and nowadays it includes secondary vegetation and original forest remnants (Mantovani 1997).

The Águas Claras River is one of the main tributaries of the São João River, one of the main watercourses of the region (Bidegain and Völcker 2003). The Águas Claras River has its source at 800 m above sea level, and its higher and middle

TABLE 1.—Sampling of the 8 streams of the Águas Claras River subbasin, southeastern Brazil. Shown are sampling period, extension of river sampled (in m), number of traps in each trapping session, and sampling effort (in trap-nights) throughout the study period.

River	Sampling period	Extension of river trapped	No. traps	Trapping effort
Águas Claras River ^a	January 2006–October 2006	700	115	838
Small tributary Ta 1	September 2005–June 2006	200	15	95
Small tributary Ta 2	July 2005–October 2006	270	35	435
Small tributary Ta 3	October 2005–October 2006	230	15	153
Floresta River ^b	October 2004–October 2005	1200	120	784
Small tributary Tf 1	October 2005–October 2006	110	10	111
Small tributary Tf 2	October 2005–October 2006	180	20	222
Dona Rosa River	September 2005–October 2006	150	45	463
Totals				3,157/2,303 ^c

^a The Águas Claras River was sampled only along its margins.

^b The Floresta River also was sampled in the period between July and October 2006, with 15 traps for each trapping session.

^c The number before the slash refers to total sampling effort and the number after the slash refers to trapping effort excluding the traps placed at in Águas Claras River margins.

course still present well-preserved conditions, with stony substrate and presence of runs, riffles, and occasional deep pools (Bidegain and Völcker 2003). Near the confluence with the Dona Rosa River, there is a 3-m-high inactive dam. After it is joined by the Floresta River, the lower course of the Águas Claras River flows through agricultural fields and pastures (Bidegain and Völcker 2003). In this part of the Águas Claras River, the stream has a sandy substrate, slow and shallow water, and long lengths without riparian forest. The Águas Claras River has 8 main tributaries, among them the Floresta and Dona Rosa rivers. The Floresta River has its source at 700 m above sea level (Bidegain and Völcker 2003), flowing 4.8 km until it joins the Águas Claras River. It has well-preserved habitats along its entire course, with few areas without riparian forest, and consists of runs and riffles with stony substrate. Along its course there is a sequence of 3 waterfalls up to 12 m high. The Dona Rosa River is 2.0 km in length with well-preserved conditions along its entire course, and consists of runs and riffles with stone substrate and riparian forest. Within the study area, the Águas Claras River and Floresta River are joined by many tiny, permanent tributaries up to 1.5 m wide, with substrates composed of stone and sand. The Águas Claras River tributary Ta 1 is an exception because it is composed of sand only, and it dries in the dry season.

Trapping methods.—We conducted a trapping session every month from October 2004 to October 2006, except in November 2004 and March 2006. The areas sampled included 1 stretch of the Águas Claras River and 3 tributaries (Ta 1, Ta 2, and Ta 3), 1 stretch of the Floresta River and 2 tributaries (Tf 1 and Tf 2), and 1 stretch of the Dona Rosa River (Table 1). Methods for trapping and handling animals met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Each trapping session comprised 5 consecutive nights of livetrapping. We placed trap stations in favorable river sites, in order to maximize capture success (see below). The distance between consecutive trap stations varied between 20 and 200 m. Each trap station had 1–3 traps. According to this sampling design, we set 10–120 traps in different river stretches in each trapping session (Table 1).

Following the method developed by Bressiani and Graipel (2008), we placed double-door wire-mesh live traps (90.0 ×

21.0 × 21.0 cm; Gabrisa Ltda., Cafelândia, Brazil; 96.6 × 15.2 × 15.2 cm and 81.3 × 22.9 × 22.9 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) in the rivers in a way that the trip pan stood out of the water. We built barriers in suitable places in the rivers, using stones and branches, in a way to direct the water flow through the trap, inducing the animal to enter. After each trap session, traps were removed and barriers undone. Up to March 2006, we used no bait in the traps. From April 2006, we baited the traps with different types of bait. In April and May, the bait was bacon and fruits, and between June and October, the bait was shrimp (*Litopenaeus vannamei*) or fish (Engraulidae). To test the null hypothesis that trapping success was not affected by the use of bait, we performed a *t*-test.

Because the Águas Claras River had a flow too large to allow suitable trapping within the river, we sampled only its margins. From January to October 2006, except March and August, we placed 23 single-door wire-mesh live traps (48.4 × 15.2 × 15.2 cm; Tomahawk Live Trap Co.) along 700 m of both Águas Claras River margins. Between January and June, we baited the traps with a mixture of peanut butter, banana, oats, and bacon. In the following months, the bait used was the same used in the double-door traps set in the other rivers.

Animals captured were individually marked using numbered ear tags (model 1005-1; National Band and Tag Co., Newport, Kentucky). For each individual captured, we recorded trap station, sex, reproductive condition (pouch young and swollen mammae for females, and testes position for males), body measurements (weight and tail length), and age (by tooth-eruption sequence). Because the tooth-eruption pattern for *C. minimus* is not well known, age was based on the classification proposed by Rocha (2000) for *Didelphis* and *Philander*, 2 genera phylogenetically close to *Chironectes* (Jansa and Voss 2000). This classification divides the individuals into juveniles (with deciduous premolars), subadults (definitive premolars and 3 molars), and adults (definitive premolars and 4 molars). After recording data, we released each individual at the point of capture.

Population structure.—We assessed the population density of water opossums in the study site by dividing the minimum number known to be alive (Krebs 1966) by the extent of river that was effectively trapped, estimated by adding half of

a mean home length to each end of the stretch of river trapped (Otis et al. 1978). We used a chi-square test with Yates correction to test the null hypothesis that sex ratio was 1:1 for all individuals captured, and Mann–Whitney *U*-test to test the null hypotheses that recapture frequencies and body weights did not differ between sexes. To analyze the reproductive seasonality of water opossums, we 1st used a Spearman correlation to verify if the number of juveniles captured was correlated with the number of nonjuveniles captured, to test the hypothesis that temporal variation in the number of juveniles captured merely reflected the variation in sample sizes. Then we used circular statistics to test the null hypothesis that recruitment was randomly distributed throughout the year, by applying Rayleigh's test (program ORIANA 2.0; Kovach Computing Service, Anglesey, Wales) to the number of captured juveniles. All statistics followed Zar (1999).

Radiotagging and tracking methods.—We fitted individuals weighing more than 350 g with radiocollar transmitters with activity sensors (SOM-2380A; Wildlife Materials, Inc., Murphysboro, Illinois). Radiocollars weighed approximately 15 g, corresponding to up to 5% of the animal's weight, as recommended by Jacob and Rudran (2003). There were no obvious adverse effects of the radiocollars on the animals. We monitored individuals during the night, using the “homing-in on the animal” technique and a TR-4 handheld receiver (Telonics, Inc., Mesa, Arizona) and an RA-14K antenna (Telonics, Inc.). This technique consists of following the transmitter signal until visual contact with the animal tracked is achieved (White and Garrott 1990). A location also was recorded when it was possible to hear the radiosignal with the antenna disconnected from the receiver, following Lira et al. (2007). To prevent autocorrelated locations of the same individual, we obtained locations at intervals of at least 1 h (Endries and Adler 2005; Linders et al. 2004), which is enough time for an individual to traverse its entire home length. We recorded locations in the field using a Garmin-12 global positioning system handheld receiver (Garmin, Olathe, Kansas), in Universal Transverse Mercator (UTM) coordinates.

Spatial patterns.—To calculate the home length of individual water opossums, we plotted the locations obtained for each individual over a georeferenced map containing the river courses, using the program ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). Although many techniques are available to analyze how an individual uses the landscape (Harris et al. 1990; Jacob and Rudran 2003), none is suitable for animals that use linear habitats (Durbin 1998; Somers and Nel 2004). Therefore, we estimated home length of each individual as the distance in meters along the river course between the most widely separated locations of that individual (van der Ree and Bennett 2003). We used locations obtained both through radiotelemetry and trapping to estimate home lengths. We assessed static home-length overlaps for individuals that were tracked simultaneously (Dunn and Gipson 1977; Powell 2000; White and Garrott 1990). Overlaps were estimated by the proportion of the home length of individual A overlapped by that of individual B, and by the proportion of the home length of individual B overlapped by that of individual A (van der Ree and Bennett 2003).

Activity period.—Each radiotracking session started when the individual left its den, usually just after sunset, and lasted until sunrise, with the individual already back in its den. We obtained occasional diurnal fixes to check for possible diurnal activity. We detected activity as fluctuations in the transmitter's signal strength. For each individual, we grouped the number of active locations, beginning at the sunset, in 4 periods of 3 h. To test the null hypothesis that both sexes had the same activity pattern, we used the *G*-test. To test the null hypothesis that water opossums showed uniform activity over the night we also used the *G*-test, for both sexes separately.

RESULTS

With a trapping effort of 3,157 trap-nights, we obtained 47 captures of 21 individuals of *C. minimus*. Captures were concentrated in 3 streams: Dona Rosa River (22 captures), Floresta River (12), and tributary Ta 2 (11). In each of the tributaries Tf 1 and Tf 2 there was a single capture of a water opossum, and in tributaries Ta 1 and Ta 3 there were no captures. Between January and May 2005, there were no captures of water opossums. However, in the same period of the following year, we obtained 8 captures. During the 1st months of 2005, strong rains occurred that must have affected trappability. The trapping success increased 34% when baits were used, in relation to the previous period when no bait was used, but the difference was not significant ($t = -1.25$, $d.f. = 12$, $P = 0.24$). When bait was offered to trapped water opossums, they accepted only shrimp and fish.

Besides water opossums, we captured neotropical water rats (*Nectomys squamipes*, $n = 141$ captures) and the opossums *Didelphis aurita* ($n = 8$), *Metachirus nudicaudatus* ($n = 3$), and *Philander frenatus* ($n = 3$). The first 2 species were captured both in traps within the river and at the margin; the latter 2 were captured only in traps at the margin. We also found signs of the presence of the neotropical otter (*Lontra longicaudis*) in Águas Claras and Floresta rivers, the largest streams in the study area.

Population structure.—The estimated population density of water opossums ranged from 0 to 1.34 individuals/km of river in November 2005 and in July 2006, respectively. However, the variation in density did not follow a seasonal pattern (Fig. 2). Throughout the study, the sex ratio was strongly biased toward males. Out of 47 captures, 38 were of 18 males and 9 were of 3 females (individuals: χ^2 with Yates correction = 9.33, $d.f. = 1$, $P < 0.01$). However, there was no difference between sexes in the number of recaptures per individual (0–10 and 1–4 recaptures/individual of males and females, respectively; $U = 12$, $n_1 = 18$, $n_2 = 3$, $P = 0.13$). Adult weights did not differ between sexes (weights: 405–595 g and 395–420 g for males and females, respectively; $U = 12$, $n_1 = 10$, $n_2 = 2$, $P = 0.13$). The residence time (time between the 1st and last capture) for individuals captured in at least 2 trapping sessions ranged between 28 and 245 days.

The only 2 reproductive females were captured in August, September, and October (Fig. 2); on all occasions, they had 3 pouch young each. We captured juvenile individuals in

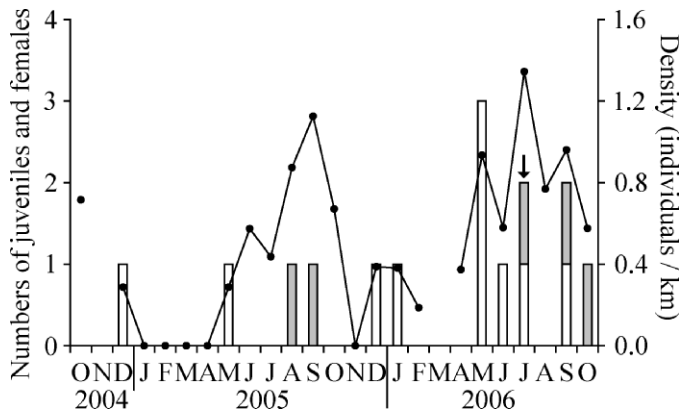


FIG. 2.—Variation in population density, juvenile recruitment, and presence of females in the population of *Chironectes minimus* in 2004–2006 in the Águas Claras River subbasin, southeastern Brazil. The line represents the density, in number of individuals per kilometer of river. White and gray bars represent the numbers of juveniles and females captured, respectively. The arrow indicates the only female that was not reproductive.

both dry and wet seasons (Fig. 2), and their number was not correlated with the number of nonjuveniles captured (Spearman correlation: $r_s = -0.04$, $P = 0.85$, $n = 24$). There was no evidence of seasonality on recruitment (length of the mean vector = 0.27; Rayleigh's $Z = 0.72$, $P = 0.50$, $n = 10$; Fig. 2).

Spatial patterns.—We radiocollared 10 adult individuals; however, only 3 males and 2 females could be monitored because of failure of the radiocollars of the other 5 individuals. We obtained 174 locations between July 2005 and October 2006 (Table 2), with a large variation in the number of locations (12–70) and in the length of tracking period (1–9 nights) of each individual. The home length was not related to sampling effort (Spearman correlation: $r_s = 0.10$, $P = 0.87$, $n = 5$) and an asymptote in the plot of home length against number of locations was not reached for any individual. The end of each tracking period occurred mainly because of transmitter failure, with the exception of female F1, which was found dead.

Home lengths varied between 844 and 3,388 m (Table 2) and, although males had home lengths up to 4 times larger than those of females, we could not test for statistical differences between sexes because of the small sample size. In the night that female F2 was tracked carrying pouch young, it was

restricted to the inner portion of its home length. Female F2 was the only one to use just 1 stream; all others used 3 or more streams (Table 2; Fig. 3). Small tributaries with riparian forest, closed canopy, stony substrate, and riffles were used by all individuals tracked, comprising 10.4–100% of the home length of each individual (Table 2). Only male M1 also used the lower stretch of the Águas Claras River, which presents pools, sandy substrate, and little remaining riparian forest. This stretch represented 10.8% of the home length of M1 (Table 2). The small tributary Ta 1 was never used by any radiotracked individual. This tributary was narrow, with a sandy substrate, and it dried during the dry season. The inactive dam on Águas Claras River was not a barrier to individuals M2 and M3, which used river stretches both upstream and downstream from the dam (Fig. 3). However, no individual tracked at Floresta River ever went upstream of the waterfall sequence in that river (Fig. 3).

At all locations when we sighted monitored individuals ($n = 28$ locations), water opossums were either in the river, getting out of the den, or at the margin (<1.0 m from the water). Only individuals M1 and F1 used a marshy area (approximately 1,000 m²) between the Águas Claras River and the small tributary Ta 3 (Fig. 3). Female F2 crossed 20 m by land until it reached its den near another tributary.

We located 21 dens of 9 individuals. Most dens ($n = 15$) were in holes formed by stones and tree roots by the river margin. The other dens were either in tree roots in the river margin ($n = 3$) or in holes in the ground in the riparian forest near the streams ($n = 3$). Male M2 used 7 dens during its tracking period, but it used mostly 2 dens located in each extreme of its home length (63.7% of its locations inside dens were at these 2).

When 2 or more individuals were tracked simultaneously, there was intersexual overlap ($n = 3$ occasions) and male–male overlap ($n = 1$ occasion) of home lengths. We simultaneously tracked individuals M1, M2, and F1 in 2005, and individuals M3 and F2 in 2006. Males had between 19.0% and 41.2% ($\bar{X} = 26.6\%$) of their home lengths overlapped by females, whereas females had between 44.2% and 49.3% ($\bar{X} = 46.6\%$) of their home lengths overlapped by males. Individuals M3 and F2 were located together and used dens close to each other. The same occurred with individuals M1 and F1, and they were located in the same den when the female was lactant. The male–male overlap between individuals M1 and M2 corre-

TABLE 2.—Home lengths of 5 individual *Chironectes minimus* estimated from trapping data (number of captures) and radiotracking data (number of locations) in the Águas Claras River subbasin, southeastern Brazil. M = male, F = female. River abbreviations: Ar = Águas Claras River, Fr = Floresta River, Dr = Dona Rosa River, Ta 2 and Ta 3 = Águas Claras River tributaries, Tf 1 = Floresta River tributary.

Individual	Tracking period	Rivers used	No. captures	No. locations	Home length (m)	Proportion of home length in small tributaries (%)
M1	July 2005–September 2005	Fr, Tf 1, Ar, Ta 2, and Ta 3	3	70	3,388	15.1
M2	August 2005–February 2006	Fr, Ar, Ta 2, and Dr	4	12	3,724	10.4
F1	August 2005–September 2005	Ar, Ta 2, and Ta 3	2	20	844	33.2
M3	April 2006–October 2006	Dr, Ar, and Ta 2	11	30	2,616	56.8
F2	May 2006–October 2006	Dr	5	42	1,126	100.0

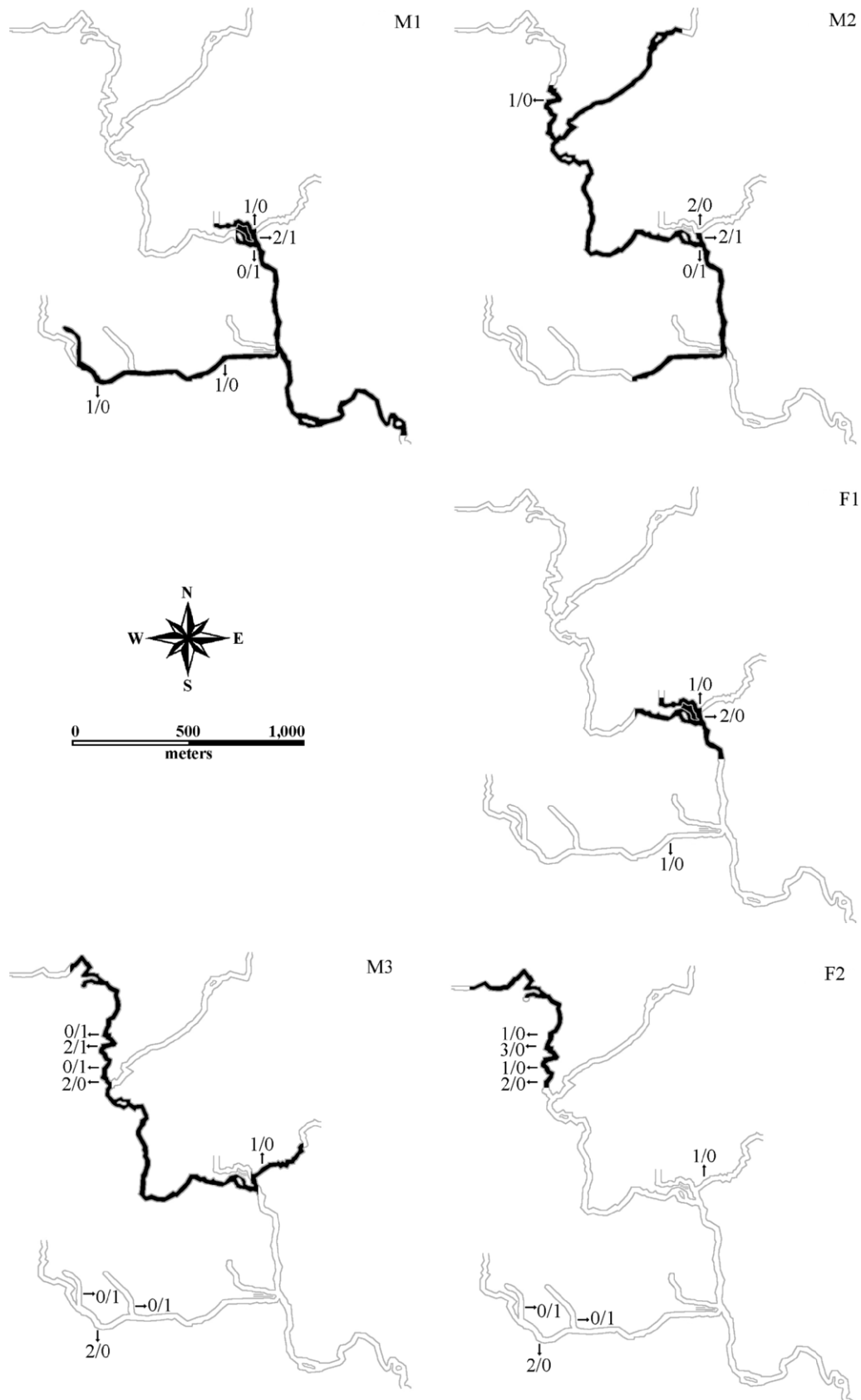


FIG. 3.—Home lengths (in black) of 5 individual *Chironectes minimus* tracked by capture-mark-recapture and radiotelemetry in rivers of the Águas Claras River subbasin, southeastern Brazil. M1, M2, and M3 were males, and F1 and F2 were females. Numbers in the figure are the numbers of other males and females captured in each trapping station during the period of radiotracking of each individual.

sponded to 27.5% and 66.4% of their home lengths, respectively. The spatial overlap between males also was shown by captures of different males in the same trap station or in adjacent trap stations within a single trapping session ($n = 5$ occasions).

Activity period.—Activity of water opossums was exclusively nocturnal. In all diurnal locations ($n = 20$), the individuals were inactive inside their dens. The activity period of all individuals began just after sunset, and we recorded higher activity in the 1st one-half of the night (Fig. 4). Activity patterns varied among males and females ($G = 12.76$, $d.f. = 3$, $P < 0.01$). Females were more active in the 1st period of the night ($G = 7.49$, $d.f. = 3$, $P < 0.01$) and there was a trend toward males being more active in the 1st and 2nd periods of the night ($G = 7.49$, $d.f. = 3$, $P = 0.06$). Only individuals M1 and M2 were active in the last period of the night (Fig. 4).

DISCUSSION

The variation in population density found for *C. minimus* in the study area seems to have been overestimated by a methodological artifact. The trapping method used (Bressiani and Graipel 2008), with traps placed in the river, suffers great influence from fluctuations in river flow. In periods of high rainfall, when the river levels are high, water opossums are seldom captured and therefore population levels are underestimated. We believe that the true population densities of water opossums are closer to those estimated for the months with higher numbers of captures, which means that true densities would be close to 1.34 water opossums/km of river in our study area.

Regarding reproductive seasonality, the number of lactating females captured was too small to allow firm conclusions. However, we captured juveniles throughout the year, showing no evidence of seasonality in recruitment. This agrees with previous anecdotal information for water opossums, according to which females with offspring were captured in all seasons (Mondolfi and Padilla 1958; Monteiro-Filho et al. 2006; Nowak 1991). These findings do not corroborate the hypothesis that water opossums breed seasonally, as do most neotropical marsupials (Fleming 1972; Fonseca and Kierulff 1989; O'Connell 1989; Quental et al. 2001). However, breeding throughout the year also has been recorded for didelphids in areas characterized by unpredictable (Streilein 1982) or nonseasonal (Julien-Laferrière and Atramentowicz 1990) climates, as well as in fragmented landscapes (Barros et al. 2008). In the case of water opossums, their environment can be described as unpredictable, because Atlantic Forest rivers present an unstable hydrological regimen and storms tend to happen rather stochastically (Mazzoni and Silva 2006). In the study area, rainfall in a given month can vary up to 3,000% between years (Mantovani 1997). In addition, fishes and prawns, the major prey types for water opossums (Medellín 1991; Mondolfi and Padilla 1958; Zetek 1930), reproduce throughout the year in Atlantic Forest rivers (fishes—Mazzoni et al. 2002; Mazzoni and Iglesias-Rios 2002; Menezes and Caramaschi 1994; prawns—Mossolin and Bueno 2002).

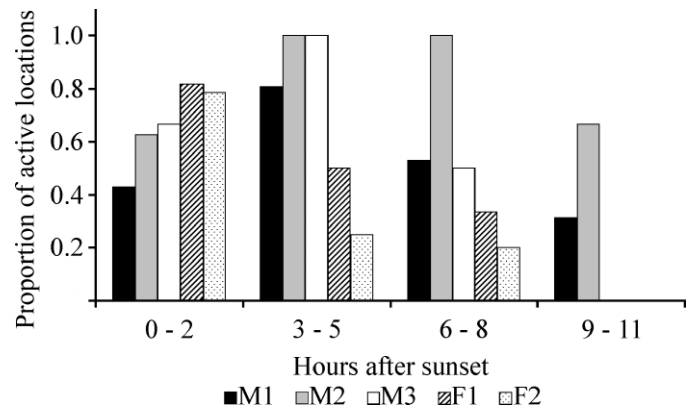


FIG. 4.—Activity pattern of *Chironectes minimus* (proportion of active locations in relation to the total number of locations, in each class of hours after sunset) in the Águas Claras River subbasin, southeastern Brazil. Number of locations of each individual in each class varied from 36 to 58 (for M1), from 6 to 9 (for M2), from 4 to 15 (for F1), from 1 to 29 (for M3), and from 10 to 22 (for F2).

Therefore, the lack of seasonality in the recruitment of water opossums seems consistent with the hypothesis that their reproductive patterns reflect mostly the specific characteristics of their aquatic environment. Additional data on reproductive patterns of water opossums in the wild are surely needed to corroborate this hypothesis.

We found a male-biased sex ratio for water opossums. Mondolfi and Padilla (1958) found a similar bias in the litters of 3 females. However, sex ratio biases are rare in mammalian populations (Seger and Stubblefield 2002). The sex ratio bias we found for water opossums may be a sampling artifact, reflecting differential trappability of sexes. As in many other marsupials (Bradshaw and Bradshaw 2002; Cáceres 2003; Fisher 2000; Lira et al. 2007; Pires and Fernandez 1999; Sunquist et al. 1987; van der Ree and Bennett 2003) and semiaquatic mammals (Durbin 1998; Ludwig 1984; Medina-Vogel et al. 2007; Somers and Neil 2004), males showed home ranges or home lengths larger than those of females. Home lengths of males were 4 times longer than those of females and overlapped extensively with each other. Thus, by travelling longer river sections, males are exposed to more traps than females; correspondingly, several males, but few females, travel each stream section. This pattern would make males easier to capture than females.

The spatial patterns presented by water opossums are similar to patterns found in many other didelphids, as well as in other small mammals, in which females have small, exclusive ranges, whereas males have larger, overlapping ranges (e.g. Magnusson et al. 1995; Ostfeld 1986, 1990; Pires and Fernandez 1999). In our study, it was not possible to determine whether females had exclusive home lengths, because on no occasion were 2 females radiotracked at the same time. However, on all occasions when a female was tracked, no other female was ever captured within its home length, which is consistent with the expected pattern. Therefore, the hypothesis that the specificity of water opossums' habitat would play the major role in shaping its spatial patterns found no support,

whereas mating systems seem to be a more important determinant of those patterns. In many species of mammals, the use of space by females reflects the abundance, distribution, and renewal rate of the resources, whereas the use of space by males reflects a strategy to maximize access to females (Ostfeld 1990). Because there is a cost for a female to maintain its territory, smaller and less-costly territories would be selected, whereas for males it would be advantageous to have a larger home length in order to overlap the territories of several females. This pattern, originally described for small mammals, seems to apply to many semiaquatic mammals as well (Johnson et al. 2000; Ludwig 1984; Medina-Vogel et al. 2007; Somers and Neil 2004). Such a spatial pattern is consistent with either a promiscuous or a polygynous mating system (Ostfeld 1990). Our finding that individual males were located near or using the same den as females bearing offspring is contradictory with the promiscuous mating system, and it may indicate either parental care or mate guarding by males.

The home lengths of water opossums are comparable to or larger than those of other small semiaquatic mammals. Neotropical water rats (*N. squamipes*; 200- to 430-g rodents) have home ranges from 0.3 to 1.6 ha and the longest distance between captures up a river course was 450 m (Ernest and Mares 1986). Water voles (*Arvicola terrestris*; 200–300 g) have home lengths between 50 and 162.5 m (Stoddart 1970). Giant African water shrews (*Potamogale velox*; 300–400 g) have home lengths between 500 and 1,000 m (Nowak 1991). Male aquatic tenrecs (*Limnogale mergulus*; 80–100 g) have home lengths of up to 1,000 m in a single night (Benstead et al. 2001). All comparisons between these studies and our own are hindered by methodological differences, but some patterns can be cautiously pointed out. The longer home lengths of water opossums as compared with neotropical water rats and water voles was expected, because carnivorous animals usually need greater ranges than herbivores or omnivores of similar mass (Sanderson 1966). Although it can be argued that the difference may reflect the larger body size of water opossums, in our study the mean adult body mass for this species was only 462.5 g, not much heavier than that of a large neotropical water rat. Home lengths of giant African water shrews and aquatic tenrecs are comparable to those of water opossums, especially taking in account the smaller size of aquatic tenrecs. This can be explained by the water shrew and the aquatic tenrec having high trophic level and high metabolic rates (Macdonald 1984).

The activity period of water opossums was strictly nocturnal, beginning after sunset and ending before sunrise. Mondolfi and Padilla (1958) and Zetek (1930) found similar activity periods in captivity. Only Marshall (1978) reported that a captive animal was occasionally active during the day. In the Águas Claras River subbasin, water opossums showed a unimodal activity pattern, being active mostly at the beginning of the night. This pattern does not corroborate the hypothesis that water opossums have a bimodal activity pattern as often found for mammals, in which the animal forages right after it starts activity and right before it returns to its den (Carrillo et al. 2002; Julien-Laferrière 1993; Valenzuela and Ceballos 2000). However, activity of water opossums was not homogeneously

distributed throughout the night, but was concentrated in its 1st hours. Thus, nocturnal censuses for water opossums should sample preferentially the first 6 h after sunset in order to maximize the probability of sightings.

The habitat used by water opossums in the Águas Claras River subbasin included mostly well-preserved rivers, with riparian vegetation, stony substrate, and clear, fast-flowing water, and small tributaries of the Águas Claras River and Floresta River. The use of the small and shady tributaries may be related to the occurrence of prawns, which prefer this kind of environment (Lobão et al. 1978). Handley (1976), Mondolfi and Padilla (1958), and Zetek (1930) captured water opossums in streams similar to the ones we studied, and Voss et al. (2001) captured individuals in small streams similar to the small tributaries Ta 2 and Tf 2. Mares et al. (1989) and Graipel et al. (2001, 2006) captured an individual each in riparian forests. Only Mondolfi and Padilla (1958) also captured individuals in rivers with different characteristics, that is, without riparian forest, and with sandy substrate and slow-moving, muddy water. If it is true that water opossums are more sensitive to river degradation than other semiaquatic mammals, such as neotropical otters and water rats, then the species can be a useful indicator of the preservation status of rivers.

In our study area, about 80% of the Águas Claras River subbasin is well preserved, but its final portion is highly degraded (Bidegain and Völcker 2003). With the degradation of areas of confluence of rivers, water opossums may be prevented from moving among adjacent subbasins, blocking gene flow and isolating populations in each subbasin. The situation is similar to fragmentation of terrestrial habitats, which prevents dispersal and accelerates the extinction rate of isolated populations (Fahrig 2003; Viveiros de Castro and Fernandez 2004). Other risks to water opossums are pollution and eutrophication of rivers and the introduction of exotic species, common processes in Brazil (Agostinho et al. 2005). Additionally, in some regions, water opossum fur is appreciated (Rocha-Mendes et al. 2005). Therefore, it is an important conservation concern to understand the factors that determine the occurrence of this unique species and the effects of river degradation on its populations.

RESUMO

Nós estudamos a estrutura populacional, os padrões espaciais e o período de atividade da cuíca d'água (*Chironectes minimus*), através de captura-marcação-recaptura e radio-telemetria, durante outubro de 2004 e outubro de 2006, em rios da Mata Atlântica no sudeste do Brasil. Nós testamos a hipótese de sazonalidade reprodutiva, o padrão mais comum para marsupiais neotropicais, utilizando o recrutamento de juvenis. A hipótese foi rejeitada, corroborando a hipótese alternativa, na qual a reprodução da cuíca d'água é melhor explicada pelas características de seu habitat e disponibilidade de presas. A razão sexual foi significativamente desviada para machos. As extensões de uso dos indivíduos de cuíca d'água variaram entre 844 e 3.724 m. Machos possuíram extensões de uso maiores que as fêmeas, e ocorreram sobreposições de

macho com macho e macho com fêmea. A maior extensão de uso dos machos pode explicar o desvio da razão sexual observado, uma vez que machos estão mais expostos às armadilhas. Todos os indivíduos utilizaram trechos de rios com vegetação ripária preservada, corredeiras e substrato pedregoso. Com relação aos padrões de atividade, a hipótese de que a atividade da cuíca d'água era homogeneamente distribuída pela noite foi rejeitada; a atividade começou logo após o pôr do sol e terminou antes do nascer do sol, com picos de atividade nas primeiras 6 horas da noite. Devido às alterações nas bacias hidrográficas, a cuíca d'água pode estar ameaçada pela redução do seu principal habitat, rios com corredeiras e substrato pedregoso.

ACKNOWLEDGMENTS

We thank colleagues at Laboratório de Ecologia e Conservação de Populações, Universidade Federal do Rio de Janeiro, for their help in fieldwork and discussions; M. and C. Amorim and A. Mantovani for allowing us to work within their Águas Claras Botanical Reserve; V. Bressiani for instructing us on his method to trap *Chironectes*; A. V. de Araujo, P. K. Lira, M. T. M. Széchy, É. Caramaschi, H. Bergallo, M. V. Vieira, and G. Mourão for their suggestions; R. Medellín and 3 anonymous referees for their useful comments on the manuscript; C. G. Penna for his enthusiastic support; Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (from the Brazilian Ministry of Environment) for allowing us to do research on *Chironectes* (license 060/05-RJ); Associação Mico-Leão Dourado for logistic support; and Fundação O Boticário de Proteção à Natureza, Critical Ecosystems Partnership Funding, Idea Wild, and Conselho Nacional de Desenvolvimento Científico e Tecnológico for funding.

LITERATURE CITED

- AGOSTINHO, A. A., S. M. THOMAZ, AND L. C. GOMES. 2005. Conservation of biodiversity of Brazil's inland waters. *Conservation Biology* 19:646–652.
- BAES, P. O., S. SÜHRING, AND G. CEBALLOS. 2002. Mamíferos de Uruguay. Pp. 551–565 in *Diversidad y conservación de los mamíferos neotropicales* (G. Ceballos and J. A. Simonetti, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Universidad Nacional Autónoma de México, México, D. F.
- BARROS, C. S., R. CROUZEILLES, AND F. A. S. FERNANDEZ. 2008. Reproduction of the opossums *Micoureus paraguayanus* and *Philander frenata* in a fragmented Atlantic Forest landscape in Brazil: is seasonal reproduction a general rule for neotropical marsupials? *Mammalian Biology* 73:463–467.
- BENSTEAD, J. P., K. H. BARNES, AND C. M. PRINGLE. 2001. Diet, activity patterns, foraging movement and responses to deforestation of the aquatic tenrec *Limnogle mer gulus* (Lipotyphla: Tenrecidae) in eastern Madagascar. *Journal of Zoology (London)* 254:119–129.
- BIDEGAIN, P. P., AND C. M. VÖLCKER. 2003. Bacias hidrográficas dos rios São João e das Ostras: águas, terras e conservação ambiental. www.riolagos.com.br/calsj/publicacoes.htm. Accessed 10 January 2005.
- BRADSHAW, S. D., AND F. J. BRADSHAW. 2002. Short-term movements and habitat use of the marsupial honey possum (*Tarsipes rostratus*). *Journal of Zoology (London)* 258:343–348.
- BRESSIANI, V. B., AND M. E. GRAIPEL. 2008. Comparação de métodos para captura da cuíca d'água, *Chironectes minimus* (Zimmerman, 1780) (Mammalia, Didelphidae) no sul do Brasil. *Mastozoologia Tropical* 15:33–39.
- CÁCERES, N. C. 2003. Use of the space by the opossum *Didelphis aurita* Wied-Newied (Mammalia, Marsupialia) in a mixed forest fragment of southern Brazil. *Revista Brasileira de Zoologia* 20: 315–322.
- CARRILLO, E., J. C. SAENZ, AND T. K. FULLER. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. *Biological Conservation* 108:317–324.
- CEBALLOS, G., AND D. NAVARRO L. 1991. Diversity and conservation of Mexican mammals. Pp. 167–198 in *Latin American mammalogy—history, biodiversity, and conservation* (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman.
- DUNN, J. E., AND P. S. GIPSON. 1977. Analysis of radio telemetry data in studies of home range. *Biometrics* 33:85–101.
- DURBIN, L. S. 1998. Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. *Journal of Zoology (London)* 245:85–92.
- EMMONS, L. H., AND F. FEER. 1997. Neotropical rainforest mammals: a field guide. University of Chicago Press, Chicago, Illinois.
- ENDRIES, M. J., AND G. H. ADLER. 2005. Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), in Panama. *Journal of Zoology (London)* 265:147–155.
- ENGSTROM, M. D., AND B. K. LIM. 2002. Mamíferos de Guyana. Pp. 329–375 in *Diversidad y conservación de los mamíferos neotropicales* (G. Ceballos and J. A. Simonetti, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Universidad Nacional Autónoma de México, México, D. F.
- ERNEST, K. A., AND M. A. MARES. 1986. Ecology of *Nectomys squamipes*, the neotropical water rat, in central Brazil: home range, habitat selection, reproduction and behaviour. *Journal of Zoology (London)* 210:599–612.
- FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34:487–515.
- FISHER, D. O. 2000. Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. *Journal of Applied Ecology* 37:660–671.
- FLEMING, T. H. 1972. Aspects of the population dynamics of three species of opossums in the Panama Canal Zone. *Journal of Mammalogy* 53:619–622.
- FONSECA, G. A. B., AND M. C. KIERULFF. 1989. Biology and natural history of Brazilian Atlantic Forest small mammals. *Bulletin of Florida State Museum, Biological Sciences* 34:99–152.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GRAIPEL, M. E., J. J. CHEREM, E. M. A. MONTEIRO-FILHO, AND L. GLOCK. 2006. Dinâmica populacional de marsupiais e roedores no Parque Municipal da Lagoa do Peri, Ilha de Santa Catarina, sul do Brasil. *Mastozoologia Neotropical* 13:31–49.
- GRAIPEL, M. E., J. J. CHEREM, AND A. XIMENEZ. 2001. Mamíferos terrestres não voadores da Ilha de Santa Catarina, sul do Brasil. *Biotemas* 14:109–140.
- HANDLEY, C. O., JR. 1966. Checklist of the mammals of Panama. Pp. 753–795 in *Ectoparasites of Panama* (V. J. Jipton and R. L. Wenzel, eds.). Field Museum of Natural History, Chicago, Illinois.
- HANDLEY, C. O., JR. 1976. Mammals of the Smithsonian Venezuelan Project. *Brigham Young University Science Bulletin—Biological Series* 20:1–89.
- HARRIS, S., W. J. CRESSWELL, P. G. FORDE, W. J. TREWHELLA, T. WOOLLARD, AND S. WRAY. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97–123.

- JACOB, A. A., AND R. RUDRAN. 2003. Radiotelemetria em estudos populacionais. Pp. 285–342 in *Manejo e conservação da vida silvestre no Brasil* (C. B. Valladares-Padua, R. E. Bodmer, and L. Cullen, Jr., eds.). Editora da Universidade Federal do Paraná, Curitiba, Brazil.
- JANSA, S. A., AND R. S. VOSS. 2000. Phylogenetic studies on didelphid marsupials I. Introduction and preliminary results from nuclear IRBP gene sequences. *Journal of Mammalian Evolution* 7:43–77.
- JOHNSON, D. D. P., D. W. MACDONALD, AND A. J. DICKMAN. 2000. An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Review* 30:171–196.
- JULIEN-LAFERRIÈRE, D. 1993. Radio-tracking observations on ranging and foraging patterns by kinkajous (*Potos flavus*) in French Guiana. *Journal of Tropical Ecology* 9:19–32.
- JULIEN-LAFERRIÈRE, D., AND M. ATRAMENTOWICZ. 1990. Feeding and reproduction of three didelphid marsupials in two neotropical forests (French Guiana). *Biotropica* 22:404–415.
- KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36:239–273.
- LINDERS, M. J., S. D. WEST, AND W. M. V. HAEGEN. 2004. Seasonal variability in the use of space by western gray squirrels in southcentral Washington. *Journal of Mammalogy* 85:511–516.
- LIRA, P. K., F. A. S. FERNANDEZ, H. S. A. CARLOS, AND P. L. CURZIO. 2007. Use of a fragmented landscape by three species of opossum in south-eastern Brazil. *Journal of Tropical Ecology* 23:427–435.
- LOBÃO, V. L., P. SAWAYA, AND L. E. SANTOS. 1978. Influência da temperatura, precipitação pluviométrica e insolação na reprodução de *Macrobrachium holthuisi* Genofre and Lobão, 1976 (Crustácea, Decapoda). *Boletim do Instituto de Pesca* 5:109–118.
- LUDWIG, D. R. 1984. *Microtus richardsonii*. *Mammalian Species* 223:1–6.
- MACDONALD, D. (ED.). 1984. The encyclopedia of mammals. Andromeda Oxford, Abingdon, United Kingdom.
- MAGNUSSON, W. E., A. L. FRANCISCO, AND T. M. SANAIOTTI. 1995. Home-range size and territoriality in *Bolomys lasiurus* (Rodentia: Muridae) in an Amazonian savanna. *Journal of Tropical Ecology* 11:179–188.
- MANTOVANI, A. 1997. Considerações iniciais sobre a conquista do hábito epífítico na família Araceae. M.S. thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
- MARES, M. A., J. K. BRAUN, AND D. GETTINGER. 1989. Observations on the distribution and ecology of the mammals of the Cerrado grasslands of central Brazil. *Annals of Carnegie Museum* 25:1–60.
- MARSHALL, L. G. 1978. *Chironectes minimus*. *Mammalian Species* 109:1–6.
- MAZZONI, R., E. P. CARAMASCHI, AND N. FENERICH-VERANI. 2002. Reproductive biology of a Characidiinae (Osteichthyes, Characidae) from the Ubatiba River, Maricá-RJ. *Brazilian Journal of Biology* 62:487–494.
- MAZZONI, R., AND R. IGLESIAS-RIOS. 2002. Environmentally related life history variations in *Geophagus brasiliensis*. *Journal of Fish Biology* 61:1606–1618.
- MAZZONI, R., AND A. P. F. SILVA. 2006. Aspectos da história de vida de *Bryconamericus microcephalus* (Miranda Ribeiro) (Characiformes, Characidae) de um riacho costeiro de Mata Atlântica, Ilha Grande, Rio de Janeiro, Brasil. *Revista Brasileira de Zoologia* 23:228–233.
- MEDELLÍN, R. A. 1991. Ecomorfología del cráneo de cinco didélfos: tendencias, divergencias e implicaciones. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Zoología* 62:269–286.
- MEDELLÍN, R. A. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, México. *Conservation Biology* 8:780–799.
- MEDINA-VOGEL, G., F. BOHER, G. FLORES, A. SANTIBAÑEZ, AND C. SOTO-AZAT. 2007. Spacing behavior of marine otters (*Lontra felina*) in relation to land refuges and fishery waste in central Chile. *Journal of Mammalogy* 88:487–494.
- MENEZES, M. S., AND E. P. CARAMASCHI. 1994. Características reprodutivas de *Hypostomus* grupo *H. punctatus* no rio Ubatiba, Maricá, RJ (Osteichthyes, Siluriformes). *Revista Brasileira de Biologia* 54:503–513.
- MONDOLFI, E., AND G. M. PADILLA. 1958. Contribución al conocimiento del "perrito de agua" (*Chironectes minimus* Zimmermann). *Memoria de la Sociedad de Ciencias Naturales La Salle* 17: 141–155.
- MONTEIRO-FILHO, E. L. A., M. E. GRAIPEL, AND N. C. CÁCERES. 2006. História natural da cuíca-d'água *Chironectes minimus* e da cuíca-marrom *Lutreolina craussicaudata*. Pp. 287–295 in *Os marsupiais do Brasil—biologia, ecologia e conservação* (N. C. Cáceres and E. L. A. Monteiro-Filho, eds.). Editora Universidade Federal do Mato Grosso do Sul, Campo Grande, Brazil.
- MORAES JUNIOR, E. A., AND A. G. CHIARELLO. 2005. A radio tracking study of home range and movements of the marsupial *Micoureus demerarae* (Thomas) (Mammalia, Didelphidae) in the Atlantic forest of south-eastern Brazil. *Revista Brasileira de Zoologia* 22: 85–91.
- MOSSOLIN, E. C., AND S. L. S. BUENO. 2002. Reproductive biology of *Macrobrachium olfersi* (Decapoda, Palaemonidae) in São Sebastião, Brazil. *Journal of Crustacean Biology* 22:367–376.
- NOWAK, R. M. 1991. Walker's mammals of the world. 5th ed. Johns Hopkins University Press, Baltimore, Maryland.
- O'CONNELL, M. A. 1989. Population dynamics of neotropical small mammals in seasonal habitats. *Journal of Mammalogy* 70:532–548.
- OJEDA, R. A., C. E. BORCHI, AND V. G. ROIG. 2002. Mamíferos de Argentina. Pp. 23–63 in *Diversidad y conservación de los mamíferos neotropicales* (G. Ceballos and J. A. Simonetti, eds.). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Universidad Nacional Autónoma de México, México, D. F.
- OSTFELD, R. S. 1986. Territoriality and mating system of California voles. *Journal of Animal Ecology* 55:691–706.
- OSTFELD, R. S. 1990. The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* 5:411–415.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:1–135.
- PIRES, A. S., AND F. A. S. FERNANDEZ. 1999. Use of space by the marsupial *Micoureus demerarae* in small Atlantic Forest fragments in south-eastern Brazil. *Journal of Tropical Biology* 15:279–290.
- POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in *Research techniques in animal ecology: controversies and consequences* (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.
- QUENTAL, T. B., F. A. S. FERNANDEZ, A. T. CORRÊA, AND F. S. ROCHA. 2001. Population dynamics of the marsupial *Micoureus demerarae* in small fragments of Atlantic Forest in Brazil. *Journal of Tropical Biology* 17:339–352.
- ROCHA, F. S. 2000. Ecologia reprodutiva de pequenos mamíferos (com ênfase no marsupial *Micoureus demerarae*) em fragmentos de Mata Atlântica no sudeste do Brasil. M.S. thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
- ROCHA-MENDES, F., S. B. MIKICH, G. V. BIANCONI, AND W. A. PEDRO. 2005. Mamíferos do município de Fênix, Paraná, Brasil: etnozootologia e conservação. *Revista Brasileira de Zoologia* 22:991–1002.

- SANDERSON, G. C. 1966. The study of mammal movements—a review. *Journal of Wildlife Management* 30:215–235.
- SEGER, J., AND W. STUBBLEFIELD. 2002. Models of sex ratio evolution. Pp. 2–25 in *Sex ratios—concepts and research methods* (I. C. W. Hardy, ed.). Cambridge University Press, Cambridge, United Kingdom.
- SOMERS, M. J., AND J. A. J. NEL. 2004. Movement patterns and home range of Cape clawless otters (*Aonyx capensis*), affected by high food density patches. *Journal of Zoology* (London) 262:91–98.
- STODDART, D. M. 1970. Individual range, dispersion and dispersal in a population of water voles (*Arvicola terrestris* (L.)). *Journal of Animal Ecology* 39:403–425.
- STREILEIN, D. E. 1982. The ecology of small mammals in the semi-arid Brazilian Caatinga. III. Reproduction biology and population ecology. *Annals of Carnegie Museum* 51:251–269.
- SUNQUIST, M. E., S. N. AUSTAD, AND F. SUNQUIST. 1987. Movement patterns and home range in the common opossum (*Didelphis marsupialis*). *Journal of Mammalogy* 68:173–176.
- TERBORGH, J. W., J. W. FITZPATRICK, AND L. EMMONS. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana: Zoology* (New Series) 21:1–29.
- TYNDALE-BISCOE, C. H., AND R. B. MACKENZIE. 1976. Reproduction in *Didelphis marsupialis* and *D. albiventris* in Colombia. *Journal of Mammalogy* 57:249–265.
- VALENZUELA, D., AND G. CEBALLOS. 2000. Habitat selection, home range, and activity of the white-nosed coati (*Nasua narica*) in a Mexican tropical dry forest. *Journal of Mammalogy* 81:810–819.
- VAN DER REE, R., AND A. BENNETT. 2003. Home range of the squirrel glider (*Petaurus norfolcensis*) in a network of remnant linear habitats. *Journal of Zoology* (London) 259:327–336.
- VIVEIROS DE CASTRO, E. B., AND F. A. S. FERNANDEZ. 2004. Determinants of differential extinction vulnerabilities of small mammals in Atlantic Forest fragments in Brazil. *Biological Conservation* 119:73–80.
- VOSS, R. S., D. P. LUNDE, AND N. B. SIMMONS. 2001. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna, part 2—nonvolant species. *Bulletin of the American Museum of Natural History* 263:1–236.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- ZAR, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey.
- ZETEK, J. 1930. The water opossum—*Chironectes panamensis* Goldman. *Journal of Mammalogy* 11:470–471.

Submitted 7 December 2007. Accepted 25 May 2008.

Associate Editor was Rodrigo A. Medellín.