Wildlife Research http://dx.doi.org/10.1071/WR11176

First telemetry study of bush dogs: home range, activity and habitat selection

Edson de Souza Lima^{A,B,G,I}, Karen E. DeMatteo^{C,D}, Rodrigo S. P. Jorge^{B,E,G}, Maria Luisa S. P. Jorge^{F,G}, Julio Cesar Dalponte^G, Herson Souza Lima^A and Stuart A. Klorfine^H

^AUNEMAT, Departamento de Ciência Biológicas, Nova Xavantina, MT, Brazil.

^BCentro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade (CENAP/ICMBio), Atibaia, SP, Brazil.

^CUniversity of Missouri-St Louis, Department of Biology, St Louis, Missouri, USA.

^DUniversity of Missouri-Columbia, Division of Biological Sciences, Columbia, Missouri, USA.

^EInstituto Brasileiro para a Medicina da Conservação – TRÍADE, Recife, PE, Brazil.

^FInstituto de Biociências, Departamento de Ecologia, UNESP – Campus Rio Claro, Rio Claro, SP, Brazil.

^GInstituto para a Conservação dos Carnivoros Neotropicais/Pro-Carnívoros, Atibaia, SP, Brazil.

^HUniversity of Washington, Department of Professional and Continuing Education, Seattle, Washington, USA.

¹Corresponding author. Email: edsolima@hotmail.com

Abstract

Context. The bush dog (*Speothos venaticus*) is difficult to observe, capture, and study. To date, indirect evidence and opportunistic field observations have been the primary sources of information about the species' ecology. Field data are urgently needed to clarify the species' ecological requirements, behaviour and movement patterns.

Aims. The present study uses 13 months of telemetry data from a group of bush dogs to begin to address questions about area requirements, habitat preferences and movement patterns of this difficult-to-study species.

Methods. We tracked a group of bush dogs (two adults, one juvenile, four young) in an area of intact and altered Cerrado (woodland–savanna biome) in eastern Mato Grosso, Brazil (Nova Xavantina District).

Key results. The group had a total home range of 140 km^2 (fixed kernel 95%), with smaller seasonal 'subareas' (areas used for 1–2 months before moving to another area, with repetition of some areas over time) and demonstrated a preference for native habitats.

Conclusions. The bush dog's home range is greater than that of other canids of the same size, even correcting for group size. Patterns of seasonal movement are also different from what has been observed in other South American canids.

Implications. From our observations in the Brazilian savanna, bush dogs need large tracks of native habitat for their long-term persistence. Although the present study is based on a single pack, it is highly relevant for bush dog conservation because it provides novel information on the species' spatial requirements and habitat preferences.

Additional keywords: canid, habitat use, social living, Speothos venaticus.

Received 18 October 2011, accepted 17 May 2012, published online 1 August 2012

Introduction

The bush dog (*Speothos venaticus*), a highly social South American canid, is considered *Threatened* by the Brazilian Ministry of Environment (MMA 2003) and *Near Threatened* by the IUCN (Zuercher *et al.* 2008). They hunt in groups of 2–10 individuals (Aquino and Puertas 1997; Barnett *et al.* 2001; Beisiegel and Zuercher 2005) for a variety of small- and medium-sized prey (Zuercher *et al.* 2005; DeMatteo 2008; Lima *et al.* 2009). The species appears to be naturally rare (Beisiegel and Zuercher 2005; DeMatteo 2008) and difficult to observe, frequently hiding under low vegetation (Lima *et al.* 2009). Most information about bush dogs, including behaviour

and reproduction, comes from captive animals (Kleiman 1972; Porton *et al.* 1987; Montalli and Kelly 1989; DeMatteo *et al.* 2006). Knowledge of its ecology has been primarily gained through indirect evidence (scats and footprints, DeMatteo *et al.* 2004; Zuercher *et al.* 2005; Lima *et al.* 2009; interviews, DeMatteo 2008; DeMatteo and Loiselle 2008; detection dogs, DeMatteo *et al.* 2009) or opportunistic field observations (Peres 1991; Beisiegel 2009; Oliveira 2009; Michalski 2010).

Systematic field data are urgently needed to clarify the species' ecological requirements, behaviour and movement patterns. For example, bush dogs are associated with a variety of intact (fields, savannas, forest and flooded areas, Zuercher *et al.*

2005; DeMatteo 2008; Lima *et al.* 2009; Oliveira 2009) and modified habitats (DeMatteo and Loiselle 2008; Oliveira 2009); however, it is unknown whether their ecological requirements vary within those. In addition, although estimates of homerange size exist, they vary tremendously (4.56–150 km²; Silveira *et al.* 1998; Van Humbeck and Pérez 1998; Beisiegel 1999) and are indirectly inferred from body size and diet. The present study uses 13 months of telemetry data from a group of bush dogs to begin to address questions related to area requirements, habitat preferences and movement patterns.

Materials and methods

Study area

The study was conducted between the São Rafael and Índio Rivers, ~27 km north of the municipal district of Nova Xavantina (between 14.365°S, 52.554°W and 14.549°S, 52.354°W). Nova Xavantina is located in the state of Mato Grosso in the eastern basin of the Mortes River that flows into the Araguaia River and has an economy based on agriculture and cattle raising. Since 1970, a large portion of its native vegetation has been cleared for cultivation; however, some native vegetation still remains, especially where the terrain is elevated, because local ranchers lack equipment to clear it. In the study area, elevation varies and Cerrado (woodland-savanna biome) is the typical native vegetation. The soils are predominantly Red-Yellow Dystrophic Oxisols, with a moderate horizon, medium texture, with or without lateritic concretions (MME 1981). The climate is characterised as type Aw in the Köppen system, with average annual rainfall of 1600 mm (Nimer 1989), and two distinct seasons, namely, wet (October-March) and dry (April-September).

Animal live-trapping

Initial capture attempts were made with leg-hold (Soft Catch Spring Trap, Forestry Suppliers, Jackson, Mississippi, USA) and cage (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) traps in areas with high potential for presence of bush dogs, such as locations where groups were observed by local ranchers. Additionally, we opportunistically surveyed burrows looking for fresh signs of recent burrow activity by bush dogs (e.g. scat, tracks). When an active burrow was located, its entrance was hand-excavated until the animals were within ~1.5 m and could be captured with a restraining pole lasso. Once restrained, adults were removed from the burrow and sedated with a 5 mg kg⁻¹ intramuscular injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil 50, Virbac, France).

Each adult was sedated and fit with a radio-collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) that had a design specific for the species (DeMatteo and Kochanny 2004), weight of 65 g, VHF frequency of 164 MHz and an activity switch. After a full recovery from sedation, individuals were released into the burrow system where they were captured. Individuals were noted to remain in the burrow until the following day when their daily movement patterns resumed. All handling of live animals was approved by the Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renováveis (Licence 02027.002452/2004-95).

Monitoring and activity pattern

For 13 months (from 13 July 2004 to 13 August 2005), radiocollared animals were monitored on the ground with a TR4 radio receiver and RA-14 H-directional antenna (Telonics, Mesa, Arizona, USA). Even though two individuals were radiocollared, they were considered a single unit for all movement analyses because they typically travelled together. Twenty-fourhour monitoring sessions took place 3-4 days per week, with an average of 13.9 ± 2.9 sampling days per month. During each monitoring session, locations were taken every 3 h, so as to ensure an unbiased sampling of overall space use (Aebischer et al. 1993). All coordinates were recorded with a Rino 110 GPS (Garmin, Olathe, Kansas, USA). The location of each individual was determined either directly (recording the point where the group was determined to be present, such as resting in a den site) or by triangulation (Jacob and Rudran 2003). Estimated location by triangulation was determined using geographic coordinates and respective angular direction of two points of high-quality signal and visual angle of ~90° to each other relative to the animal. Magnetic corrections were made in all directions for each point with the program GPS TrackMaker 12.0 (http:// www.gpstm.com/eng/contract.htm, verified 1 December 2010). Activity pattern of each marked individual was monitored every 15 min, during 24-h monitoring sessions by listening to the activity switch on the radio-collar and scoring as either active (moving) or inactive (at rest).

Home range and habitat use

The home-range size of the monitored animals was determined with fixed kernel 95% (FK 95%; Worton 1987, 1989), using the Animal Movement Extension of ArcView 3.1 (ESRI, Redlands, California, USA). FK is considered to be a more accurate estimator of the area an animal uses during its normal activities (Worton 1989). Although home-range estimates can be affected by sample size (Harris et al. 1990; Seaman et al. 1999; Börger et al. 2006; Wauters et al. 2007), our FK estimates were calculated with >30 locations, the recommended minimum, and most with \geq 50 locations, the preferred minimum (Seaman et al. 1999). The area (km²) used by a single animal in the monitored group was calculated by dividing the home-range size for the group by the weighted average number of individuals in the group during the monitoring period. This calculation, when compared with data collected in future field studies, can be used to understand how group size affects the species' spatial requirements.

To evaluate whether habitat use was random in relation to availability, proportions of use were generated from an utilisation distribution (UD) instead of the direct locations, because the UD quantifies use within the home range with a probabilistic and continuous metric and eliminates concerns about independence between points (Marzluff *et al.* 2004; Millspaugh *et al.* 2006). We also calculated the proportion of resources from a vegetation grid, which correlates, cell-by-cell, with the grid generated for the UD.

The vegetation grid was derived from a colour composition, created with Spring 4.3.3. (Ministério da Ciência e Tecnologia (MCT) – Instituto de Pesquisas Espaciais (INPE)), of a 2004 CBERS image (INPE), using ArcView 3.2 (Esri). By using an

image from 2004, versus a more recent image, we were able to accurately access habitat use relative to availability for the period the group was monitored. The image was classified into the following three vegetation categories: savanna (all native grassland formations, including swampy grassland, grassland, shrub grassland, grassland with scattered short trees, Cerrado *sensu stricto* and dense Cerrado), forest (gallery forest, dry forest, valley forest and Cerradão) and cultivated areas (pasture and agricultural crops).

We then created a resource utilisation function (RUF) with the Focal Patch extension of ArcView 3.2 (Marzluff *et al.* 2004; Millspaugh *et al.* 2006). The RUF expresses the correlation between the UD (group's relative use of space within its home range) and the three vegetation categories. The program extension creates a table, with use and vegetation values for each cell of the home-range grid. The use values vary from 1 to 99 (1 being the lowest use) and the vegetation categories from 1 to 3 (each being a single vegetation category). We separated relative use into two (low *v*. high – 50% of the cells each) and three categories (low, medium, and high – 33% of the cells each) and tested for statistically significant differences in proportion of use and availability per vegetation type with a G-test.

Movement patterns

To evaluate bush-dog movement patterns, we considered the following three possibilities: (1) nomadic, if the group never repeated the use of a single area and constantly moved to a different area; (2) semi-nomadic, if the group used an area for a short period (1-2 months) before moving to another area, with the group repeating previous sites over time and (3) territorial, if the group repeatedly used the same overall area. All burrows used by the monitored group were geo-referenced to evaluate the use and reuse of individual burrows.

Results

Animal live-trapping

On 13 July 2004, a group of three individuals (a pair of adults and a juvenile about 6 months of age) was captured inside a giant armadillo (*Priodontes maximus*) burrow. Radio-collars were placed on the two adults. On 20 November 2004, the group grew in size with the birth of four pups (two males, one female and one unknown). On 20 December 2004, the juvenile (approximately 1-year old) disappeared from the group and was never found. Approximately 1 week later, the pup of unknown sex disappeared and was assumed deceased. Two of the three remaining pups (one female and one male) were noted absent from the group in February 2005 and April 2005, respectively.

In March 2005, the adult female began to lose hair, evolving to a severe generalised hair loss. In April 2005, both males (adult and 7-month juvenile) also started to lose hair, progressing more gradually to a severe generalised hair loss, similar to the female, with the loss more apparent in the adult male. The female died on 13 June 2005 and both males died ~13 August 2005.

Monitoring and activity pattern

During the 13 months when the group was monitored, a total of 1002 point locations was recorded, with 860 (85.8%) as exact

locations and 142 (14.2%) as triangulations, and estimated distance to the animal of ~300 m. In total, 20 211 activity records were collected (adult male = 10 770 and adult female = 9441). An average of 112 ± 8.5 records (range: 91–125) and 98 ± 6.5 records (range: 82–105) were collected in each monitoring session for the male and female, respectively. Both animals were primarily active during early morning (0600 hours to 0700 hours) and night (2000 hours to 2300 hours), with a higher proportion of activity during the morning than the night period (Fig. 1).

Home range and habitat use

The home-range estimate using 95% FK (n=1002) was 140.86 km². The average area used per individual in the monitored group was 40 km² (weighted average number of individuals in the group=3.5) and ranged from 20 km² (140 km² per 7 individuals) to 47 km² (140 km² per 3 individuals). The 95% minimum convex polygon estimate for the entire period was 160.97 km² and not statistically different from 95% FK ($\chi^2 = 1.272$, P = 0.260).

Focal patch analysis (ArcView 3.2) generated 6656 cells, each of them with a correspondent intensity-of-use value (going from 1 to 99, based on the FK home-range estimate) and a resource categorical-value (based on the vegetation grid with 1 = cultivated land, 2 = forest, and 3 = savanna). Cell size was 130 m² and it was determined in the FK analysis of home range, through a least-square cross-validation. The vegetation grid was classified as 14% cultivated land (n=961), 14% forest (n=930) and 72% savanna (n=4765).

In both analyses (two and three categories), habitat use was not proportional to habitat availability for two habitat types, namely, cultivated lands and savanna (Fig. 2). In cultivated lands, there was a higher-than-expected proportion of low-use cells and a lower-than-expected proportion of medium- and highuse cells ($G_{2cat} = 212.28$, d.f. = 1, P < 0.001; $G_{3cat} = 232.89$, d.f. = 2, P < 0.001). The opposite pattern was found in savanna habitat, with a lower-than-expected proportion of low-use cells and a higher-than-expected proportion of medium- and high-use cells ($G_{2cat} = 51.22$, d.f. = 1, P < 0.001; $G_{3cat} = 40.76$, d.f. = 2, P < 0.001). In the forest habitat, results diverged depending on the number of categories. With two categories (low and high use), results were marginally significant, with low-use cells marginally more frequent than was expected (O/E = 1.06, or 6% more, $G_{2cat}=3.01$, d.f.=1, P=0.08). With three categories (low, medium and high), the marginal significance disappeared $(G_{3cat}=0.135, d.f.=2, P=0.935).$

Movement patterns

During 12 of the 13 months that the group was monitored, it covered five separate sites within the larger home range ('subareas' or 'temporary areas'; Table 1, Fig. 3). The 'subareas' were defined on the basis of the concentration of locations in a given area for periods of 1-3 months. The overall movement pattern did not involve the group repeatedly covering the entire area within few weeks (territorial), nor did it involve the group moving from one area to another without ever repeating the same area (nomadic). Instead, the group stayed for 1-2 months in one area, moved to another, stayed

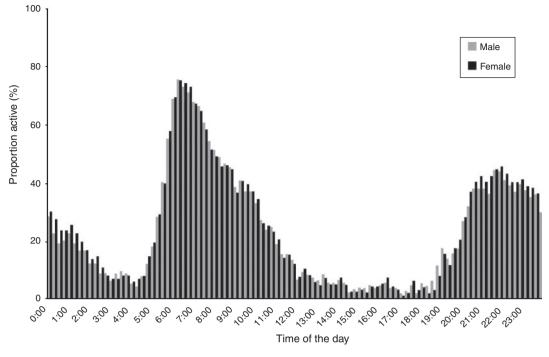


Fig. 1. Daily activity patterns for both adult bush dogs where records were collected every 15 min during a 24-h monitoring session. The male (grey) had an average of 112 ± 8.5 records each 24-h monitoring session and the female (black) had an average of 98 ± 6.5 records each 24-h monitoring session.

for another 1–2 months, and either returned to a previous area, or moved to another adjacent area, staying for another 1–2-month period, and moving again, on a semi-nomadic movement pattern (Fig. 3). The average 95% FK per 'subarea' was $17.9 \pm 12.8 \text{ km}^2$ (Table 2).

It was very rare for bush dogs to use a den for more than a single day or to return to a den that they had previously used. Of the 150 geo-referenced lairs that the group used, 147 were used once, one was used twice and two were used three times. The reused dens were associated with reproduction, specifically mating and birthing. The group used dens of three armadillo species (nine-banded armadillo/Dasypus novemcinctus, giant armadillo/*Priodontes* maximus, six-banded armadillo/ Euphractus sexcinctus) and was observed digging and cleaning out abandoned armadillo dens, using them as a night shelter, and then leaving the burrow the following morning. Although the entire group was typically found in a single den, there were exceptions when the pups were 2-3 months of age, namely, the adults would leave them in a separate den during the day and retrieve them when starting their night-time activity. During the day, the pups were unprotected and free to exit the den, which could explain some of the losses of young (e.g. predation).

Discussion

Home-range estimate $(95\% \text{ FK} = 140.86 \text{ km}^2)$ for the group of bush dogs (three to seven individuals) monitored in the present study is very close to indirect estimates of bush-dog home ranges $(150.31 \text{ km}^2 \text{ per a group of six animals; Beisiegel 1999})$. When the bush-dog home range is compared with other

sympatric South American canids, which differ in degree of sociality (solitary or live in pairs) and diet (omnivorous), bushdog home range is dramatically higher, irrespective of body size, e.g. maned wolf (Chrysocyon brachyurus) = 67.69 km² (95% MCP) or 80.18 km² (FK; Jácomo et al. 2009), crabeating fox (*Cerdocyon thous*) = 5.32 km^2 (restricted polygon (RP); Macdonald and Courtenay 1996) and hoary fox (Pseudalopex vetulus)=456 ha (95% RP; Courtenay et al. 2006). It is possible that the bush dog's extensive home range is associated with its sociality (group living) and restricted diet (hyper-carnivorous - Zuercher et al. 2005). Although additional data are needed to develop a population-level model for the species and understand how home range may vary with habitat type, degree of fragmentation, prey density and group size, this value provides an important baseline for initiating speciesspecific conservation efforts.

We believe that this semi-nomadic movement pattern is tightly associated with the bush dog's observed intensive predation rates (1 armadillo per 1–2 days); however, additional studies on prey density are needed to confirm whether their constant movement within an area and rotational movement among areas functions to minimise negative effects on prey density. The group's constant changing of den sites may be an energy-saving adaptation to this semi-nomadic pattern, because the group uses readily available local dens when they are ready to rest instead of traveling back to their previous den, which can be kilometres away. The only period when they change their pattern of den use is when newborns are present. In those periods, the group utilises the same burrow for a longer period, possibly to lower the pup's exposure to predators.

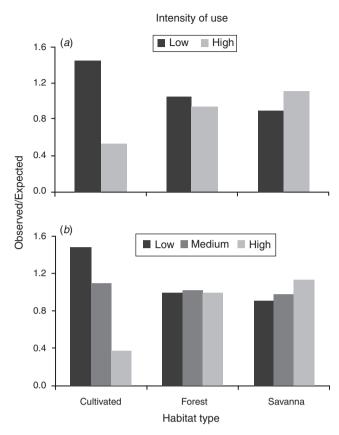


Fig. 2. Habitat-use analyses (*a*) with two categories of use (low *v*. high) or (*b*) with three categories of use (low, medium and high) demonstrated that the monitored bush dogs used cultivated areas less than expected by their availability, forests at the same level as expected by their availability, and savannas more than expected by their availability (see text for results of statistical analyses).

The daily activity pattern of the bush dog is similar to three other South American canids (maned wolf, crab-eating fox, hoary fox, Jácomo et al. 2004); however, unlike for these other canids, the bush dog's morning peak is more intense (shorter in total duration) than the night period. These activity peaks are possibly associated with their prey's observed activity patterns. Ninebanded armadillos were observed to be the main prey of bush dogs in the present study (97.6%, or 41 of the 42 predation observations) and in another study in a similar habitat (94.1%) occurrence in scats; Lima et al. 2009). Nine-banded armadillos are primarily nocturnal but return to their burrows in early morning (Emmons and Feer 1990). Bush dogs have a body structure well adapted to remove prey from burrows (Lima et al. 2009) and observations of the monitored group indicate that once the group located an armadillo in its den, they could very efficiently dig to remove and kill it. The majority of the observed predation events (armadillos removed from their burrows) occurred during the morning activity peak when fresh armadillo routes might be easier to track. Few predation events were recorded during the night, when armadillos were outside their burrows. Overall, observations indicated that it seemed more difficult for the bush dogs to secure an armadillo foraging in open areas than it was to secure one confined in a burrow.

 Table 1. Period that the monitored group of bush dogs visited each of the five separate sites over a 12-month period

The pattern of staying temporarily in different locations but repeatedly visiting one of the areas (Area 2) indicates a semi-nomadic movement pattern

Date	Duration of stay (days/months)	Subarea no.
13 Jul. 2004 to 14 Aug. 2004	33/1.1	1
15 Aug. 2004 to 28 Oct. 2004	74/2.5	2a
11 Nov. 2004 to 17 Jan. 2005	67/2.2	3 - birth
18 Jan. 2005 to 31 Mar. 2005	73/2.4	2b
7 Apr. 2005 to 21 Apr. 2005	14/0.5	4
4 May 2005 to 24 May 2005	20/0.7	2c
3 Jun. 2005 to 13 Jul. 2005	40/1.3	5
14 Jul. 2005 to 13 Aug. 2005	31/1.0	А

^AAlthough the adult male and juvenile remained within the overall home range of the group during the last 31 days of monitoring, they shifted to an aberrant movement pattern. Specifically, they moved among Areas 2, 1, and 4, before returning to Area 5, where both died (13 August 2005). This could be a side-effect of losing the adult breeding female (13 July 2005) in the group and possibly searching for a female companion, and we decided to error on the side of caution and not include this data as an independent subarea.

The group used savanna habitat more than predicted by its availability, and cultivated lands less than predicted by their availability. The group's movement and behaviour support this higher-than-expected savanna use, which we believe is associated with widely available shelters (e.g. high grass for hiding, dens for escape), and more abundant prey in native than in cultivated habitats. The latter is supported by the group's lower observed kill rate in cultivated areas (32 armadillo-predation events were in the savanna, eight were in the forest and one was in the cultivated habitat), possibly an indication of low armadillo abundance, which appears to be their preferred prey. In general, when the group was encountered in cultivated habitat, they never stayed for extended periods of time, and instead travelled quickly until native habitat was reached. The group's avoidance of cultivated habitat and preference for native habitat demonstrated the importance for understanding the range of effects that fragmentation may have on the ecological requirements of the bush dog. With fragmentation continually increasing throughout much of the bush-dog distribution (DeMatteo and Loiselle 2008), it is possible that the bush dog will require larger home ranges so as to compensate for lower density of basic ecological requirements (e.g. prey, shelter) in cultivated habitats.

During this 13-month study, there were several changes in group size. Although predation is the possible cause of the disappearance of the pups, it is not the only explanation for the disappearance of the 1-year-old juvenile. With the latter, it is possible that the individual dispersed from the group. Although this contradicts captive data (extended family groups) and other opportunistic field observations (e.g. 10-12 individuals per group; Beisiegel and Zuercher 2005), pack size may be a plastic trait dependent on many factors (habitat quality, time since pack formation, prey density; Sillero-Zubiri *et al.* 2004); however, additional field data are needed to clarify this question.

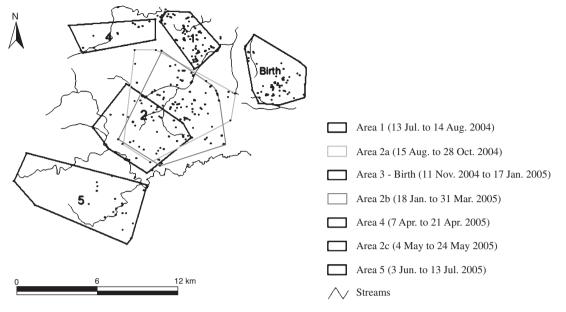


Fig. 3. Map of the five separate sites, or 'subareas', within the larger home range of the monitored bush-dog group. Each black dot represents a location recorded between 13 July 2004 and 13 August 2005. The duration of stay, number of locations and estimated area for each 'subarea' are presented in Tables 1 and 2. The last period of monitoring (14 July to 13 August 2005) was not defined as a subarea (see Table 1).

 Table 2.
 Summary of total home-range size and area for each separate site, or 'subarea', with 95% fixed kernel (FK 95%)

Subarea no.	FK 95% (km ²)	No. of points
1	9.9	122
2a	33.9	255
3 – birth	13.6	181
2b	33.6	152
4	6.8	40
2c	20.2	61
5	40	74

Another possible explanation for the loss or disappearance of individuals from the group is the generalised hair loss that was seen in the individuals from the study group. Although it was not possible to definitely determine the cause of the generalised hair loss, it is suspected that it was a type of mange, one of the diseases reported to occur in bush dogs (DeMatteo 2008). This is supported by the diagnosis of *Sarcoptes scabiei* in two bush dogs in an area near the area of the monitored group (Jorge *et al.* 2008). Additional research is also needed to understand the range and impact of diseases which bush dogs are susceptible to, especially with the increasing loss of habitat and their inevitable interactions with domestic dogs.

In summary, although only one group of bush dogs was monitored, our study is the first to shed light on important questions related to ecological requirements of the species, helping develop more sounding conservation and management plans. Continued effort is greatly needed if we want to better understand the responses of one the least known species of Neotropical canid to the increasing fragmentation and degradation of native habitats.

Acknowledgements

This project was conducted with the help of Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros of the Instituto Chico Mendes de Conservação da Biodiversidade (CENAP/ICMBio). We thank Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) for the necessary permits to conduct this study. We are grateful to the generous financial support provided by the Zoological Society of Chicago, Palm Beach Zoo Conservation Fund, Cleveland Metroparks Zoo Small Grants Program, Pittsburgh Zoo & PPG Aquarium Conservation Fund, and Idea Wild. The CBERS satellite image was kindly provided by the Instituto Nacional de Pesquisas Espaciais (INPE). We thank all of the field assistants who help with the collection of data, including R. Sollmann and N. Luz. We appreciate the services provided by both veterinarians in the capture and handling of animals, namely, D. H. de Morais and M. R. Santos. A special thanks goes to all the private land owners that allowed the research to occur in their properties, especially the family of D. Stanke, who also aided in many other aspects of the research project. We appreciate the time and effort of two anonymous reviewers whose comments helped improve earlier drafts of the manuscript.

References

- Aebischer, N. J., Robertson, P. A., and Kenward, R. E. (1993). Compositional analyses of habitat use from animal radio-tracking date. *Ecology* 74, 1313–1325. doi:10.2307/1940062
- Aquino, R., and Puertas, P. (1997). Observations of *Speothos venaticus* (Canidae: Carnivora) in its natural habitat in Peruvian Amazonia. *Zeitschrift für Saugetierkunde* 62, 117–118.
- Barnett, A., Shapley, R., and Engstrom, M. (2001). Records of the bush dog, Speothos venaticus (Lund, 1842) from Guyana. Mammalia 65, 232–237.
- Beisiegel, B. M. (1999). Contribuição ao estudo da história natural do cachorro do mato, Cerdocyon thous, e do cachorro vinagre, Speothos venaticus. Ph.D. Thesis, Universidade de São Paulo, São Paulo, Brazil.

- Beisiegel, B. M. (2009). First camera trap record of bush dogs in the state of São Paulo, Brazil. *Canid News* 12.5 [online]. Available at http://www. canids.org/canidnews/12/Bush_dogs_in Sao_Paulo.pdf [verified 20 January 2011].
- Beisiegel, B. M., and Zuercher, G. L. (2005). Speothos venaticus. Mammalian Species 783, 1–6. doi:10.1644/783.1
- Börger, I., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology* **75**, 1393–1405. doi:10.1111/j.1365-2656.2006.01164.x
- Courtenay, O., Macdonald, D. W., Gillingham, S., Almeida, G., and Dias, R. (2006). First observations on South America's largely insectivorous canid: the hoary fox (*Pseudalopex vetulus*). *Journal of Zoology* 268, 45–54. doi:10.1111/j.1469-7998.2005.00021.x
- DeMatteo, K. E. (2008). Using a survey of carnivore conservationists to gain insight into the ecology and conservation status of the bush dog. *Canid News* 11.3 [online]. Available at http://www.canids.org/canidnews/11/ Bush_dog_data_survey.pdf [verified 20 December 2010].
- DeMatteo, K. E., and Kochanny, C. (2004). Determining an effective and safe radio-tracking collar for bush dogs (*Speothos venaticus*) Canid News 7.7 [online]. Available at http://www.canids.org/canidnews/ 7/Radiotracking_collar_for_bush_dogs.pdf [verified 12 January 2011].
- DeMatteo, K. E., and Loiselle, B. A. (2008). New data on the status and distribution of the bush dog (*Speothos venaticus*): evaluating its quality of protection and directing research efforts. *Biological Conservation* 141, 2494–2505. doi:10.1016/j.biocon.2008.07.010
- DeMatteo, K. E., Carrillo, O., Zuercher, G. L., Ramírez, S., Smith, K., and Porton, I. J. (2004). A technique for attracting bush dogs (*Speothos venaticus*) in the wild. *Canid News* 7.6 [online]. Available at http:// www.canids.org/canidnews/7/Attracting_bush_dogs.pdf [verified 10 December 2010].
- DeMatteo, K. E., Porton, I. J., Kleiman, D. G., and Asa, C. S. (2006). The effect of the male bush dog (*Speothos venaticus*) on the female reproductive cycle. *Journal of Mammalogy* 87, 723–732. doi:10.1644/05-MAMM-A-342R1.1
- DeMatteo, K. E., Rinas, M. A., Sede, M. M., Davenport, B., Argüelles, C., Lovett, K., and Parker, P. G. (2009). Detector dogs: an effective technique for bush dogs (*Speothos venaticus*) surveys. *The Journal of Wildlife Management* **73**, 1436–1440. doi:10.2193/2008-545
- Emmons, L. H., and Feer, F. (1990). 'Neotropical Rainforest Mammals: a Field Guide.' (University of Chicago Press: Chicago, IL.)
- Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., and Wray, S. (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. doi:10.1111/j.1365-2907.1990.tb00106.x
- Jacob, A. A., and Rudran, R. (2003). Radiotelemetria em estudos populacionais. In 'Métodos de Estudos em Biologia da Conservação e Manejo da Vida Silvestre'. (Eds L. Cullen Jr, R. Rudran and C. Valladares-Padua.) pp. 285–342. (Editora UFPR: Curitiba, Brazil.)
- Jácomo, A. T. A., Silveira, L., and Diniz-Filho, J. A. F. (2004). Niche separation between the maned wolf (*Chysocyon brachyurus*), the creab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in Central Brazil. *Journal of Zoology* 262, 99–106. doi:10.1017/S0952836903004473
- Jácomo, A. T. A., Kashivakura, C. K., Ferro, C., Furtado, M. M., Astete, S. P., Tôrres, N. M., Sollmann, R., and Silveira, L. (2009). Home range and spatial organization of maned wolves in the Brazilian grasslands. *Journal* of Mammalogy **90**, 150–157. doi:10.1644/07-MAMM-A-380.1
- Jorge, R. S. P., Lima, E. S., and Lucarts, L. E. B. (2008). Sarna sarcóptica ameaçando cachorros-vinagres (*Speothos venaticus*) de vida livre em Nova Xavantina – MT. In 'Proceedings of the Annual Meeting of the Brazilian Society of Zoos (SZB)'. Available at http://www.szb.org.br/ [verified 15 December 2010].

- Kleiman, D. G. (1972). Social behavior of the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. *Journal of Mammalogy* 53, 791–806. doi:10.2307/1379214
- Lima, E. S., Jorge, R. S. P., and Dalponte, J. C. (2009). Habitat use and diet of bush dogs, *Speothos venaticus*, in the northern Pantanal, Mato Grosso, Brazil. *Mammalia* 73, 13–19. doi:10.1515/MAMM.2009.002
- Macdonald, D. W., and Courtenay, O. (1996). Enduring social relationships in a population of crab-eating zorros, *Cerdocyon thous*, in Amazonian Brazil (Carnivora, Canidae). *Journal of Zoology* 239, 329–355. doi:10.1111/ j.1469-7998.1996.tb05454.x
- Marzluff, J. M., Millspaugh, J. J., Hurvitz, P., and Handcock, M. S. (2004). Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology* 85, 1411–1427. doi:10.1890/03-0114
- Michalski, F. (2010). The bush dog Speothos venaticus and short-eared dog Atelocynus microtis in a fragmented landscape in southern Amazonia. Oryx 44, 300–303. doi:10.1017/S0030605309990871
- Millspaugh, J. M, Nielson, R. M., McDonald, L., Marzluff, J. M., Gitzen, R. A., Rittenhouse, C. D., Hubbard, M. W., and Sheriff, S. L. (2006). Analysis of resources selection using utilization distributions. *The Journal* of Wildlife Management **70**, 384–395. doi:10.2193/0022-541X(2006)70 [384:AORSUU]2.0.CO;2
- MMA (Ministry of the Environment of Brazil) (2003). Instrução normativa, n°. 3. In 'Diário Oficial de União', 101. (Ed. Brazilian Government.) pp. 88–97 (Imprensa Nacional: Brasília, Brazil.)
- MME (Ministry of Mining and Energy of Brazil) (1981). Goias: geologia, geomorfologia, vegetação, uso potencial da terra. In 'Projeto RADAMBRASIL. Levantamento de Recursos Naturais'. (Ed. Ministry of Mining and Energy of Brazil.) p. SD.22. (Ministry of Mining and Energy of Brazil: Rio de Janeiro.)
- Montalli, R. J., and Kelly, K. (1989). Pathologic survey and review of diseases of captive maned wolves (*Chrysocyon brachyurus*) and bush dogs (*Speothos venaticus*). *Erkrankungen Der Zootiere* **61**, 67–79.
- Nimer, E. (Ed.) (1989). 'Climatologia do Brasil.' (Fundação IBGE: Rio de Janeiro.)
- Oliveira, T. G. (2009). Distribution, habitat utilization and conservation of the vulnerable bush dog *Speothos venaticus* in northern Brazil. *Oryx* 43, 247–253. doi:10.1017/S0030605307002347
- Peres, C. A. (1991). Observations on hunting by small-eared (*Atelocynus microtis*) and bush dogs (*Speothos venaticus*) in central-western Amazonia. *Mammalia* 55, 635–639.
- Porton, I., Kleiman, D. G., and Rodden, M. (1987). Aseasonality of bush dog reproduction and the influence of social factors on the estrous cycle. *Journal of Mammalogy* 68, 867–871. doi:10.2307/1381569
- Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., and Gitzen, R. A. (1999). Effects of sample size on kernal home range estimates. *The Journal of Wildlife Management* 63, 739–747. doi:10.2307/3802664
- Sillero-Zubiri, C., Hoffmann, M., and Macdonald, D. W. (2004). 'Canids: Foxes, Wolves, Jackals, and Dogs.' (IUCN Publication Services Unit: Cambridge, UK.)
- Silveira, L., Jácomo, A. T. A., Rodrigues, F. H. G., and Diniz-Filho, J. A. F. (1998). Bush dogs (*Speothos venaticus*), in Emas National Park, Central Brazil. *Mammalia* 62, 446–449.
- Van Humbeck, J., and Pérez, N. (Eds.) (1998). 'Estudios del Jagua Yvyguy, Speothos venaticus, en el Centro de Investigación de Animales Silvestres de Itaipu, CIASI.' (Superintendência de Médio Ambiente de la Itaipu Binacional: Ciudad del Este, Paraguay.)
- Wauters, L. A., Preatoni, D. G., Molinari, A., and Tosi, G. (2007). Radiotracking squirrels: performance of home range density and linkage estimators with small range and sample size. *Ecological Modelling* 202, 333–344. doi:10.1016/j.ecolmodel.2006.11.001
- Worton, B. J. (1987). A review of models of home range for animal movement. *Ecological Modelling* 38, 277–298. doi:10.1016/0304-3800(87)90101-3

- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168. doi:10.2307/ 1938423
- Zuercher, G. L., Gipson, P. S., and Carrillo, O. (2005). Diet and habitat associations of bush dogs *Speothos venaticus* in the Interior Atlantic Forest of eastern Paraguay. *Oryx* **39**, 86–89. doi:10.1017/S0030605305 000153
- Zuercher, G. L., Swarner, M., Silveira, L., and Carrillo, O. (2008). Speothos venaticus. In 'IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1'. Available at http://www.iucnredlist.org/apps/redlist/details/ 20468/0 [verified 17 October 2011].