

How rare is rare? Quantifying and assessing the rarity of the bush dog *Speothos venaticus* across the Amazon and other biomes

TADEU G. DE OLIVEIRA, FERNANDA MICHALSKI, ANDRÉ L. M. BOTELHO
LINCOLN J. MICHALSKI, ARMANDO M. CALOURO and ARNAUD L. J. DESBIEZ

Abstract The bush dog *Speothos venaticus* is a medium-sized Neotropical canid. It is considered to be rare and its biology and population parameters are still poorly understood. The Amazon is one of the main strongholds of this species and is important for maintaining viable populations, as the region still holds extensive tracts of pristine habitat. We gathered field data from camera-trap studies throughout the Brazilian Amazon to estimate the relative abundance of the species and gain an understanding of its rarity, and how this compares with estimates from other vegetative formations and for sympatric hypercarnivores. We focused on three pristine or partially disturbed sites and one fragmented site. The estimated relative abundance of the species was 0.060–0.185 individuals per 100 trap-days, confirming that the species is rare. The bush dog's abundance in the Amazon is equivalent to that in all other areas outside the Basin. The mean group size recorded was c. 2.5 individuals. There were no differences in group sizes between forests in the Amazon and in other regions of Central America; however, there were significant differences between forests and open habitats. A combination of competition/predation, habitat structure/integrity, and disease may be acting synergistically in determining the abundance and rarity of bush dogs.

Keywords Amazon, bush dog, camera trap, conservation, group size, rarity, relative abundance, *Speothos venaticus*

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Introduction

The bush dog *Speothos venaticus* is a medium-sized (c. 6 kg) Neotropical canid that lives in packs. The species' biology and population characteristics are poorly understood, and it is one of the least known carnivores in South America (Eisenberg & Redford, 1999; Zuercher et al., 2004; DeMatteo & Loiselle, 2008). Most information available on the species in Brazil comes from opportunistic observations (e.g. Peres, 1991; Silveira et al., 1998; Rocha et al., 2015; Michalski et al., 2015a), and it has only recently become the subject of longer-term studies (Lima et al., 2009, 2012, 2015).

The bush dog is recognized as being a rare carnivore (Zuercher et al., 2004; Oliveira, 2009; DeMatteo et al., 2011), and is categorized as Near Threatened on the IUCN Red List (DeMatteo et al., 2011) and Vulnerable in Brazil (Jorge et al., 2013). The Amazon Basin represents the species' main geographical range and is important for its long-term conservation (e.g. Zuercher et al., 2004; Oliveira, 2009). Currently, the Amazon has sufficient suitable habitat to maintain a genetically viable population of bush dogs (Oliveira, 2009).

The Amazon Basin is the largest tract of lowland rainforest, although many areas are under pressure from ongoing habitat loss and fragmentation as a result of human encroachment and development activities, especially along the so-called deforestation arc (Nogueira et al., 2015; Silva et al., 2015). To date, 18.8% of the original forest cover has been lost in the Brazilian Amazon alone (INPE, 2015) and further decline is predicted (e.g. a reduction to 53% of the original cover by 2050; Soares-Filho et al., 2006). The Amazon provides a safe haven for species that range within its boundaries (Rodrigues & Oliveira, 2006), by a combination of extensive tracts of primary forest and a network of protected areas. However, given the current rate of deforestation and the number of existing and proposed hydroelectric dams (Tundisi et al., 2014; INPE, 2015) there is

TADEU G. DE OLIVEIRA* (Corresponding author) Departamento de Biologia, Universidade Estadual do Maranhão, Cidade Universitária Paulo VI – Caixa Postal 09, São Luís, Maranhão, 65055-000, Brazil. E-mail tadeu4@yahoo.com

FERNANDA MICHALSKI† Instituto Pró-Carnívoros, Atibaia, São Paulo, Brazil

ANDRÉ L. M. BOTELHO‡ Mestrado em Ecologia e Manejo de Recursos Naturais, Campus Universitário Rodovia, Rio Branco, Acre, Brazil

LINCOLN J. MICHALSKI Faculdade de Itaituba, Itaituba, Pará, Brazil

ARMANDO M. CALOURO Universidade Federal do Acre, Centro de Ciências Biológicas e da Natureza, Campus Universitário–Rodovia, Rio Branco, Acre, Brazil

ARNAUD L. J. DESBIEZ Royal Zoological Society of Scotland, Murrayfield, Edinburgh, UK

*Also at: Instituto Pró-Carnívoros, Parque Edmundo Zanon, Atibaia, São Paulo, Brazil

†Also at: Laboratório de Ecologia e Conservação de Vertebrados, Universidade Federal do Amapá, Macapá, Amapá, Brazil

‡Also at: Instituto Federal de Educação, Ciência e Tecnologia do Acre. Campus Avançado Baixada do Sol, Rio Branco, Acre, Brazil

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likely to be a major shift in the ecological landscape towards many isolated and fragmented habitats; for example, > 10 million ha of forest are expected to be flooded as a result of the construction of hydroelectric dams (Fearnside, 2006), representing 2% of the total area of the Brazilian Amazon (FAO, 2005), which will contribute directly to widespread extinction of vertebrates (Benchimol & Peres, 2015).

The detection and study of cryptic or elusive species has become easier and more reliable with the advent of camera trapping. Although the technique has drawbacks for certain species, such as arboreal or very small species, it has been utilized effectively to study several mammalian carnivores and has proved a reliable source of data for estimating relative abundance and population density (Carbone et al., 2001; O'Brien et al., 2003; O'Connell et al., 2011; Oliveira, 2011; Kasper et al., 2015). Although the rarity of bush dogs is widely acknowledged, there is no specific quantitative measure of abundance, nor has the abundance of bush dogs been compared with that of other sympatric hypercarnivores. The apparent rarity and distribution of this canid could be a product of competitive interactions with the puma *Puma concolor*, jaguar *Panthera onca*, and possibly ocelot *Leopardus pardalis* (Oliveira & Pereira, 2014), as they share similar prey species (Oliveira, 2002; Zuercher et al., 2005; Lima et al., 2009; Oliveira et al., 2010). To address these issues we estimated the relative abundance of bush dogs in the Brazilian Amazon and compared it with those in other biomes and potential sympatric competitors/predators to assess the long-term conservation and persistence prospects of the species in this area.

Study area

The study focused on four sites in the south-west, central, south-central, and north-east of the Brazilian Amazon (Fig. 1). Three of these were mostly pristine (with slight disturbance; i.e. < 5% alteration by human activity, such as fire or logging) and one was fragmented. The study site at Alto Tarauacá Extractive Reserve, in the south-west, is in an area of open and closed rainforest with alluvial seasonally flooded forest and some degree of disturbance related to the latex extraction industry. The sites surveyed in the Reserve included areas where subsistence hunting had low and high impact (Botelho, 2013). The mid-Tapajós/Amazonia National Park area in central Amazonia is characterized by a humid equatorial climate and hilly terrain with a mosaic of rainforest vegetation types. We used study areas both within and outside the park. The area is dominated by tall terra firme forest (15–30 m) interspersed by areas of lower forest and lianas (10–15 m). There is also an area of seasonally flooded riverine forest (*igapó*) occupying a narrow strip along the banks of the Tapajós River and its

tributaries (George et al., 1988). The Amapá National Forest, in the north-east, is a sustainable-use area comprising continuous tropical rainforest vegetation, predominantly never-flooded terra firme forest, with some areas of flooded forest, bamboo and rocky outcrops (Michalski et al., 2015b). The Alta Floresta site is located along the deforestation arc of the Amazon and includes terra firme forest fragments of varying sizes, shapes and degrees of connectivity (Michalski et al., 2008).

Methods

Defining rarity

A rare species is one that is uncommon, scarce or encountered infrequently (Gaston, 1994). For the purpose of this study we define a rare species as one for which the number of camera-trap records is low, which is an inherent reflection of low density and small population size (Rabinowitz, 1981). This definition has been used in other studies of mammals (Cofré & Marquet, 1999; Yu & Dobson, 2000; Harcourt et al., 2002). We assessed camera-trap data (photographic records) from our study sites (Fig. 1) and for several uncommon and elusive species in the Neotropics (e.g. Martins et al., 2007; Tobler et al., 2008; Negrões et al., 2011; Pimenta, 2012; Botelho, 2013; Oliveira et al., 2014; Borges et al., 2015). Difficult-to-detect species such as the short-eared dog *Atelocynus microtis*, giant armadillo *Priodontes maximus* and giant anteater *Myrmecophaga tridactyla* were all recorded at rates of no more than 0.300 records per 100 trap-days. Thus, we considered species with < 0.300 records per 100 trap-days to be rare.

Bush dog abundance

The location and arrangement of cameras was targeted towards mammalian carnivores. All cameras were spaced 0.5–1 km apart and typically positioned at 20–30 cm height along forest trails, riparian forest/stream banks, and at other sites where carnivores were likely to be detected. The protocol used for camera placement was based on the objective of gathering data on the abundance of carnivores and other mammals, and cameras were placed at optimum distances from the focal area to capture all mammals, and particularly bush dogs (mean shoulder height 25–30 cm; Zuercher et al., 2004). This protocol was also followed to capture data on smaller (< 1 kg) mammals, such as small rodents and marsupials. Thus, we predicted the camera-trap sampling protocol would provide a robust representation of how common or rare carnivores were in these areas. As bush dogs are gregarious, we considered the total number of individuals captured on video or in photographic records to represent

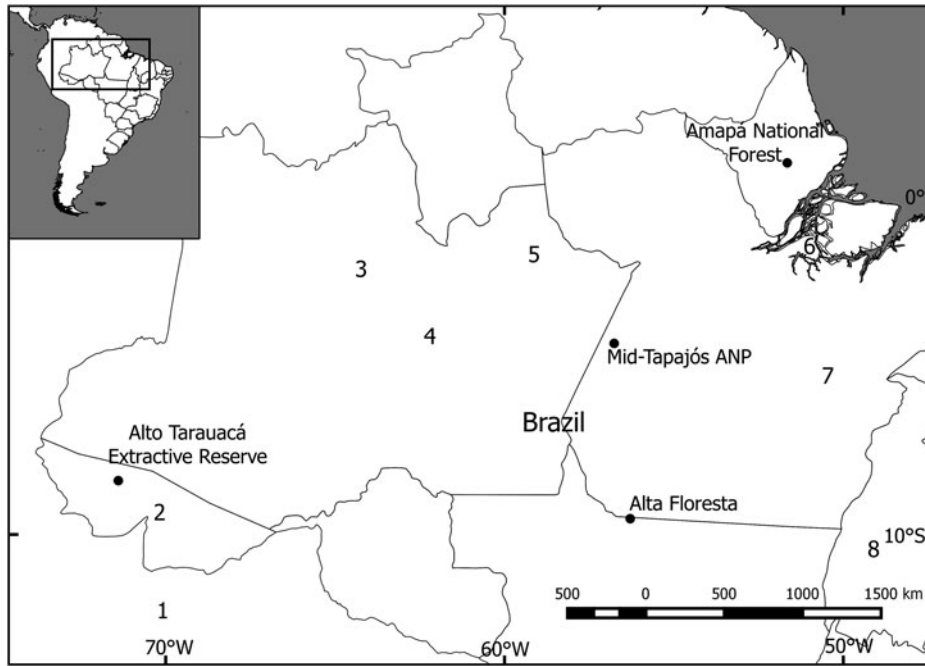


FIG. 1 Locations of the four study sites in the Amazon Basin where camera-trap surveys of the bush dog *Speothos venaticus* were conducted. Other camera-trap studies have been conducted at (1) Los Amigos Conservation Concession, Peru (Tobler et al., 2008), (2) Chandless State Park (Borges et al., 2015), (3) Amanã Sustainable Development Reserve (Rocha et al., 2015), (4) Piagaçu-Purus Sustainable Development Reserve (Pimenta, 2012), (5) Balbina Hydroelectric Dam (Benchimol & Peres, 2015), (6) Caxiuanã National Forest (Martins et al., 2007), (7) Carajás National Forest (Bergallo et al., 2012), and (8) Cantão State Park (Negrões et al., 2011).

relative abundance, reported as individuals per 100 trap-days. Consecutive photographic records of the same species were defined as independent occurrences if the individual(s) could be distinguished unambiguously or if the interval between records was > 30 minutes (O'Brien et al., 2003). Bush dog group size was determined from the number of individuals recorded on camera or observed by researchers at the study sites during fieldwork. We assessed bush dog abundance in relation to the abundance of other sympatric hypercarnivores and the bush dog's main prey species, agouti *Dasyprocta* spp., paca *Cuniculus paca* and armadillo *Dasyurus* spp. (Zuercher et al., 2004, 2005; Lima et al., 2009).

Analytical procedures

We present data as mean \pm standard deviation per sampling unit. We conducted normality tests to determine whether to use parametric or non-parametric statistics. To compare the abundance of bush dogs with that of their potential intra-guild predators or competitors we used ANOVA on ranks, and Tukey's test for all pairwise multiple comparisons. We used ANOVA to compare bush dog group size among various vegetative formations, and the Holm-Sidak method for all pairwise multiple comparisons. We applied *t*-tests to compare bush dog abundance in the Amazon with all other areas in the species' range as well as abundance in fragmented and non-fragmented sites. We used a Mann-Whitney rank sum test to compare group size from camera-trap data and visual observations, and conducted regression analyses to determine the relationship between bush dog

abundance and number of records with trap effort. The significance level was considered to be $\alpha = 0.05$.

Results

Rarity

Trapping effort at our four study sites was 15,888 trap-days in total, which yielded a mean relative abundance of $0.117 \pm$ SD 0.052 bush dogs per 100 trap-days (range 0.060 – 0.185 ; Table 1). In pristine areas mean abundance was $0.136 \pm$ SD 0.067 individuals per 100 trap-days, more than double that found at the fragmented Alta Floresta site (0.060 individuals per 100 trap-days). The species' rarity was confirmed by a lack of records in several other similar camera-trap studies across the Amazon, which accounted for an additional 40,949 trap-days (Table 2). Thus, considering the other sites where the focal species was observed (Table 2), the relative abundance of bush dogs in the Amazon was estimated to be 0.013 – 0.185 individuals per 100 trap-days (mean $0.107 \pm$ SD 0.064 ; Negrões et al., 2011; Bergallo et al., 2012; Rocha et al., 2015; this study). The mean abundance in fragmented and non-fragmented areas across the Amazon Basin was 0.060 and $0.117 \pm$ SD 0.067 individuals per 100 trap-days, respectively. The mean for all camera-trap sites evaluated in the Amazon (including non-detection sites) was $0.058 \pm$ SD 0.072 individuals per 100 trap-days (range 0 – 0.185 ; Martins et al., 2007; Tobler et al., 2008; Negrões et al., 2011; Pimenta, 2012; Benchimol & Peres, 2015; Borges et al., 2015; Rocha et al., 2015; this study). Bush dog abundance in the Amazon was equivalent to

TABLE 1 Details of our camera trap study to estimate the relative abundance (number of individuals per 100 trap-days) of bush dogs *Speothos venaticus* and their potential intraguild competitors/predators and prey species at four sites throughout the Brazilian Amazon (Fig. 1).

	Alto Tarauacá Extractive Reserve	Mid-Tapajós/Amazonia National Park	Amapá National Forest	Alta Floresta
Sampling effort (trap-days)	2,467	4,000	2,700	6,721
Camera stations	59	140	30	49
Survey area (km ²)	43	106	25	2,580
Study period	May–Dec. 2012	June 2012–Nov. 2013	Oct. 2013–Oct. 2014	June 2003–Dec. 2004; Oct. 2007–Dec. 2008
Forest type	Pristine/lightly disturbed	Pristine/lightly disturbed	Pristine/lightly disturbed	Highly fragmented
Bush dog abundance				
No. of individuals per 100 trap-days	0.122	0.100	0.185	0.060
No. of photographs per 100 trap-days	0.081	0.025	0.074	0.030
No. of sightings	2	6		
Intraguild competitors/predators				
Jaguar <i>Panthera onca</i>	0.081	0.675	1.6	0.253
Puma <i>Puma concolor</i>	0.365	1.2	1.7	0.208
Ocelot <i>Leopardus pardalis</i>	1.216	1.1	1.0	1.131
Prey species				
Agouti <i>Dasyprocta</i> spp.	16.133	10.775	15.7	4.612
Paca <i>Cuniculus paca</i>	10.418	3.8	2.0	3.050
Armadillo <i>Dasygus</i> spp.	1.784	2.48	1.1	7.008

that in all other areas outside the Basin (mean $0.092 \pm$ SD 0.061 individuals per 100 trap-days; $t = 0.460$, $df = 12$, $P = 0.654$; Table 2). Additionally, no difference in abundance was found when comparing fragmented/disturbed and non-fragmented areas at any of the study sites ($t = 1.351$, $df = 12$, $P = 0.202$). As abundance was equivalent across all vegetation formations, we conducted regression analyses of bush dog abundance against camera-trap effort across all vegetation types. The expected relative abundance in relation to camera-trap effort was determined as follows: bush dog abundance = $0.130 - (0.0000577^{\text{effort}})$ ($r = 0.557$, $R^2 = 0.311$, $F_{1, 12} = 5.409$, $P = 0.038$). Considering the number of records, we expected the following: bush dog photographic records = $1.240 + (0.000137^{\text{effort}})$ ($r = 0.6777$, $R^2 = 0.458$, $F_{1, 12} = 10.160$, $P = 0.008$).

Group size and activity

All photographic records and some of the visual observations of bush dogs were from terra firme forest. Bush dogs were mostly recorded along trails (Plate 1) but were also sighted at road crossings, on stream banks and in *igapó* (flooded forest). The majority of both visual ($n = 8$, 100%) and camera-trap ($n = 7$, 71.4%) records occurred during the day. There was no significant difference between group sizes estimated from camera-trap and visual records ($T = 56.00$, $P = 1.00$; Fig. 2). We found no significant differences between sizes of bush dog groups in Amazonian forests and in Central America ($T = 286.5$, $P = 0.393$; Table 3). However, there were significant differences between forested environments and open formations of the Pantanal floodplains and savannahs ($F_{3, 67} = 3.397$, $P = 0.023$).

Species interactions

The mean relative abundances of jaguars, pumas and ocelots in the study areas were $0.652 \pm$ SD 0.679 , $0.868 \pm$ SD 0.705 and $1.112 \pm$ SD 0.089 , respectively (Table 1; Supplementary Table S1). All of these species, which are potential intraguild competitors or predators of the bush dog, were significantly more abundant than the bush dog ($H = 14.623$, $df = 3$, $P = 0.002$). Pairwise comparisons of relative abundances between hypercarnivores and bush dogs were also significantly different ($P < 0.05$). In addition, relative abundances of the main prey species of the bush dog were relatively high at the four study sites (Table 1).

Discussion

Bush dog rarity

The relative abundances of bush dogs in the four study areas were low, corroborating previous observations and

TABLE 2 Relative abundance of bush dogs recorded in camera-trap studies in major vegetation formations of the Amazon and Atlantic rainforests, the Pantanal floodplains and savannahs in Brazil, and the Central American forests in Panama, with sampling effort, no. of individuals per 100 trap days, habitat integrity, and data source.

Site	Sampling effort (days)	Individuals per 100 trap-days	Photographs per 100 trap-days	Habitat integrity	Source
Amazon (rainforest)					
Alto Tarauacá Extractive Reserve	2,467	0.122	0.081	Pristine/lightly disturbed	This study
Mid-Tapajós/Amazonia National Park	4,000	0.100	0.025	Pristine/lightly disturbed	This study
Amapá National Forest	2,700	0.185	0.074	Pristine/lightly disturbed	This study
Alta Floresta	6,721	0.060	0.030	Highly fragmented	This study
Amanã Sustainable Development Reserve (Amazonas, Brazil)	4,894	0.163	0.061	Pristine/lightly disturbed	Rocha et al. (2015)
Carajás National Forest (Pará, Brazil)	3,572	Data unavailable	0.084	Pristine/lightly disturbed	Bergallo et al. (2012)
Cantão State Park (Tocantins, Brazil)	7,929	0.013	0.013	Pristine/lightly disturbed	Negrões et al. (2011)
Caxiuanã National Forest (Pará, Brazil)	2,838	*	*	Pristine/lightly disturbed	Martins et al. (2007)
Chandless State Park (Acre, Brazil)	3,213	*	*	Pristine/lightly disturbed	Borges et al. (2015)
Piagaçu-Purus Sustainable Use Reserve (Amazonas, Brazil)	3,743	*	*	Pristine/lightly disturbed	Pimenta (2012)
Balbina Hydroelectric Dam (Amazonas, Brazil)	12,420	*	*	Highly fragmented	Benchimol & Peres (2015)
Los Amigos Conservation Concession (Peru)	2,340	*	*	Pristine/lightly disturbed	Tobler et al. (2008)
Atlantic Forest					
Carlos Botelho State Park (São Paulo, Brazil)	4,818	0.042	0.021	Pristine/lightly disturbed	Beisiegel (2009)
Natural Reserves complex (Paraná, Brazil)	4,112	0.097	0.073	Lightly disturbed but with fragments	Fusco-Costa & Ingberman (2013)
Pantanal floodplains/forest mosaic					
Nhumirim Ranch (Mato Grosso do Sul, Brazil)	2,238	0.179	0.045	Lightly–moderately disturbed	Bianchi (2009)
Cerrado (savannah)					
Veredas do Peruaçu State Park (Minas Gerais, Brazil)	6,000	0.017	0.017	Secondary savannah with old Eucalyptus plantation	Ferreira et al. (2015)
Central American forests (Panama)					
Pirre	3,119	0.160	0.096	Pristine/lightly disturbed	Meyer et al. (2015)
Nusagandi	830	0.120	0.120	Pristine/lightly disturbed	Meyer et al. (2015)
Donoso	24,641	0.024	0.020	Pristine/lightly disturbed	Meyer et al. (2015)
Santa Fé	3,165	0.095	0.063	Pristine/lightly disturbed	Meyer et al. (2015)

* Species present but not detected by camera traps

conclusions that the species is rare (e.g. Zuercher et al., 2004; Oliveira, 2009; DeMatteo et al., 2011; Jorge et al., 2013). Although the abundance estimated from camera-trap records at the mid-Tapajós/Amazonia National Park site was lower compared to the other undisturbed areas, the number of visual records at this site was higher than at the other sites. Thus, relative abundance was similar across the study sites, except for the fragmented Alta Floresta area, where it was approximately half that at the other sites. Even with the limited number of records of the bush dog, it is clear that habitat fragmentation is a major conservation

issue for this species. Previous studies of the species based on radio tracking have showed a trend of increasing home range with increasing degree of fragmentation of habitat (Lima et al., 2012, 2015; E. Lima, pers. comm.). We found a similar trend at our sites, with higher relative abundances of bush dogs in pristine or only slightly disturbed areas compared with fragmented areas. However, we found no differences when comparing camera-trap records from fragmented/disturbed and non-fragmented areas at any of the study sites. Given the generally low number of records of the species, caution is warranted regarding this issue.



PLATE 1 A bush dog *Speothos venaticus* pack at the disturbed and fragmented study site of Alta Floresta, Brazil (Fig. 1). Photograph by Fernanda Michalski.

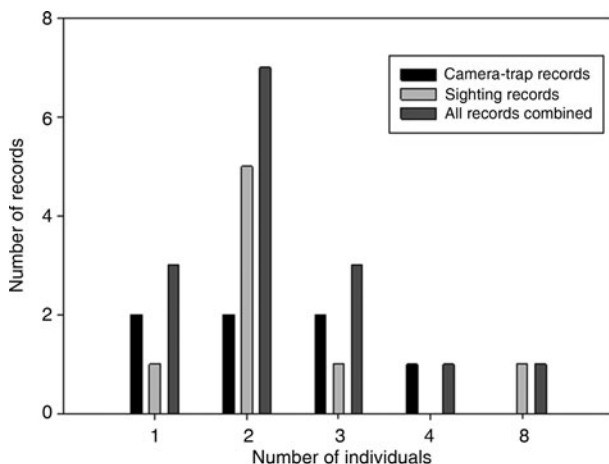


FIG. 2 The total number of bush dogs recorded by camera traps, sightings, and both methods combined, at the four study sites combined (Alto Tarauacá Extractive Reserve, Mid-Tapajós/Amazonia National Park, Amapá National Forest and Alta Floresta; Fig. 1).

The inherent rarity of bush dogs was also highlighted by the fact that despite a large sampling effort (2,340–12,420 trap-days) the species was not recorded in 42% (5 of 12) of other systematic and robust camera-trap studies across the Amazon (Martins et al., 2007; Tobler et al., 2008; Pimenta, 2012; Benchimol & Peres, 2015; Borges et al., 2015), most of which were conducted in areas with good habitat integrity. Nevertheless, it is important to highlight that absence of detection by camera-trapping does not prove that the species is absent in an area, only that the low numbers make it difficult to detect. It has been shown that the use of detection dogs is more accurate for locating this rare canid (DeMatteo et al., 2009).

Relative abundance estimates were from areas where bush dogs were considered to be relatively common (based on visual and/or other evidence). As such, this species is rare even when recorded in greater numbers (Bianchi,

2009; Meyer et al., 2015; Rocha et al., 2015; this study). Of all the carnivores that occur in the Amazon Basin only the so-called phantom species, the Amazon weasel *Mustela africana* and the northern tiger cat *Leopardus tigrinus*, may be rarer than the bush dog (Oliveira et al., 2013; Rodrigues, 2013).

This general pattern of rarity observed for the bush dog is not restricted to the Amazon Basin but is characteristic of the species throughout its range. Abundance estimates from the Amazon are similar to those from the Atlantic and Central American forests and the Pantanal floodplains and savannahs. Thus, the species is rare in all its habitats, irrespective of the area, biome or method of detection (camera trap, radio telemetry, detection dogs). This rarity is probably related to the species' inherently low population density, large home range and secretive behaviour (Zuercher et al., 2004; Beisiegel, 2009; DeMatteo et al., 2009; Lima et al., 2012, 2015; Fusco-Costa & Ingberman, 2013; Ferreira et al., 2015; this study).

Camera-trap records are considered to be a consistent and reliable means of estimating the relative abundance of cryptic mammals (Carbone et al., 2001; Goulart et al., 2009; Negrões et al., 2011), although a linear relationship between the rate of photographic records and true abundance is assumed, as is a constant detection probability across space and time (O'Connell et al., 2011). Thus, it is possible that low abundance estimates reflect low detectability (Lima et al., 2012; Ferreira et al., 2015), in which case alternative methods, such as detection dogs, may be more cost-efficient for detecting rare species, including the bush dog (Long et al., 2007; DeMatteo et al., 2009). However, detection dogs may not be appropriate for population assessment of all species or in all areas, especially as there are no data on the use of dogs to detect Neotropical carnivores with which to make comparisons. Nevertheless, camera-trapping studies of carnivores, even rare ones, have proven to be effective for detecting and estimating abundance when compared to other techniques, such as telemetry, especially when trapping effort is high (e.g. > 2,000 trap-days; Soisalo & Cavalcanti, 2006; T.G. Oliveira, 2011, unpubl. data; L.P. Meira et al., unpubl. data; this study). Additionally, bush dog behaviour in the study areas and elsewhere did not suggest avoidance of camera traps or camera locations. The number of records from our study areas also supports this argument. We therefore concur with previous, similar studies and conclude that bush dogs are rare.

In this study we considered any estimates of abundance < 0.300 individuals per 100 trap-days to be indicators of rarity. We are confident that this is an accurate indicator when compared to camera-trap records for other Neotropical carnivores and rare or uncommon Neotropical mammals that were accurately sampled using the same technique (e.g. Tobler et al., 2008; Negrões et al., 2011; Botelho, 2013; Oliveira et al., 2014; L.P. Meira et al., unpubl. data).

TABLE 3 Group sizes of bush dogs recorded in various vegetation formations throughout the species' range.

Area/formation	Mean \pm SD	Range	No. of observations	Source
Amazon forest				This study
Camera trap	2.286 \pm 1.113	1–4	7	
Sighting	2.75 \pm 2.188	1–8	8	
Combined	2.533 \pm 1.727	1–8	15	
Central American forests	2.421 \pm 1.712	1–8	19	Meyer et al. (2015)
Northern Pantanal floodplains/ forest/pastureland mosaic	2.75 \pm 1.07	1–7	24	Lima et al. (2009)
Savannahs & Pantanal floodplains	4.556 \pm 2.833	1–10	9	Silveira et al. (1998), Lima et al. (2012, 2015), Teribele et al. (2012), Ferreira et al. (2015), M. Buonato (unpubl. data)

Group size and activity

All photographic records were from terra firme forest; however, we also recorded sightings and track records in other areas, including at highway crossings, on stream banks and in *igapó*. Lima et al. (2012, 2015) reported that radio-tracked groups of bush dogs did not utilize roads, whereas Fusco-Costa & Ingberman (2013) observed that they did. In any case, at our study sites cameras were not placed along roads, only on narrow trails. Similar to Rocha et al. (2015), the majority of our records suggest that this canid is predominantly diurnal. However, in the savannahs of Mato Grosso state (Brazil) a radio-tracked pack showed higher levels of activity both early in the morning and at night (Lima et al., 2012).

Typical groups of bush dogs are estimated to comprise 2–12 individuals, and most observations suggest group sizes of 2–6 (Zuercher et al., 2004). Previous camera-trap studies of the bush dog recorded groups of 1–8 individuals (Beisiegel, 2009; Bianchi, 2009; Negrões et al., 2011; Fusco-Costa & Ingberman, 2013; Meyer et al., 2015; Rocha et al., 2015), which is similar to our results. Mean group sizes recorded in the Amazon and Panamanian forests were c. 2.5 individuals (Meyer et al., 2015). In a Pantanal floodplain savannah/forest/pastureland mosaic the mean group size (2.75) was only slightly larger than in forested areas (Lima et al., 2009). However, limited data from other open habitats in seasonally flooded floodplains and savannahs suggest larger and significantly different group sizes than those in forested areas (Lima et al., 2012, 2015; Teribele et al., 2012; Ferreira et al., 2015; Meyer et al., 2015; this study). Differences in group size between savannahs and forests may reflect differences in the availability or accessibility of the bush dog's main prey species between these vegetative formations. The predominantly small group size may be explained in part by the more solitary behaviour of Neotropical hypercarnivores (Oliveira & Pereira, 2014), with the formation of groups being related to the need to subdue larger prey in some habitats (Zuercher et al., 2004, 2005).

Species interactions

The abundance of bush dogs at the study sites was low, and up to 10 orders of magnitude lower compared to intraguild competitors and predators. However, the highest abundance estimates for large felids in the study area are for Amapá National Forest, where the highest abundance of bush dogs was also recorded. Conversely, in the Tarauacá Extractive Reserve, where bush dog abundance was almost as high as in Amapá, large felids were uncommon. Although this appears to be contradictory, we suggest that our data can neither confirm nor deny the existence of intraguild interactions, which have been demonstrated for smaller Neotropical felids (Oliveira et al., 2010; Oliveira, 2011). Negative impacts of dominant competitors on subordinate competitors include decreases in niche breadth, restriction of habitat to less favourable areas, changes in activity patterns, and localized extinction, in addition to being preyed upon. Thus, subordinates tend to have smaller population sizes than dominant competitors (e.g. Miquelle et al., 2005; St-Pierre et al., 2006; Saleni et al., 2007; Oliveira et al., 2010; Oliveira, 2011). Thus, bush dog rarity may be a result of competitive interactions with jaguars, pumas and perhaps ocelots, as they share a similar prey base (Oliveira, 2002; Zuercher et al., 2005; Lima et al., 2009; Oliveira et al., 2010; Oliveira & Pereira, 2014). Predation by domestic dogs could also be a threat in some areas (Ferreira et al., 2015; E. Lima, pers. comm.).

Relative abundances of the bush dog's main prey items (i.e. agouti, paca and armadillo) were relatively high at all of our study sites. Although prey availability is a defining factor of carnivore abundance, we suggest it may not be the limiting factor determining inherent bush dog rarity, as this would not explain their low abundance at our study sites or elsewhere (Ferreira et al., 2015; this study).

Conservation issues

The expansion of hydroelectric energy projects in the Amazon Basin, where most of the viable populations of

bush dogs occur, will continue and possibly accelerate in the future. Current estimates vary from 94 to 151 additional dam projects planned for Amazonia (Tundisi et al., 2014). This will introduce large-scale changes to the hydrological cycle, inland connectivity and ecosystem services, which will in turn affect the persistence and maintenance of several species populations. This future scenario for the Amazon Basin in Brazil is of particular concern (Soares-Filho et al., 2006). The population viability assessment conducted for Amazonia National Park showed a 50% probability of extinction of the bush dog in < 100 years if populations become isolated (Godoy et al., 2015). The overall scenario for this area is predicted to worsen as the population size and carrying capacity decrease as a result of the suppression of flooded riverine forest following the installation and operation of a hydroelectric dam (Godoy et al., 2015). Simulations indicate that isolation, which has already begun in some places (Nogueira et al., 2015; Silva et al., 2015), reduces the likelihood that even forest reserves of > 10,000 km² would be adequate to maintain viable populations of bush dogs and to provide the conditions necessary for the long-term conservation of this rare canid.

Conclusions

Extensive tracts of undisturbed forest with low levels of human impact dominated the study areas, except for Alta Floresta, yet even in pristine areas the bush dog is naturally rare and threatened by predation and disease. Sarcoptic mange in particular is one of the main threats to the species in all Brazilian biomes (e.g. Jorge et al., 2013; Godoy et al., 2015). Disease can cause the loss of species from some areas for prolonged periods, as observed for short-eared dogs in Peru (Leite-Pitman & Williams, 2011). Diseases affecting wild canids tend to be transmitted from domestic dogs, which are commonly brought into protected and unprotected forested areas by local and indigenous people (Leite-Pitman et al., 2003; Leite-Pitman & Williams, 2011). However, it is unlikely that disease alone could pose a simultaneous threat across the entire range of the bush dog, or be the sole cause of its rarity. Rather, the inherent rarity of the bush dog (defined here as < 0.300 individuals per 100 trap-days) appears to be attributable to a combination of competitive pressure and predation (intraguild or otherwise), habitat structure and integrity, and disease, acting synergistically (but not separately) to determine the abundance and degree of rarity in any particular area.

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Author contributions

TGO, FM, ALMB and LJM collected and analysed the data, and co-wrote the article with AMC and ALJD.

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Biographical sketches

TADEU DE OLIVEIRA’s main research interests are the ecology and conservation of Neotropical carnivores. FERNANDA MICHALSKI’s research interests are in conservation biology and the ecological consequences of habitat fragmentation on large and mid-sized vertebrates. ANDRÉ BOTELHO is a wildlife ecologist and is interested in the ecology and conservation of medium-to-large sized mammals. LINCOLN MICHALSKI is a wildlife ecologist whose main research interests are in the ecology and conservation of mammals. ARMANDO CALOURO is interested in the effects of anthropogenic perturbations on mammals in the south-western Brazilian Amazon. ARNAUD DESBIEZ’s research focuses on sustainable use of natural resources and species conservation.