Camera trapping Cerrado mammals: assessing protected area effectiveness, influence of anthropogenic pressure and the occupancy-abundance relationship

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“Mas, o senhor a sério tenciona devassar a raso este mar de territórios, para sortimento de conferir o que existe?”

“Sertão: estes seus vazios. O senhor vá. Alguma coisa ainda encontra.”

Excerpts from the book *Grande Sertão: Veredas*, by João Guimarães Rosa. This classic of the Brazilian literature describes in detail the region where I conducted field work for this thesis.

Declaration

I, Guilherme Braga Ferreira, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis. Assistance received in each chapter is detailed below:

- Chapter 1: Chris Carbone, Marcus Rowcliffe and Tim Newbold provided comments on this chapter.
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Abstract

Protected areas (PAs) are a cornerstone of conservation policy and have been established worldwide in order to mitigate the current environmental crisis. Although PAs are usually effective at avoiding habitat conversion, their effectiveness at safeguarding local biodiversity is less clear. Furthermore, a substantial number of PAs face threats related to anthropogenic pressures that can erode the biodiversity they aim to protect. In this thesis, I use camera trap data from a mosaic of protected areas in the Brazilian Cerrado to investigate PA effectiveness and the influence of human disturbance on mammal species. Additionally, I assess the relationship between occupancy and density estimates to improve the understanding of camera trap-derived metrics in wildlife research. Overall, I surveyed 517 camera trap sites distributed across seven PAs under two contrasting types of management, totalling more than 25,000 survey days. My results revealed that PA type has a strong effect on the mammal community studied, with much higher species richness and occupancy probability in strict than in multiple-use PAs, particularly for larger and threatened mammals. I also found that succession stage of the savanna vegetation (old growth vs secondary) in a strict PA did not have a negative impact on species occupancy, and that secondary savannas supported a diverse mammal community. Despite the strong effect of PA type on the spatial distribution of mammals, I found little evidence that anthropogenic pressure influenced species' activity patterns, with few species shifting to being more nocturnal in multiple-use PAs or closer to households. Finally, my results indicated that occupancy and density estimates obtained from camera trap data tend to have a species-specific positive relationship and that under certain circumstances camera trap-derived occupancy can reflect variation in species' abundance across the landscape.

Impact statement

The results presented in this thesis have implications for mammal conservation in the Neotropics, as well as for protected area policy and management in Brazil. They also have practical implications for the use of camera traps in wildlife research globally. Furthermore, at a local scale some results can be used to inform current land use conflicts in the mosaic of protected areas studied.

One of the main conclusions of this thesis is that strict PAs play a vital role in maintaining Cerrado wildlife and without them the conservation of larger and threatened mammal species would be compromised. Results from the analysis of an extensive camera trap dataset clearly demonstrate the importance of formal habitat protection at a time when the future existence of many Brazilian PAs is not secure. However, these results also suggest that large parts of the Cerrado that are not subject to strict management and have higher human pressure than the study region may provide limited contribution to the conservation of large-sized sensitive mammals. This has important implications for PA policy in Brazil, as strict PAs only cover 3% of the Cerrado and 60% of the PA coverage in the biome is conferred by the least restrictive category of PA. The findings presented here suggest that the policy of favouring less restrictive types of management requires reassessment and that the creation of strict PAs should be prioritised in the Cerrado if large mammals of conservation concern are to be effectively protected. Furthermore, the difference in conservation performance between PA types highlights the need to go beyond simple metrics of PA coverage when assessing PA effectiveness. This thesis provides a local scale example of PA assessment using indicators directly linked to conservation outcomes, which could be scaled up to the biome or national level.

Results presented here also revealed the conservation value of secondary savanna that has regenerated from clear cut, indicating that under adequate conditions areas of secondary habitats may still support a diverse mammal community in the Cerrado. Given the resilience of some savanna formations, such results give reason for cautious optimism about the conservation potential of vast areas of the Cerrado that could be restored to comply with national environmental law.

Finally, it was demonstrated here that a camera trapping protocol widely used to survey tropical forest mammals is also adequate to produce precise occupancy estimates for globally threatened mammal species in the Cerrado. Additionally, this thesis presents the first implementation of the Random Encounter Model (a method used to estimate density from camera trap images without the need for individual recognition) in the Neotropics and illustrates the great potential of this technique to provide abundance data currently lacking for many mammal species in this region. Furthermore, analyses conducted here provided empirical evidence that occupancy estimates from a single camera trapping design can adequately reveal the effect of covariates on the abundance of multiple species. This suggests that, under certain circumstances, camera trap-derived occupancy will often reflect changes in species' abundance across the landscape, being a useful metric in the study and monitoring of mammal populations globally.

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I started collecting the data used in this thesis in 2012, but the starting point of this PhD project can be traced back to February 2004, when I first visited Grande Sertão Veredas National Park as an undergrad intern with Instituto Biotrópicos. In the 15 years between that first visit and finishing this thesis I had the opportunity to work in almost all protected areas in the Sertão Veredas-Peruaçu mosaic (SVP), serve as a member of SVP's advisory board and live close to some of the protected areas I studied. During this period I got to know hundreds of people and many organisations who helped shape this research and my understanding of northern Minas Gerais. I cannot possibly name everyone in this section, but I am sincerely grateful to all of them. Therefore, I have to focus here on those who were most influential to this work.

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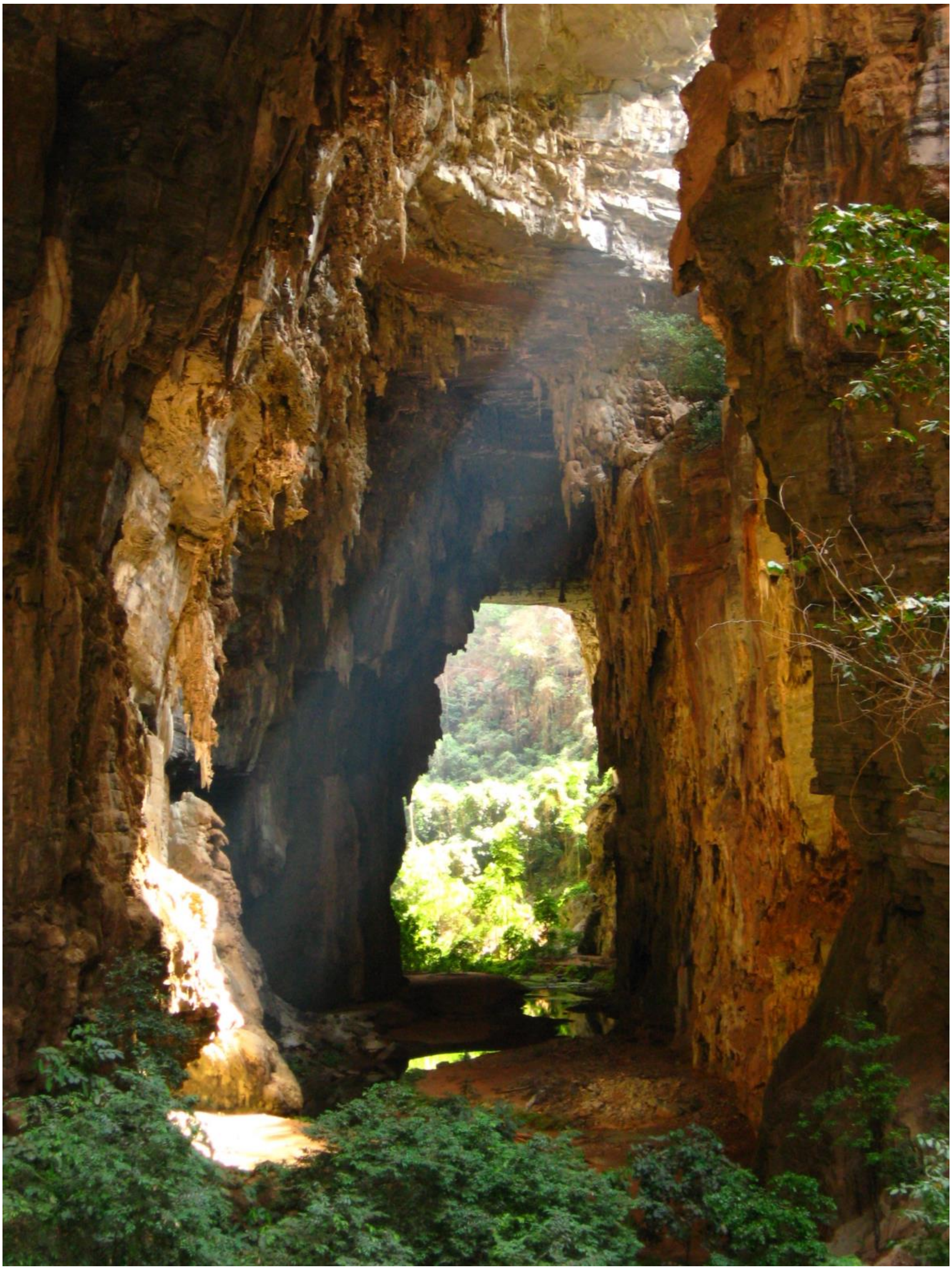
Chapter 1: Introduction



Janelão cave at Cavernas do Peruaçu National Park

1.1. Biodiversity crisis and protected areas

Human impacts have caused a dramatic loss in biodiversity, both in terms of species numbers and abundance of individuals (Dirzo et al. 2014). On average, vertebrate populations have declined 60% since 1970 (WWF 2018), human pressure is increasing in areas of high biodiversity (Venter et al. 2016) and 75% of the world's terrestrial surface is significantly altered (IPBES 2019). The establishment of protected areas (PAs) has been a key policy to mitigate this current biodiversity crisis, which would be even more extreme without them (Watson et al. 2014). As of 2018 terrestrial PAs covered approximately 20 million km^2, representing 14.9% of the earth's land surface (UNEP-WCMC et al. 2018). This is close to the Aichi Target 11 of protecting 17% of land and inland waters by 2020 – one of the targets in the strategic plan adopted by the Convention on Biological Diversity in 2010 (www.cbd.int/sp/).

However, Aichi Target 11 is more nuanced than the areal indicator suggests and also states that the PA system should to be "effectively and equitably managed, ecologically representative and well-connected" (CBD 2013), recognising that a single measure of coverage alone could not ensure that conservation end-goals would be achieved (Barnes 2015). In fact, despite global PA coverage being close to the 17% target, Butchart et al. (2015) estimated that the current PA system would require an expansion to cover approximately 28% of the earth's terrestrial surface if national, ecoregion and species-specific targets were to be met. In addition to adequately represent biodiversity values, it is important that established PAs are able to retain these values. However, PAs very frequently face threats related to the use of biological resources, modification of ecosystems and other anthropogenic disturbances (Schulze et al. 2018) that can erode the biodiversity values they should be protecting. Indeed, one-third of the area covered by terrestrial PAs worldwide is under intense human pressure, potentially undermining their contribution to conservation (Jones et al. 2018).

1.2. Protected area effectiveness

Because simply creating PAs does not necessarily equate to safeguarding the species and ecosystems within their borders, assessing PA effectiveness is key to ensure the objectives of habitat protection are being achieved (Mascia et al. 2017). Such assessments are useful both in retrospective performance evaluations of current PAs (e.g. Craigie et al. 2010) and also to inform the best strategies for future expansion of the system (e.g. Venter et al. 2014). There are several ways of measuring PA effectiveness, but they can be broadly divided in three groups: coverage of species geographic range (e.g. Rodrigues et al. 2004; Venter et al. 2018), evaluation of management capacity (e.g. Leverington et al. 2010; Geldmann et al. 2015), and counterfactual comparisons of ecological outcomes (e.g. Andam et al. 2008; Geldmann et al. 2013; Gray et al. 2016). In short, these assessments address distinct but complementary questions crucial to the success of PAs: Were PAs established in the right place? How well are PAs being managed? Are PAs actually safeguarding biodiversity and ecosystems?

Assessments of the adequacy of PA locations are most frequently based on analyses of the spatial overlap between PAs and species' geographic range. Since the beginning of this century scientists have known that some species were left out of the global PA system and that creation of new areas should be more targeted (Rodrigues et al. 2004). Nevertheless, a more recent assessment revealed that 17% of the world's threatened vertebrates were still not covered by a single PA and that 85% were not covered in a way likely to ensure their persistence in the future (Venter et al. 2014). This mismatch occurs because the creation of PAs is not only driven by knowledge about biodiversity values, but also by economic, political and social pressures. This is illustrated in the results of a recent analysis revealing that mean species richness of threatened vertebrates is very similar among recently created PAs (after 2004), older PAs (established before 2004), and even across the whole globe (Venter et al. 2018), indicating that creation of PAs have not targeted areas with high concentration of species of conservation concern. Indeed, economic reasons seem to play an important role in the establishment of PAs worldwide, with protection biased towards lands of low economic value, located in remote areas and on high terrain (Joppa & Pfaff 2009; Venter et al. 2018). Despite the fact that PAs could have been created in more strategic locations, they are not completely random in relation to biodiversity. For example, proportion of PA cover in centres of vertebrate diversity, although still insufficient, is higher than the global proportion of land protected (Jenkins et al. 2013) and concentration of endemic species seems to have influenced the establishment of PAs globally (Loucks et al. 2008).

A second type of effectiveness assessment investigates the management capacity of PAs and usually relies on questionnaire-based evaluations collectively termed Protected Area Management Effectiveness (PAME). PAME assessments assign scores to PAs based mostly on qualitative or ordinal data collated from questions about their management cycle, including elements of planning, inputs, process, outputs and outcomes (Hockings 2003; Leverington et al. 2010). These evaluations have revealed that many PAs face major deficiencies in their management (Leverington et al. 2010), but scores seem to be improving over the years (Geldmann et al. 2015).

When PAME assessments are robustly implemented they can be useful for the adaptive management of PAs, but it is unclear whether the evaluation scores correlate well with ecological outcomes (Coad et al. 2015). A few studies have failed to find any relationship between results from PAME evaluations and direct measures of PA performance. For instance, an assessment in the Amazon found no correlation between PAME scores and PA’s ability to avoid forest fires, with high-scoring and low-scoring PAs being similarly effective (Nolte & Agrawal 2013). Similarly, an investigation of PA effectiveness in mitigating deforestation in the Brazilian Cerrado showed that PAME scores, either aggregated or of individual components of the evaluation, did not correlate with avoided conversion (Carranza et al. 2014b). On the other hand, however, a recent global analysis found an association between animal population trends and PAME scores for the component of the evaluation related to staff and resources, with PAs that scored higher in this component being more likely to see an increase in abundance of species (Geldmann et al. 2018). Nonetheless, authors of this study noted that their model explained only a relatively small part of the variance in the data and also highlighted the limited spatial overlap between the two global databases used, calling for a more concerted effort in data collection on management capacity and ecological outcomes of PAs.

A third group of assessments evaluate PA effectiveness via comparisons of ecological outcomes, such as deforestation or species abundance, between protected and unprotected land. These assessments are known as impact evaluation and they try to understand what would have happened in the absence of protection (Gertler et al. 2016). In other words, they attempt to make a causal link between the establishment of PAs and the outcome observed (e.g. reduced deforestation rates).

To infer causality this type of evaluation needs to control for confounding factors that may influence the outcome being measured. For example, because PAs are usually biased towards marginal lands that are less likely to be converted to anthropogenic land uses than the average patch of vegetation on unprotected land (Joppa & Pfaff 2009), a direct comparison between randomly selected locations inside and outside PAs may overestimate the effect of protection simply because for reasons other than protection the location inside a PA has lower probability of losing its natural vegetation cover. A more adequate approach is to explicitly account for other factors that influence conversion, such as accessibility and suitability for agriculture (e.g. Andam et al. 2008; Joppa & Pfaff 2011). In impact evaluation of PAs this is usually achieved through a matching process (counterfactual unprotected sites are selected to match relevant characteristics of protected sites) or including confounding factors as covariates in statistical analysis (Mascia et al. 2017). Most counterfactual studies of PA effectiveness so far have focused on loss of natural vegetation (as data on extensive areas can be obtained remotely via satellite images) and have provided overwhelming evidence that legal protection reduces land conversion in distinct regions and ecosystems (Andam et al. 2008; Joppa & Pfaff 2011; Nolte et al. 2013; Geldmann et al. 2013; Carranza et al. 2014a; Françoso et al. 2015; Ament & Cumming 2016).

On the other hand, the effect of habitat protection on biodiversity is less clear than its impact on vegetation cover. Due to logistical, financial and technical challenges of obtaining accurate and precise biodiversity metrics in large areas under contrasting managements, data that allow this type of assessment has not been collected widely. Nonetheless, there is some evidence that PAs have a positive impact on local biodiversity. A review of 42 studies investigating the effect of protection on species population trends (change over time) found that in 31 of them PAs had a positive impact – even if in some cases the population was still declining under protection, it was at a lower rate than outside PAs (Geldmann et al. 2013). A global meta-analysis investigating the effect of protection on local biodiversity levels showed that on average PAs support higher abundance and species richness of terrestrial vertebrates and arthropods than nearby unprotected lands (Coetzee et al. 2014). Similarly, Gray et al. (2016) used a global database of species records to estimate that samples from PAs contained 10% more species and almost 15% more individuals than samples from outside PAs.

Although this general pattern is encouraging, these assessments have limitations related to the relative scarcity of field studies that collected suitable data to perform counterfactual comparisons of local biodiversity. The most recent global meta-analysis on this topic found only 86 publications between 1975 and 2011 that relied on such data (Coetzee et al. 2014), an average of less than 2.5 papers/year. Likewise, Geldman et al. (2013) highlighted that the low number of studies matching their inclusion criteria revealed a lack of sufficient evaluation of PA effectiveness at safeguarding local biodiversity, and cautioned against the generalisation of their findings. This lack of studies is particularly acute in the Neotropical region: the review investigating effect of protection on population change had only one study conducted in the Neotropics (Geldmann et al. 2013). Moreover, although the meta-analysis relied on data from 27 published studies in this zoogeographic region (Coetzee et al. 2014), only two of them had the original objective of assessing the effect of habitat protection, which may lead to comparisons between areas with distinct natural characteristics.

1.3. Camera trapping in biodiversity assessments

Given that the gaps in knowledge about the effect of PAs on biodiversity is in part caused by the logistical and technical challenges of collecting local-scale data to perform counterfactual assessments, remote sensors such as camera traps and acoustic devices are well-suited to help overcome this barrier. Surveys using remote sensors can be easily standardised and designed to cover relatively large areas in a cost-effective manner (e.g. Rovero & Ahumada 2017), two important features in assessing PA effectiveness based on local biodiversity metrics. Standardisation allows meaningful comparisons across distinct locations, whereas large cover ensures the locations surveyed are representative of the PAs assessed and of the regional landscape. Large-scale standardised camera trap surveys are being conducted in tropical forests across the globe to uncover patterns in mammal community structure (Ahumada et al. 2011), to monitor population trends over time (Ahumada et al. 2013; Beaudrot et al. 2016) and to understand the influence of local temperature change on species distribution (Beaudrot et al. 2019a). Such approaches readily accommodate counterfactual thinking (i.e. what would have happened in the absence of a conservation intervention) and can be adapted to answer questions about PA effectiveness. Indeed, the integration of local and regional camera trap initiatives has the potential not only to address issues of PA performance, but to tackle many of the global biodiversity challenges that require large-scale standardised data (Steenweg et al. 2017).

Automatic cameras were being deployed to photograph wildlife as early as the 1890s (Kucera & Barrett 2011), but it was the use of camera traps to estimate tiger density a century later (Karanth 1995; Karanth & Nichols 1998) that probably marked the beginning of more systematic scientific applications. Since then camera traps have constantly grown in popularity among scientists, especially after digital units became widely available at a reasonable cost (Rowcliffe & Carbone 2008; Burton et al. 2015). Besides the decrease in costs in the last 10-15 years, camera trapping benefitted from the development of occupancy modelling (MacKenzie et al. 2002, 2006) that enabled more complex hierarchical analysis of data from unmarked species (e.g. O'Connell et al. 2006; Linkie et al. 2007; McShea et al. 2009). Camera traps lend themselves naturally to occupancy estimation and modelling due to their cost-effectiveness in gathering presence-absence data on species usually difficult to observe and/or occurring at low densities (O'Connell & Bailey 2011). Occupancy is broadly defined as the proportion of sites occupied or used by a species (MacKenzie et al. 2002, 2004) and has been adopted in camera trap studies to understand trends in species populations (O'Brien et al. 2010; Ahumada et al. 2013; Andresen et al. 2014; Beaudrot et al. 2019b), habitat use (Gray 2012; Cassano et al. 2012; Rovero et al. 2014; Tobler et al. 2015), effect of land use and management schemes (Kinnaird & O'brien 2012; Rich et al. 2016; Deere et al. 2018; Boron et al. 2019), niche partitioning and species interaction (Sollmann et al. 2012; Schuette et al. 2013; Rich et al. 2017b; Ferreguetti et al. 2018), and impact of anthropogenic factors (Erb et al. 2012; Zimbres et al. 2013; Reilly et al. 2017; Oberosler et al. 2017), among many other topics.

Despite being widely adopted, occupancy modelling in camera trap studies has been criticised by some authors due to the influence of animal movement on estimates (Efford & Dawson 2012). Variation in movement rates and home range can result in occupancy not adequately reflecting change in abundance (Neilson et al. 2018), therefore losing part of its appeal as a metric to monitor wildlife populations. Evaluations of the relationship between occupancy and abundance estimates derived from camera trap surveys have been conducted on very few occasions, always finding a positive correlation but with various levels of predictive power (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017). Therefore, an empirical in-depth understanding of the occupancy-abundance relationship is still greatly needed for a broader range of contexts and species, and it will certainly help improving the application of occupancy modelling to camera trap data.

1.4. Large mammals and protected areas

Camera traps can be used to study amphibians, reptiles and birds (e.g. O'Brien & Kinnaird 2008; Ariefiandy et al. 2013; Barata et al. 2018), but they are most effective in surveys of medium- to large-sized mammals (Burton et al. 2015). Although large mammals represent only a fraction of species present in a location, they are linked to important ecological processes, such as dispersal of large-seeded plants that disproportionally influence the carbon stock in a forest (Bello et al. 2015) and regulation of prey populations (Terborgh et al. 2001; Owen-Smith 2019). Moreover, some of these large animals may act as ecosystem engineers, creating habitats for other vertebrates (e.g. Beck et al. 2010; Reider et al. 2013; Desbiez & Kluyber 2013) and changing the vegetation structure, either directly via trampling, rooting and grazing (Roldán & Simonetti 2001; Levick & Rogers 2008; Davies et al. 2018) or indirectly via the influence of mammalian predators over herbivores (Terborgh et al. 2006; Beschta & Ripple 2016; Morris & Letnic 2017).

Additionally, large mammals have higher extinction risk than smaller species of this taxonomic group (Cardillo et al. 2005; Cooke et al. 2019), are disproportionally affected by bushmeat hunting (Ripple et al. 2016b; Benítez-López et al. 2019), and severely threatened by habitat loss and fragmentation (Woodroffe & Ginsberg 1998; Chiarello 1999; Morrison et al. 2007; Ripple et al. 2015, 2016a). Therefore this group of species can greatly benefit from conservation interventions that mitigate anthropogenic threats. Among possible interventions, establishment of PAs is one that has been adopted widely (Watson et al. 2014). However, the extent to which PAs are effective in safeguarding local animal populations is not completely clear (see 'Protected Area effectiveness' section of this chapter), and this general knowledge gap also applies to large mammals. Craigie et al. (2010) observed severe population declines in large mammals inside African PAs, but noted wide geographic variation, with some regions showing more positive trends and other suffering sharp declines. Barnes et al. (2016) using a global dataset revealed a positive population trend inside PAs for mammals with larger body size, but also found that the relationship between body size and population trend was u-shaped, indicating declines in species of intermediate size. In Brazil, a recent longitudinal assessment of Iguaçu National Park indicated the park was successful in maintaining a largely intact mammal community, as there was no evidence of decline in large mammal occupancy over the monitoring period (Xavier da Silva et al. 2018). Nevertheless, none of those studies (i.e. Craigie et al. 2010; Barnes et al. 2016; Xavier da Silva et al. 2018) had counterfactuals to compare population trends against locations without protection, precluding a more informative assessment of PA effectiveness.

Although still challenging, snapshot assessments of biodiversity levels in areas under distinct management regimes are more feasible than long-term monitoring of trends. Such assessments have showed that larger animals in Africa and India tend to benefit from stricter protection (e.g. Kinnaird & O'brien 2012; Rich et al. 2016; Velho et al. 2016; Drouilly et al. 2018), but seldom has the diversity of Neotropical mammals been compared in locations with distinct levels of protection. Carrillo et al. (2000) found that relative abundance of mammals, particularly of hunted and globally threatened species, was higher in a Costa Rican national park where resource extraction was prohibited than in a nearby forest reserve that allowed some types of economic activity. Similarly, density of pumas (*Puma concolor*) in the Atlantic Forest of Argentina was found to be higher in a better-managed national park than in two other PAs where logging and illegal hunting occurred (Paviolo et al. 2009). On the other hand, Negrões et al. (2011), comparing two areas under distinct management in the Amazonian arc of deforestation, observed that species richness and relative abundance of large mammals was higher in a private ranch's forest remnant than in a state park. These assessments, however, have evaluated just two or three contrasting areas and did not explicitly account for potential confounding factors, such as differences in environmental features, limiting inferences about the effect of protection.

Compounding this rather incomplete picture about the effect of habitat protection on large mammals in the Neotropics, results from a meta-analysis suggested a negative effect of protection status on local biodiversity in Latin America and one of the factors hypothesised to have contributed to this unexpected finding was the increase of mammals >1 kg outside PAs (Coetzee et al. 2014). As part of the Neotropical region, knowledge about the effect of Brazilian PAs on large mammals (or any other taxonomic group) is also very limited, despite the country having the largest PA network in the world (UNEP-WCMC & IUCN 2016) and being a megadiverse nation (Mittermeier et al. 2005). Indeed even basic data about species occurrence in Brazilian PAs is lacking. Oliveira et al. (2017) estimated that < 1% of all PAs in the country are well sampled and 71% of them have as few as 0.01 species record (of any taxonomic group) per km^2, with regional variation in intensity of sampling. One of the regions with low sampling intensity is the Brazilian Cerrado (Oliveira et al. 2017), which also has only a small fraction of its original area within PAs (MMA 2018) and faces higher rates of deforestation than the Amazon (INPE 2018).

1.5. Brazilian Cerrado and the Sertão Veredas-Peruaçu mosaic

The Cerrado is one of six terrestrial biomes in Brazil and the world's most biodiversity-rich savanna (Klink & Machado 2005), supporting a large number of species: 204 amphibians, 278 reptiles, 850 birds, 251 mammals and more than 13,000 plant species – which corresponds to 37% of all plants in Brazil (Fernandes et al. 2016). The typical savanna formation characteristic of the biome is formed by trees and large shrubs providing 10-60% cover and a well-developed herbaceous layer (Ratter et al. 1997). Nonetheless, the Cerrado is highly heterogeneous with variation in soil characteristics, climate and fire interacting to determine vegetation formations ranging from open grasslands to closed riparian forests (Silva et al. 2006; Bueno et al. 2018). Overall Cerrado's various vegetation formations can be broadly divided in three groups according to their structural features: grasslands, savannas and forests (Ribeiro & Walter 2008).

Due to this great heterogeneity, it has been argued that the Cerrado should not be considered a single biome (Batalha 2011) and some authors prefer to use the term 'domain' when referring to the Cerrado or any of the other five broad phytogeographic regions of Brazil (e.g. Bueno et al. 2018). I decided to use the term 'biome' as it is commonly adopted in policy, such as in national action plans (MMA 2014a), deforestation monitoring programs (INPE 2018), priority areas for conservation (MMA/PROBIO 2007; WWF-Brasil & MMA 2015) and consolidation of data on protected area coverage (MMA 2018).

The Cerrado is the second largest biome in Brazil and originally covered 25% of the country, sharing transitional zones with four other biomes (Pantanal, Atlantic Forest, Caatinga and Amazon) and with rivers that flow to 10 of the 12 Brazilian hydrographic basins (Fernandes et al. 2016). However, the fast expansion of Brazil's agricultural frontier in the second half of the 20th century, particularly after the 1970s, transformed vast areas of the biome (Klink & Machado 2005). Approximately 40% of the original area is now pasture or cropland (Sano et al. 2019) and this extensive conversion played a pivotal role in Brazil's emergence as a global agricultural powerhouse (Rada 2013). For instance, in 2010 farmland in the Cerrado was responsible for 64% of the national cattle production and 40% of the country's agricultural Gross Domestic Product (MMA 2014a).

Recent data from Brazil's National Institute for Space Research revealed that although Cerrado conversion decreased from approximately 30,000 km^2/year in the early 2000s, it is still substantial at an average of 7,000 km^2/year in 2017-2018 (INPE 2018). This deforestation rate is similar to that in the Brazilian Amazon (INPE 2018), despite the tropical forest biome occupying a much larger area. Only half of the Cerrado natural vegetation remains (MMA 2014a), but vast areas can still be legally deforested (Vieira et al. 2017) to make way for agriculture expansion. Despite PAs being effective in avoiding deforestation (Carranza et al. 2014a), only 8% of the biome's original area is designated as PAs (MMA 2018). Furthermore, over half of this protection coverage is provided by the least restrictive category of PA (MMA 2018), which has not been effective at halting land conversion (Françoso et al. 2015).

According to the Brazilian system of PAs (Brasil 2000), when PAs exist in close proximity to each other they should form a mosaic that is managed in an integrated way that promotes stakeholder participation. One such initiative is the mosaic of protected areas Sertão Veredas-

Peruaçu (SVP), the first of its kind in the Cerrado. SVP is formed by 14 PAs – eight strict PAs (IUCN categories I-IV) and six multiple-use PAs (IUCN categories V-VI) – and two indigenous lands covering approximately 18,000 km^2 (Table 1.1, Fig. 1.1). Importantly, the establishment of a mosaic does not change the regulations of individual PAs (Brasil 2000); it is just an attempt to strengthen their performance by bringing together PA staff and stakeholders that work in the same region, sharing similar objectives, problems and challenges.

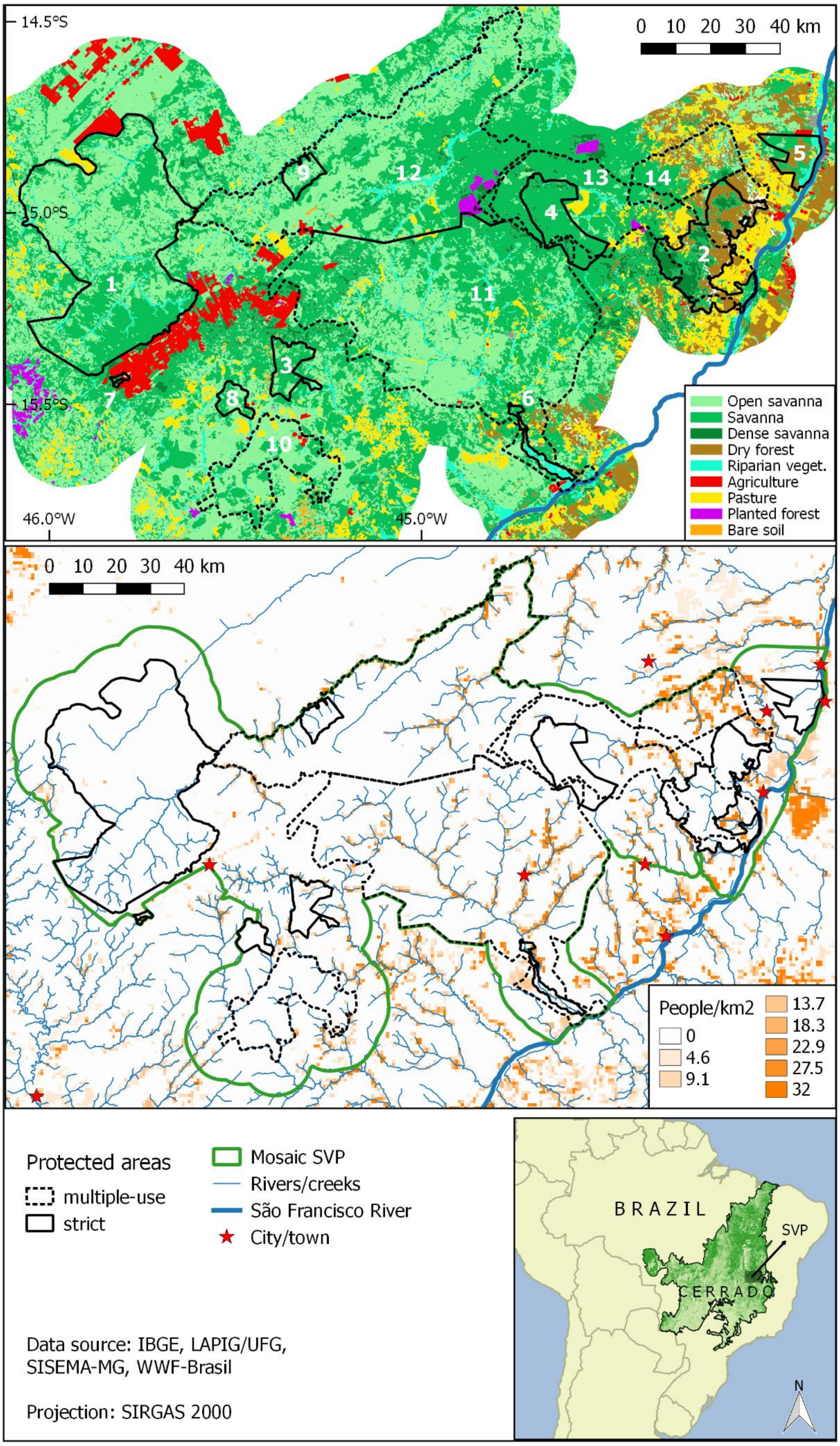
The SVP mosaic is located in the northernmost portion of Minas Gerais state and in a small area of Bahia state (due to a national park shared by both states), encompassing a number of priority areas for biodiversity conservation and scientific research (Fundação Biodiversitas 2005; WWF-Brasil & MMA 2015). It extends over 11 municipalities that have relatively low economic and development indicators and total population of 168,000 people (IBGE 2019). However, not all this population is within the limits of the mosaic, as it does not overlap completely with the area of all 11 municipalities. For example, the city of Januária has by far the largest population in the region, but its urban centre with more than 40,000 people (IBGE 2019) is outside SVP. Within the mosaic, population is distributed in six small urban centres (<15,000 inhabitants each, range: 2,000-14,000 – IBGE 2019) and scattered rural villages. In general SVP is sparsely populated (Fig. 1.1) with an average population density of 2 people/km^2, varying substantially among individual areas (Table 1.1). Road infrastructure is not well developed in the region and until the early 2000s there was only one paved road, approximately a 100-km stretch along the São Francisco River, part of it within the eastern-most portion of the mosaic. Since then other roads have been paved, but very few of them go across SVP and the vast majority remain unpaved.

Table 1.1: Protected areas of the Sertão Veredas-Peruaçu mosaic, Brazilian Cerrado.

Protected Area	IUCN category*	Area (km^2)	Year created	Human density	Management authority
Strict protected areas					
Grande Sertão Veredas National Park (1)	II	2,300	1989	0.05	ICMBio
Cavernas do Peruaçu National Park (2)	II	568	1999	0.51	ICMBio
Serra das Araras State Park (3)	II	111	1998	1.09	IEF-MG
Veredas do Peruaçu State Park (4)	II	312	1994	0.00	IEF-MG
Mata Seca State Park (5)	II	136	2000	0.00	IEF-MG
Rio Pandeiros Wildlife Refuge (6)	IV	61	2004	1.81	IEF-MG
Veredas do Pacari and Arara Vermelha Private Reserves (7)	IV	5.9	2004, 2005	0.43	Private owners
Aldeia Private Reserve (8)	IV	73	2008	0.00	Delta Sucroenergia
Porto Cajueiro Private Reserve (9)	IV	90	2004	0.01	IDESE
Multiple-use protected areas					
Veredas do Acari Sustainable Development Reserve (10)	VI	609	2003	0.20	IEF-MG
Rio Pandeiros Environmental Protection Area (11)	V	3,801	1995	2.24	IEF-MG
Cochá Gibão Environmental Protection Area (12)	V	2,844	2004	1.14	IEF-MG
Cavernas do Peruaçu Environmental Protection Area (13)	V	1,438	1989	2.74	ICMBio
Xacriabá Indigenous Land** (14)	V	530	1987	12.44	Xacriabá people

* As defined in the World Database of Protected Areas (UNEP-WCMC & IUCN 2019). For PAs not listed in the database, I assigned a category based on IUCN guidelines (Dudley 2008). **Although Indigenous Lands are not included in the national system of protected areas (Brasil 2000), they are usually incorporated in mosaics of protected areas and that is the case at Sertão Veredas-Peruaçu.

Information on area and year of creation from the websites of IEF-MG, ICMBio and FUNAI. Grande Sertão Veredas NP was expanded from 840 km^2 to its current size in 2004. Xacriabá IL is composed of two adjacent areas, the first established in 1987 with 460 km^2 and the second in 2003 with 70 km^2; The Xacraiabá people are currently claiming an additional 433 km^2 of land that partially overlaps with Cavernas do Peruaçu National Park (Ferreira 2018). Human density data is from the 2010 national census (IBGE 2017) and is given in people/km^2.



Data source: IBGE, LAPIG/UFG, SISEMA-MG, WWF-Brasil

Projection: SIRGAS 2000

Figure 1.1: Land use (top) and distribution of human density (bottom) at the Sertão Veredas-Peruaçu (SVP) mosaic. Inset shows the location in Brazil and the remnant vegetation in the Cerrado (green).

The low population density and relative distance from large economic centres prevented widespread conversion of the natural cover in the region, with up to 80% of the native vegetation left (WWF-Brasil 2011). It is important to note, however, that some of the areas currently covered with natural vegetation have been altered by anthropogenic uses, particularly grazing by cattle, collection of firewood, charcoal production and eucalyptus plantation. Larger areas converted to pasture and agriculture are found at the eastern and western extremes of the mosaic (Fig. 1.1). In general, large conversions in the west happened mostly after the 1980s following the establishment of a village that would later become the town of Chapada Gaúcha, whereas significant conversions in the east started much earlier, as the São Francisco River was a main route towards the interior of Brazil in historical times and enabled the establishment of villages, towns and farms.

Although largely within the Cerrado, SVP's eastern portion has a transitional zone with the Caatinga biome, a complex of thorn scrub and seasonally dry forests associated with semi-arid climate. Due to this location in an ecotone between two biomes, several vegetation formations are found at SVP (Fig. 1.1). In broad terms the eastern portion, influenced by the Caatinga, is dominated by dry forests and forms of very dense savanna, with gallery forests and semideciduous riparian forests along water courses. The western and central portions are dominated by savannas with a wide range of trees and shrubs densities, usually with palm swamps along creeks and rivers. These palm swamps, known as *veredas*, are strikingly beautiful and very characteristic of the region, lending their name to many of the PAs. Mean temperature in the region is 24 ^{o}C and average annual rainfall ranges between 800 and 1,400 mm (MMA/IBAMA/Funatura 2003; MMA/IBAMA/Geoclock 2005), usually increasing from east to west.

Some of SVP's PAs are relevant at a national level not only because of their biodiversity value. For example, Grande Sertão Veredas National Park is named after one of the most famous books in Brazilian literature (MMA/IBAMA/Funatura 2003), which describes in detail the landscape and animals now protected by the park. Similarly, Cavernas do Peruaçu National Park harbours a karst system of global significance, with hundreds of caves and important archaeological sites that have all the attributes to become a UNESCO world heritage site (MMA/IBAMA/Geoclock 2005). This park recently opened for visitors and the number of tourists is growing each year, although tourism is still very incipient in SVP as a whole.

The vertebrate fauna in the region is relatively well-known due to rapid inventories conducted for the management plans of some PAs (e.g. MMA/IBAMA/Funatura 2003; MMA/IBAMA/Geoclock 2005), however the discoveries of new species of frog and lizard (Nogueira & Rodrigues 2007; Teixeira et al. 2012), as well as the rediscovery of a small canid species thought to be extinct in Minas Gerais state (Ferreira et al. 2015) and the record of a previously unknown colour morph of maned wolf (Ferreira et al. 2017b) indicate that even for vertebrates there is still much diversity to uncover. SVP harbours a virtually intact large mammal community with at least 35 species >1 kg, representing 80% of all large mammals found in the Brazilian Cerrado (Ferreira & Oliveira 2014). Top predators (jaguar *Panthera onca*, puma *Puma concolor*), large herbivores (tapir *Tapirus terrestris*, marsh deer *Blastocerus dichotomus*) and insectivores (giant anteater *Myrmecophaga tridactyla*, giant armadillo *Priodontes maximus*), heavily-hunted species (white-lipped peccary *Tayassu pecari* and collared peccary *Pecari tajacu*) and rare small carnivores (bush dog *Speothos venaticus*, Pampas cat *Leopardus braccatus*) are all present in at least one of SVP's PAs. This community is also comprised of species of conservation concern: seven are globally threatened (IUCN 2017) and 11 are in the national red list (MMA 2014b).

1.6. Thesis overview and structure

The overall aim of this thesis is to contribute towards a better understanding of the effects of habitat protection and anthropogenic disturbance on the Cerrado mammal community. In addition, to improve the understanding about camera trap-derived metrics and their use in biodiversity assessments, I investigate the relationship between occupancy and density estimates obtained via the Random Encounter Model. Data used in this thesis come from specifically designed camera trap surveys I conducted at seven PAs with contrasting management regimes in SVP. The thesis is structured in the following way:

In Chapter 2, I take advantage of the quasi-experimental setting of a state park that had one-third of its natural vegetation completely removed before being designated as a PA to assess the conservation value of secondary savanna vegetation for large mammals. To my knowledge this is the first systematic comparison of the large mammal community in old growth and secondary habitats in the Cerrado.

In Chapter 3, I conduct a counterfactual assessment of PA effectiveness at safeguarding local mammal diversity. I adopt a multi-species occupancy modelling approach to estimate the impact of contrasting types of PA while controlling for confounding factors that may influence the distribution of species in the region. I present occupancy and species richness estimates demonstrating that diversity levels are much higher in strict PAs than in multiple-use PAs, particularly for larger (>15 kg) and threatened mammals, and discuss the implications of these results for the PA policy in the Cerrado.

In Chapter 4, I shift from spatial to temporal patterns and investigate the influence of anthropogenic pressure on the activity of 15 mammal species. I use approaches specifically developed to estimate activity metrics from camera trap data as well as Generalized Linear Mixed Models to reveal that activity of most species is not affected by either PA type or distance to household. Moreover, my results suggest that at SVP environmental factors have greater influence on the period mammal species are active than indicators of anthropogenic pressure.

In Chapter 5, I combine multi-species occupancy modelling and density estimation via the Random Encounter Model (REM) to investigate the occupancy-density relationship in camera trap studies and to assess how well occupancy estimates reflect change in abundance. For this assessment I estimate occupancy and density for four mammal species with a wide range of body mass and ecological requirements in five distinct areas. My results show that occupancy and density tend to have a species-specific positive relationship, and that occupancy estimates can often reflect spatial variation in animal abundance. I discuss the implications of these results for the use of camera traps in monitoring and the potential of REM to estimate density of Neotropical mammal species.

In Chapter 6, I provide an overall discussion of the thesis, highlighting the key findings and implications for conservation. Finally, I present as appendices two papers published during my PhD in which I assess the potential negative impacts for biodiversity of expanding the Xacriabá Indigenous Land over one of SVP's national parks (Appendix 1) and report the first ever record of a black-coloured maned wolf photographed by camera traps at SVP (Appendix 2).

Chapter 2: Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado

Lake at Veredas do Peruaçu State Park

This chapter has been published as:

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2.1 Introduction

The area of the planet covered by secondary vegetation is predicted to increase by between 35-75% by 2100, resulting in a large decrease in primary habitat (Hurtt et al. 2011). Given such projected changes, secondary habitats will become an essential element of longer-term conservation strategies. Currently, most of the debate about the conservation value of secondary habitats has focused on tropical forests (e.g. Chazdon et al. 2009; Gibson et al. 2011), with a great deal of research supporting the role of secondary forests in the maintenance of tropical forest biodiversity in the face of growing threats (Barlow et al. 2007; Chazdon et al. 2009; Dent & Wright 2009; Solar et al. 2015; – though see Gibson et al. 2011 on the irreplaceability of primary forests). Despite the research interest in primary and secondary forests, there remains a lack of information about the conservation value of secondary savannas, and far less attention has been devoted to such habitats. Even the definition of secondary savanna is not straightforward. Some authors (e.g. Backéus 1992; Barger et al. 2002) have adopted the term as a synonym of derived savanna, using it to describe secondary vegetation established after the destruction of a forest ecosystem. We adopt the suggestion from Veldman et al. 2015) and use the term 'secondary savanna' to characterize a savanna vegetation that regenerated in a region that historically supported savanna ecosystems.

Cerrado, the Brazilian savanna, is formed by a wide variety of vegetation physiognomies encompassing grasslands, savannas and forests (Ribeiro & Walter 2008), but the most widespread formation is a savanna composed by trees and large shrubs about 2-8 m tall generating 10-60% cover, with a grass layer in the ground level (Ratter et al. 1997). Cerrado originally covered around 25% of the country (IBGE 2004) before wide-scale conversion to anthropogenic land uses. Official estimates indicate that approximately 50% of the ecosystem has already been converted (MMA 2014). Expansion of farmland is the main driver of habitat loss in Brazilian ecosystems (Lapola et al. 2013), and this threat is even more acute in the Cerrado, where 40% of the Brazilian agricultural Gross Domestic Product is produced (MMA

2014a). In spite of its importance to the agricultural industry, some converted land may be abandoned or set aside, which could have important implications for persistence of wildlife. This land abandonment can occur for a variety of reasons, including economic changes that make an agricultural activity financially inviable or adjustment to legislation where a portion of the property must be set aside for environmental purposes.

Since most Cerrado vegetation physiognomies are, to some extent, capable of natural regeneration (Hoffmann 1999; Sampaio et al. 2007; Abreu et al. 2011), abandoned lands may recover to form secondary vegetation given time. For example, Jepson (2005) studied land cover dynamics in central Brazil Cerrado, and found that half of the land converted between 1986 and 1999 (ca. 670 km^2) regenerated into secondary native vegetation. However, secondary vegetation is structurally, floristically and functionally different from the original old growth vegetation (Pezzini et al. 2014; Whitfeld et al. 2014; Gomes & Maillard 2015). Cerrado regeneration generally follows a path from open to dense vegetation, with regeneration typified by an increase in tree density and height, and a decrease in herbaceous cover (Durigan & Ratter 2006; Maillard & Costa-Pereira 2010). However, other factors such as frequency of fire and soil conditions also influence the characteristics of the late-succession stage, which can even support a well-developed grass layer (Veldman et al. 2015). Differences in habitat structure and plant community composition between secondary and old growth vegetation could influence spatial distribution and abundance of local fauna. For example, species relying on the grassy layer for food or shelter may respond positively to an increase in secondary savanna in the landscape, especially in early regeneration stages. On the other hand, frugivorous animals could be negatively affected, as zoochoric plant species are replaced by those with abiotic dispersion syndrome in open Cerrado formations (Kuhlmann & Ribeiro 2016). These impacts on herbivores could subsequently influence higher trophic levels, ultimately affecting the whole animal community in the area.

Besides avoiding habitat conversion (Naughton-Treves et al. 2005; Carranza et al. 2014a), protected areas may also promote vegetation recovery on abandoned lands, as anthropogenic impacts are reduced and natural succession is likely to happen. These observations are borne out in the case of Veredas do Peruaçu State Park (VPSP), a protected area in the Cerrado where roughly one third of the area is secondary vegetation that regenerated after clear cut (Gomes & Maillard 2015). VPSP harbours a rich large mammal fauna, comprising at least 28 species >1kg, including globally threatened and rare species (Ferreira et al. 2011, 2015). These facets make the protected area an excellent location for studying the impact of secondary vegetation on mammal abundance and distribution.

Here, we use a quasi-experimental design in order to assess the effect of secondary vegetation on large mammal occupancy (interpreted as probability of use; Mackenzie *et al.* 2004). Since species with different ecological requirements may respond in different ways to vegetation change, we predicted that: (1) occupancy of species with wide dietary breadth (such as yellow armadillo *Euphractus sexcinctus*, maned wolf *Chrysocyon brachyurus* and puma *Puma concolor*) would not be affected by succession stage because they could shift their diets to adapt to variation in resources (e.g. Dalponte & Tavares-Filho 2004, Jacomo *et al.* 2004, Moreno *et al.* 2006). (2) occupancy would be lower in secondary savanna for species that have fruits as an important part of the diet (such as Azara's agouti *Dasyprocta azarae*, white-lipped peccary *Tayassu pecari* and lowland tapir *Tapirus terrestris*), due to a decrease in zoochoric trees and shrubs (Kuhlmann & Ribeiro 2016) and because larger (thus, older) plants generally produce more seeds and fruits (Chapman et al. 1992; Greene & Johnson 1994; Zardo & Henriques 2011). (3) occupancy would be higher in secondary savanna for herbivores that feed predominantly on the grass layer and for species that favour more open habitats (such as Pampas deer *Ozotoceros bezoarticus* and giant anteater *Myrmecophaga tridactyla*), as secondary vegetation in VPSP tend to have a more open canopy (Gomes & Maillard 2015).

Although individual species may respond differently, we predicted community occupancy (a measure of overall use by large mammals) to be higher in old growth savanna for two reasons: 1) denser savanna formations tend to have higher net primary productivity (Grace et al. 2006; Pontes 2010); and 2) few species that potentially occur in VPSP (ca. 10%) have the ecological characteristics to greatly benefit from secondary vegetation. Additionally, due to a lack of specific recommendations on occupancy study design for Brazilian mammals and also to inform the establishment of cost-effective monitoring strategies in the Cerrado, we explored the effect of different sampling schemes on the precision of occupancy estimates for the globally threatened species recorded.

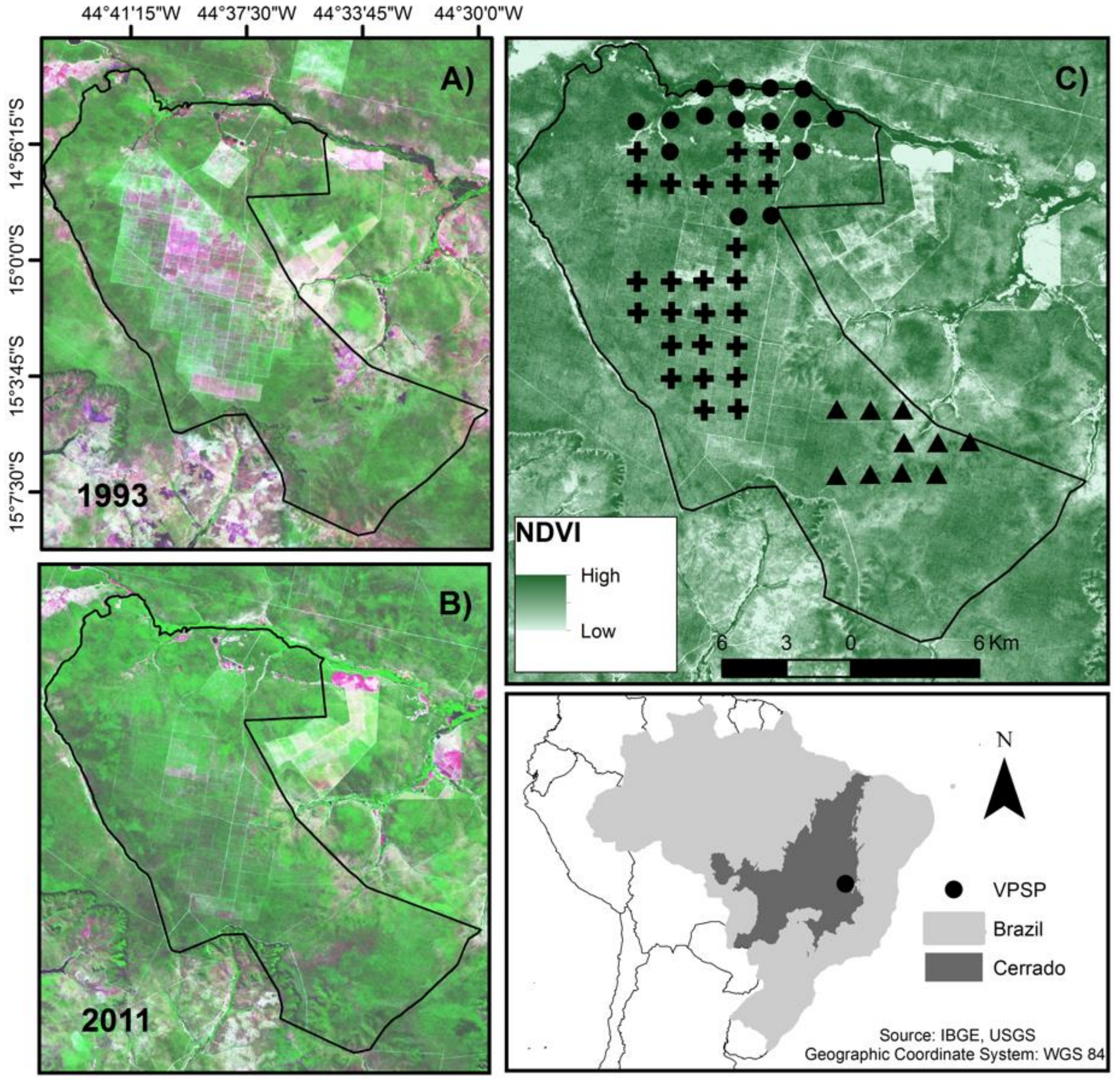
2.2 Material and methods

2.2.1 Study area

We conducted the study at Veredas do Peruaçu State Park, Minas Gerais state, south-eastern Brazil. The 310 km^2 park protects part of the upper Peruaçu River watershed, a priority area for conservation in Brazil (MMA/PROBIO 2007) embedded in the Cerrado hotspot (Myers et al. 2000) (Fig. 1.1). VPSP is predominantly covered with savanna vegetation (cerrado *stricto sensu* covering approximately 95% of the area; WWF-Brasil 2011), generally presenting a fairly dense woody layer (Maillard & Costa-Pereira 2010). *Vereda* – a humid grassland dominated by the palm species *Mauritia flexuosa* – is also an important vegetation type occurring along the Peruaçu River and is concentrated in the park's northern and north-western limits. This river, and associated lakes, is virtually the only source of water inside VPSP during the dry season. The topography is relatively flat (700 to 850 m asl) and the climate is highly seasonal, with a dry season from April to mid-October and a wet season from mid-October to March.

Before being legally protected in 1994, the area was used mainly for eucalyptus plantations, and, to a lesser extent, for charcoal production from native trees and cattle ranching. A single company was responsible for the eucalyptus plantation, which took place from late 1970s to the beginning of 1990s in more than one-third of the park's area (ca. 130 km^2) and involved the clear cut of the native vegetation (Gomes & Maillard 2015). The remainder of the company`s land was kept in its natural state with little to no direct human interference over the vegetation during the period of eucalyptus production, resulting in maintenance of old growth vegetation. Charcoal production from native trees and cattle ranching occurred diffusely in smaller properties around the eucalyptus company land, but was more frequent in the southern portion of VPSP. It is not possible to accurately determine whether only one of these two activities happened in a specific location, but it is likely that a mix of both occurred frequently, with partial removal of the woody vegetation for charcoal and then cattle being brought to browse on the herbaceous layer, with regular use of fire. For this reason, we classified these areas as having mixed-use in the past. Scattered and small patches of less disturbed savanna may have remained within these mixed-use areas.

Savanna areas used for eucalyptus plantation in the past have a more open canopy, shorter trees, lower basal area and slightly less trees and shrubs per hectare than old growth savanna (Maillard & Costa-Pereira 2010; Gomes & Maillard 2015), whereas the variation in vegetation structure within former eucalyptus areas is subtle and is likely to be better explained by fire history and other local conditions than regeneration age (Maillard & Costa-Pereira 2010). We did not have accurate information on vegetation structure of mixed-use areas, however, a lower NDVI value in portions of southern VPSP (Gomes 2006) and the general appearance of the vegetation allow us to infer that vegetation structure in sites that we classified as mixed-use is more similar to areas used for eucalyptus. Despite the difference in vegetation structure between secondary and old-growth savannas, both of them fall within a single Cerrado physiognomy (cerrado *stricto sensu*). With protected area establishment in 1994, the economic activity in the area finished and the savanna vegetation was left to naturally regenerate. The age of secondary vegetation is not homogenous throughout the study area, as eucalyptus trees were logged in different years (Maillard & Costa-Pereira 2010). At the inception of our study, the youngest secondary vegetation in VPSP had been regenerating for 16 years and the oldest for 28 years.



Source: IBGE, USGS
Geographic Coordinate System: WGS 84

Figure 2.1: Vegetation cover and location of camera trap sites at Veredas do Peruaçu State Park (VPSP), Brazil. Landsat image from 1993 (A) showing areas with sparse or degraded vegetation (in pink) and from 2011 (B) showing the recovery of native vegetation in the study area. C) Normalized Difference Vegetation Index (NDVI) from 2011 and camera trap sites surveyed at VPSP. Circles are sites in old growth vegetation, crosses are sites in secondary vegetation that regenerated from eucalyptus plantation and triangles are sites in secondary vegetation that regenerated from mixed use.

2.2.2 Data collection

We surveyed 50 sampling sites (Fig. 2.1) with camera traps (Bushnell Trophycam) following a sampling design that has been widely adopted to estimate large mammal occupancy in different regions of the world (e.g. Ahumada et al. 2011; Kinnaird & O'brien 2012; Rovero et al. 2014; Beaudrot et al. 2016). We divided the park in three sections where potential camera trap locations were established at a density of one sampling site per 2 km^2. We set the camera traps within a 100 m radius of the grid coordinates, in order to select locations with highest probability of recording large mammals. Nevertheless, due to extremely dense vegetation, placement of two camera traps was increased to a 200 m radius from the predetermined grid coordinates.

We surveyed a block of sites for approximately 30 days, and then moved the equipment to survey the next block for approximately the same amount of time. To minimize the probability of changes in occupancy during our study, sampling was conducted only in the dry season and in a relatively short period, between 9 July and 13 October 2012. No lure or bait was used to attract animals.

2.2.3 Data analysis

We assembled a detection history matrix for each of the 18 large mammal species recorded, and following previous studies, defined a sampling occasion as seven camera trap-days (Gray 2012; Ahumada et al. 2013). We analyzed data using the single season occupancy framework, an approach where occupancy and detection parameters are estimated simultaneously using replicated detection/non-detection surveys (MacKenzie et al. 2002, Mackenzie *et al*. 2006). In addition to the regular occupancy model (Mackenzie et al. 2002), we also obtained occupancy estimates using the Royle-Nichols model, an occupancy model where heterogeneity in detection results from variation in the focal organism abundance (Royle & Nichols 2003). We adopted this additional approach as a methodological comparator and to assess reliability.

In our study, it is possible that individuals of some wider ranging species were recorded in more than one camera trap site, failing to meet the assumptions of constant occupancy and of spatial independence among sampling sites (MacKenzie et al. 2006). According to MacKenzie et al. 2004) this first assumption (constant occupancy) could be relaxed if movement between locations occurred randomly (as it is expected for highly mobile species with large home-ranges), but in this case estimates of occupancy is better interpreted as an estimate of probability of use, and not as probability of occupancy. Hereafter, we interpret our estimates as the probability that a sampling site is used by a given species, an approach adopted in other occupancy studies (e.g. Zeller et al. 2011; Tobler et al. 2015). Not meeting the second assumption (spatial independence among sampling sites) can lead to underestimation of standard errors of occupancy estimates, but this problem can be detected by an assessment of model fit and corrected using a variance inflation factor (Mackenzie et al. 2006). Since none of our species models had evidence of lack-of-fit (see the end of this section), we believe this is not a major problem in our study.

We first conducted an exploratory analysis using only the null model (occupancy and detection held constant across sites) to assess each species' detection probability (Mackenzie *et al.* 2002). We defined a cut-off value for detection probability of 0.1, below which occupancy estimates could be biased, leaving ten species to be individually analysed (Table S1; we also excluded puma due to very imprecise occupancy estimates and lack of model convergence). For each of these ten species we fitted further models to investigate the effect of secondary vegetation and of other factors that could potentially affect large mammal occupancy (Table 2.1). We classified each sampling site according to vegetation succession stage, vegetation physiognomy, shortest distance from potential water sources and shortest distance from the Peruaçu River inside VPSP (Table 2.1). Within succession stage, secondary habitats were subdivided according to their use in the past: eucalyptus plantation or mixed-use. Camera trap location in relation to trails was treated as a covariate for detection probability (Table 2.1). Since the number of sampling sites is not particularly large, we fitted univariate models to avoid over parameterization (i.e. we did not use models with more than one covariate per parameter estimated).

Table 2.1: Covariates used to build occupancy models for large mammals at Veredas do Peruaçu State Park.

Covariates	Description	Code	Range of values	Source
Occupancy covariates				
Vegetation succession stage	Succession stage; further divided by type of use in the past	stage	old growth; secondary/eucalyptus; secondary/mixed-use	Gomes 2006; information from VPSP manager
Physiognomy	Broad vegetation physiognomy	physiog	cerrado; vereda	Classification in the field
Distance from Peruaçu River [a]	Distance to nearest section of Peruaçu River inside VPSP with water during the dry season peak	waterpa	0.04-16.50 km	Measured on Google Earth Pro
Distance from potential water sources [a]	Distance to nearest location with water during dry season peak	water	0.04-10.10 km	Measured on Google Earth Pro
Detection covariates				
Trail	Location of camera trap in relation to a human trail	trail	on trail; off trail	Classification in the field
Mass [a,b]	Species body mass	mass	1.75-225 kg	Marinho-Filho et al 2002
Trophic niche [b]	Species main trophic category	trophic	herbivore; carnivore; omnivore; insectivore; frugivore	Marinho-Filho et al 2002; Paglia et al 2012

[a] These covariates were standardized before running the analysis; [b] Used only in the community level models

We tested the community response by combining data from all 18 species in a single matrix, and analyzed it using the single season occupancy framework (Mackenzie et al. 2002). Since data from all species were pooled together, occupancy estimates are the probability of use by any of the species in the community, and can be seen as an overall measure of large mammal use. The same process was used as in the species level analysis (seven days grouped as a sampling occasion; occupancy estimates from the regular occupancy and the Royle-Nichols model). Additionally, we added two detection covariates: trophic guild and mass (Table 2.1). All analyses were conducted using the ‘unmarked’ package (Fiske & Chandler 2011) for R (R Development Core Team 2015) and all models presented achieved convergence.

We used Akaike Information Criterion (AIC) values to rank and compare models and considered that models with ΔAIC <2 had similar support (Burnham & Anderson 2002). We also assessed goodness-of-fit using the approach developed for occupancy models (Mackenzie & Bailey 2004), implemented in the package AICcmodavg (Mazerolle 2015). We applied the test on the best-supported model according to AIC. Because this test can have lower power in some cases (Mackenzie & Bailey 2004), we defined a significance level of 0.1, below which we considered there was a lack-of-fit for the model. We found evidence of lack-of-fit only for the community level models (*P*= 0.09; c-hat= 1.23), whereas species level models appeared to have adequate fit (*P*> 0.1 for all species). Following Mackenzie & Bailey (2004) we used the quasi-likelihood version of AIC (QAIC) and the square root of the variance inflation factor (c-hat) to adjust SEs of the estimates in the community level models.

Finally, we performed simulations using GenPres (Hines 2006; Bailey et al. 2007) to evaluate the effect of different sampling designs on the precision of occupancy estimates (measured by SE) for the four globally threatened species (Table S1). For these simulations we used the values of occupancy and detection probability obtained in the null models.

2.3 Results

We recorded 18 large mammal species during this study (Table S1), with a sampling effort of 1898 trap-days and an average of 4.6 sampling occasions per sampling site. Results from regular occupancy models (MacKenzie et al. 2002) and Royle-Nichols models were very similar for both estimates of occupancy and model ranking (Fig. S1; Table S2). Hereafter we report only the former, as it is frequently used in similar studies (e.g. Linkie et al. 2007; Ahumada et al. 2011; Kinnaird & O’brien 2012) and also provided more precise estimates (Fig. S1B).

2.3.1 Community level models

Succession stage was an important factor determining mammal community occupancy (Table 2.2). Nevertheless, there were similar levels of support for both succession stage and distance from the Peruaçu River (waterpa), though QAIC weight of the first covariate was much greater than the second (0.53 and 0.22, respectively – Table 2.2). Support for the best model where none of the covariates had an effect on occupancy was considerably smaller (ΔQAIC = 2.98; QAIC weight of 0.12 – Table 2.2).

According to the succession stage model, secondary areas formerly used for eucalyptus plantation had similar community occupancy estimate as old growth areas (Fig. 2.2A). Secondary/mixed-use areas had a lower occupancy estimate, although the 95% CI overlapped estimates for the other succession stages (Fig 2.2A). Trophic guild strongly influenced detection probability and was present in all top-ranked models (Table 2.2); herbivores had the highest and carnivores the lowest detection estimates (Fig. 2.2B). Models with mass or trail as detection covariate were not supported at the community level (ΔQAIC >60; Table S2).

Table 2.2: Top ranked models for community level occupancy modelling of large mammals at Veredas do Peruaçu State Park.

Model	K	QAIC	ΔQAIC	QAICwt
Ψ(stage)p(trophic)	8	1482.14	0	0.529
Ψ(waterpa)p(trophic)	7	1483.90	1.7	0.219
Ψ(.)p(trophic)	6	1485.13	2.98	0.119
Ψ(water)p(trophic)	7	1485.90	3.76	0.081
Ψ(physiog)p(trophic)	7	1486.81	4.66	0.051

Ψ= occupancy; p= detection probability; K= number of parameters; QAICwt= QAIC weight. Refer to Table 2.1 for covariates codes. Full set of models presented at Table S2.

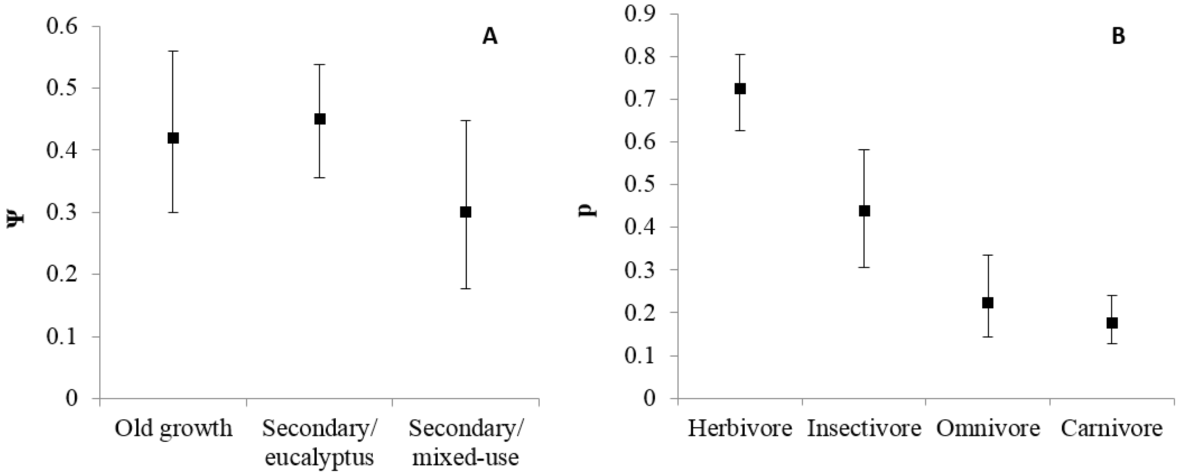


Figure 2.2: Estimates and 95% confidence intervals (corrected for overdispersion) for the Ψ(stage)p(trophic) community model. A) Effect of vegetation succession stage on occupancy estimate (Ψ); B) Effect of trophic guild on detection probability (p). Note the differences on the vertical axis.

2.3.2 Species level models

Contrary to the community level models, there was little support for the influence of succession stage on individual species' occupancy. Contradicting our predictions, none of the large mammal species that rely on fruits responded negatively to secondary savanna. Occupancy of giant anteater, a species usually favouring open habitats, was not positively affected by secondary habitats. Models with other environmental covariates or with none (null model) had much better support for all species (Table 2.3). AIC weight for models containing succession stage was lower than 0.05 for seven out of ten species assessed (maximum value for any species was 0.08), and were ranked only as the fifth best-supported model or lower (Table S3).

Table 2.3: Top ranked models for species level occupancy modelling of large mammals at Veredas do Peruaçu State Park.

Species	Ψ	p	K	AIC	ΔAIC	AICwt
Giant anteater						
Ψ(waterpa)p(trail)	+	on trail > off trail*	4	161.27	0	0.72
Ψ(.)p(trail)	NA	on trail > off trail*	3	165.4	4.13	0.09
Yellow armadillo						
Ψ(water)p(trail)	+	on trail > off trail	4	51.79	0	0.60
Ψ(water)p(.)	+	NA	3	54.21	2.42	0.18
Maned wolf						
Ψ(physiog)p(trail)	ver > cer	on trail > off trail*	4	79.13	0	0.27
Ψ(water)p(trail)	-	on trail > off trail*	4	79.42	0.29	0.24
Ψ(waterpa)p(trail)	-	on trail > off trail*	4	79.9	0.77	0.19
Ψ(.)p(trail)	NA	on trail > off trail*	3	79.98	0.85	0.18
Ocelot						
Ψ(.)p(trail)	NA	on trail > off trail	3	61.31	0	0.15
Ψ(.)p(.)	NA		2	61.39	0.09	0.15
Ψ(waterpa)p(trail)	-	on trail > off trail	4	61.61	0.30	0.13
Ψ(water)p(trail)	-	on trail > off trail	4	62.18	0.87	0.10
Oncilla						
Ψ(physiog)p(trail)	cer > ver	on trail > off trail*	4	196.13	0	0.57
Ψ(waterpa)p(trail)	-	on trail > off trail*	4	197.99	1.87	0.22
Ψ(.)p(trail)	NA	on trail > off trail*	3	199.33	3.21	0.11
Hog-nosed skunk						
Ψ(water)p(.)	+	NA	3	99.39	0	0.51
Ψ(water)p(trail)	+	on trail > off trail	4	100.14	0.76	0.35
Tapir						
Ψ(waterpa)p(trail)	-	on trail > off trail*	4	75.73	0	0.77
Ψ(waterpa)p(.)	-	NA	3	79.53	3.8	0.12
Grey-brocket deer						
Ψ(water)p(.)	-		3	232.08	0	0.23
Ψ(.)p(.)	NA	NA	2	232.18	0.1	0.22
Ψ(.)p(trail)	NA	off trail > on trail	3	233.28	1.2	0.13
White-lipped peccary						
Ψ(waterpa)p(.)	-	NA	3	105.75	0	0.62
Ψ(waterpa)p(trail)	-	on trail > off trail	4	107.43	1.68	0.27
Azara's agouti						
Ψ(physiog)p(.)	cer > ver	NA	3	255.53	0	0.50
Ψ(physiog)p(trail)	cer > ver	off trail > on trail	4	255.7	0.17	0.46

Ψ = occupancy; p = detection probability; K = number of parameters; AICw t= AIC weight; cer = cerrado; ver = vereda; + = positive effect; - = negative effect. *Denotes strong effect, where estimate does not overlap zero. Refer to Table 2.1 for covariates codes. Only top two models or models with AICwt ≥ 0.1 are presented, for full model set see Table S3.

Although for half of the species assessed (yellow armadillo, striped hog-nosed skunk - *Conepatus semistriatus* -, lowland tapir, white-lipped peccary and Azara's agouti) there is clearly only one covariate influencing occupancy (Table 2.3), the effect of the environmental factor was not strong, as the estimates overlapped zero. The effect of camera placement on detection probability was extremely strong for certain species (Table 2.3). Giant anteater, maned wolf, oncilla (*Leopardus tigrinus*) and lowland tapir were at least five times more likely to be detected if the camera trap was set up on an existing trail. The effect was similar for yellow armadillo and ocelot (*Leopardus pardalis*), though not as strong (i.e. estimates overlapped zero).

2.3.3 Sampling design simulations

Both an increase in the total number of sites and the number of sampling occasions (duration of the study) enhanced precision of occupancy estimates for the four globally threatened species recorded (giant anteater, oncilla, lowland tapir and white-lipped peccary). However, the trade-off between sampling occasions and number of sites was non-linear; increasing the number of sampling occasions from five to nine yielded similar gains in precision to increasing the number of sites from 60 to 100 (with five surveys conducted) for all species evaluated (Fig. 2.3). Standard error below 0.07 was achieved in all survey designs for lowland tapir and in the majority of designs for oncilla and white-lipped peccary, but was not achieved in any design for the giant anteater. Nevertheless, the best improvement in precision (the difference between largest and smallest SE) was found for this last species, whereas for the other three species improvements in precision were modest (Fig. 2.3).

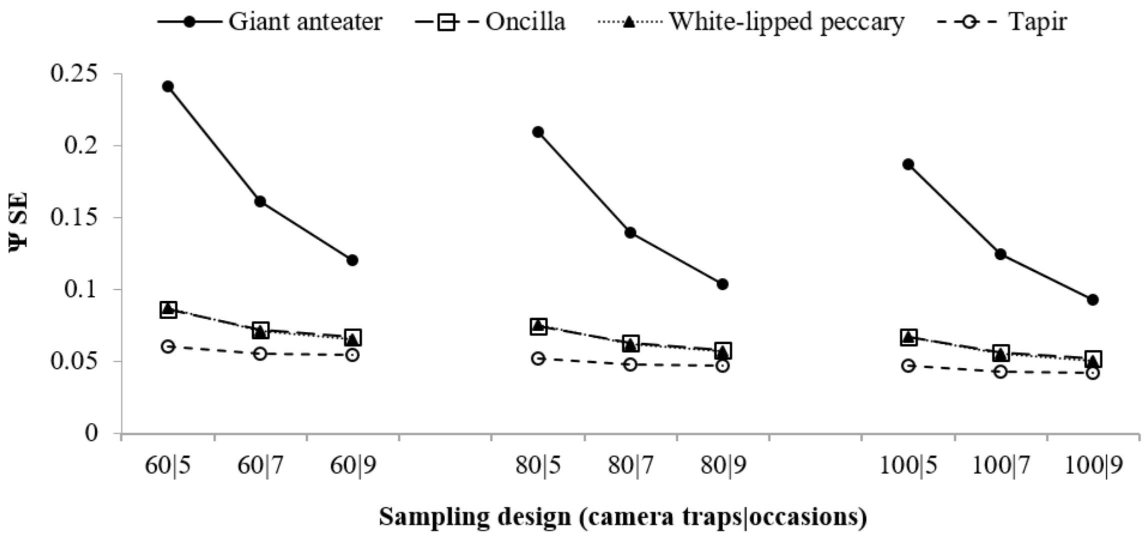


Figure 2.3: Occupancy estimate standard errors (Ψ SE) for globally threatened species obtained through simulations of sampling designs with different number of camera traps and sampling occasions.

2.4 Discussion

2.4.1 Conservation value of secondary savanna

Our study shows that probability of use by any of the individual species investigated is not strongly affected by succession stage, suggesting that secondary savanna areas do not negatively impact large mammals. Most species appeared to have responded to other environmental features, principally physiognomy and distance from water. While we recognize none of these effects are particularly strong, some of the associations suggested by these well-supported models are in line with other studies, such as preference of denser habitats by agouti (Desbiez et al. 2009), and positive relationship with water sources by white-lipped peccary (Keuroghlian et al. 2009) and lowland tapir (Padilla & Dowler 1994).

In the community level models, where succession stage may be considered an important factor determining occupancy, the effect is contrary to what we anticipated, with similar estimates for secondary areas that regenerated from eucalyptus and for old growth vegetation. This does not mean all species responded in the same way to secondary habitat; it indicates that probability of use by large mammals in general is not different between secondary savanna areas formerly used for eucalyptus plantation and old growth savanna. Similarities between old growth and secondary habitats have been found in other regions and taxonomic groups, such as amphibians and reptiles in Mexican forests (Hernández-Ordóñez et al. 2015), birds in central-African forests (Naidoo 2004) and large mammals in Amazonian forests (Barlow *et al.* 2007). Nevertheless, to our knowledge, this is the first study to explicitly test and observe some similarities in the large mammal fauna of old growth and secondary vegetation in the Cerrado.

There is, however, a suggestion of lower large mammal occupancy in secondary/mixed-use areas. Secondary habitats can be very different even within the same region if they were subjected to different land use or regeneration process (Mesquita et al. 2001; Flynn et al. 2010). Animals may subsequently respond to those differences, due to variation in resource availability. For example, Bobrowiec & Gribel (2010) found that the type of secondary habitat had a strong effect on bat community composition in the Amazon. Nevertheless, two potentially confounding effects prevent us to make strong inference on the effect of secondary/mixed-use areas. Firstly, secondary/mixed-use sites at VPSP were located further from the park's HQ and with relatively easy access by dirt roads, possibly resulting in higher external pressure, which we were unable to account for in our study. Secondly, secondary/mixed-use areas were further away from the river. Although we used distance from Peruaçu River as a covariate, the fact that secondary/mixed-used areas are clustered together in southern VPSP does not allow us to fully disentangle these two factors. This may also, at least partially, explain the support for distance from the river in the community models.

We make cautious generalizations about large mammal recovery in secondary vegetation within the Cerrado and highlight that our findings cannot be extrapolated to all secondary savannas, especially outside protected lands where the regeneration process tends to be slower and continuous anthropogenic pressure may affect the use of secondary vegetation by wildlife. Our study area might be considered a best-case scenario, as it attained the qualities of a high-value secondary habitat identified by Chazdon et al. (2009) and Dent & Wright (2009):

proximity of primary habitats, low post-abandonment disturbance and persistence of seed dispersing fauna. Additionally, the relatively short duration of most anthropogenic land-use in the area (around 15 years or less - Gomes & Maillard 2015) favoured the maintenance of a seed bank of native species, synergistically acting with seeds arriving from neighbouring remnants to promote the regeneration after the end of agriculture. As observed by Newbold et al. (2015) in a global analysis of land use effects on biodiversity, the conservation importance of secondary habitats depends critically on regeneration time, thus, the advanced state of vegetation regeneration at VPSP is also likely to contribute to its conservation value.

Our results show that Cerrado large mammals, including threatened species, can use secondary vegetation that regenerated from clear cut. This finding combined with the large extent to which secondary habitats are represented in our study area and the fact that VPSP currently harbours more than 80% of all large mammals potentially occurring in northern Minas Gerais (Ferreira & Oliveira 2014), indicates that given a favourable habitat history, areas with a large proportion of secondary savanna may still play an important role in maintaining the large mammal community. This is encouraging as, in the right conditions, part of the extensive areas that need to be restored in the Cerrado to comply with environmental legislation (Soares-Filho et al. 2014) might become potential habitats for large mammals in the future.

Cerrado large mammals are known to occur in a variety of habitats (Marinho-Filho et al. 2002) and may not perceive the environment at a finer scale to respond to the differences found between old growth and secondary savannas. Thus, while these species can thrive in secondary vegetation, we cannot assume that other animal groups would fare well in secondary savannas. In tropical secondary forests, for instance, recovery is slower for species that are more dependent on habitat structure features (Dent & Wright 2009). A similar pattern could be observed in the Cerrado, as secondary habitats can be structurally different from old-growth ones (Gomes & Maillard 2015). Furthermore, specialized nectarivorous and frugivorous animals might present a strong negative response in secondary savannas, particularly in early regeneration stages, where floristic composition tends to be more different and zoochoric dispersion of fruits is not common (Kuhlmann & Ribeiro 2016).

2.4.2 Effect of trophic guild and trail on detection probability

Similar to our study, Rovero et al. (2014) found that trophic guild is an important factor affecting detection probability for African mammals, with herbivores displaying higher detection than carnivores, an effect likely to be driven by feeding ecology. An alternative explanation is that herbivores tend to occur in higher densities than carnivores (Damuth 1987; Carbone & Gittleman 2002), and as detection probability may be affected by abundance (Royle & Nichols 2003), this could result in herbivores generally having higher detection probability than carnivores.

Although setting a camera trap on a trail had a positive effect on detection for some species, sampling only trails may yield biased results due to an interaction between patterns of animal space-use and the non-random deployment of cameras at locations chosen by researchers (Wearn et al. 2013). Similarly, Harmsen et al. (2010) showed that, while larger felids are more easily detected on trails, trails may not be well suited for detecting all Neotropical mammal species. In VPSP we recorded three species exclusively off trails. Moreover, focusing sampling on trails may result in unrealistically high occupancy estimates for ‘trail-happy’ species that cannot be extrapolated to the whole area surveyed, however, the decision on where to set up a camera trap depends largely on objectives of a study.

2.4.3 Sampling design for monitoring

We have established the baseline against which data from future monitoring initiatives in VPSP could be compared. Similar monitoring implemented in sequential years is being successfully used to evaluate trends in large mammals in protected areas across the world (e.g.

Ahumada et al. 2013; Beaudrot et al. 2016). However, the estimation of occupancy in continuous habitats has been criticized, due to the possibility of violating assumptions of constant occupancy and spatial independence (Efford & Dawson 2012). In camera trap studies of large mammals these violations can arise when a species' home-range is very large in relation to the spacing between sampling sites, allowing the same individual to be recorded in more than one site during the survey. Conducting the survey in a relatively short timeframe minimizes these problems, because during the study individuals will only use a small portion of their full home-range. Nevertheless, we adopted the precautionary view of interpreting occupancy as probability of use for all species.

We believe that surveys using 60 camera trap sites, during nine sampling occasions (7-day periods in our study), provides an effective strategy to obtain precise occupancy estimates for some species in the Cerrado. This design yields similar precision to the one surveying 100 sites during five occasions, but with substantially lower costs. However, one must take into account that precision depends on the magnitude of the occupancy estimate, and a SE of 0.07 may be large for a very small occupancy probability. Our decision to conduct more surveys in fewer sites is generally supported by assessments of design trade-offs for occupancy studies (Mackenzie & Royle 2005; Bailey et al. 2007), but for rare species maximizing both the number of occasions and sites may be necessary (Mackenzie & Royle 2005; Shannon et al. 2014). This is the case for the giant anteater in VPSP, for which a much higher number of sites and/or sampling occasions than the ones used in our simulations was needed to obtain good estimates.

We acknowledge that occupancy and detection probability estimates for a given species is not homogenous throughout its distribution. Although recent studies investigating large mammal occupancy in Brazil have been published (e.g. Sollmann et al. 2012; Zimbres et al. 2013), this type of monitoring remains rare and restricted to few localities. We believe our suggested design may be a useful starting point for new monitoring initiatives, which can then be adapted at new locations as local data becomes available.

2.5 Supporting information

Table S1: Large mammal species recorded at Veredas do Peruaçu State Park.

Species	Trophic category	Number of records [a]	Null model detection probability (p)
Pilosa			
Giant anteater(*Myrmecophaga tridactyla*)[b]	in	27	0.139
Cingulata			
Yellow armadillo (*Euphractus sexcinctus*)	in/om	9	0.366
Nine-banded armadillo (*Dasypus novemcinctus*)	in/om	1	0.004
Carnivora			
Ocelot (*Leopardus pardalis*)	ca	7	0.197
Oncilla (*Leopardus tigrinus*)[b]	ca	41	0.290
Puma (*Puma concolor*)	ca	24	0.109
Jaguarundi (*Puma yagouaroundi*)	ca	1	0.004
Crab-eating fox (*Cerdocyon thous*)	om	3	0.013
Maned wolf (*Chrysocyon brachyurus*)	om	10	0.114
Bush dog (*Speothos venaticus*)	ca	1	0.004
Lesser grison (*Galictis cuja*)	om	1	0.004
Tayra (*Eira barbara*)	om	1	0.004
Striped hog-nosed skunk (*Conepatus semistriatus*)	om	15	0.124
Crab-eating raccon (*Procyon cancrivorus*)	om	1	0.004
Perissodactyla			
Lowland tapir(*Tapirus terrestris*)[b]	fr/he	16	0.331
Artiodactyla			
White-lipped peccary (*Tayassu pecari*)[b]	fr/he	17	0.233
Gray brocket deer (*Mazama gouazoubira*)	fr/he	50	0.347
Rodentia			
Azara's agouti (*Dasyprocta azarae*)	fr	65	0.381

[a] Maximum one record per sampling occasion (7 days); [b] Denotes globally threatened species. in= insectivore; ca= carnivore; om= omnivore; he= herbivore; fr= frugivore

Table S2: Comparison of model support between regular and Royle-Nichols occupancy models at the community level modelling.

	K	QAIC	ΔQAIC	QAICwt
Mackenzie model				
Ψ(stage)p(trophic)	8	1482.15	0.00	0.53
Ψ(waterpa)p(trophic)	7	1483.90	1.76	0.22
Ψ(.)p(trophic)	6	1485.13	2.98	0.12
Ψ(water)p(trophic)	7	1485.91	3.76	0.08
Ψ(physiog)p(trophic)	7	1486.81	4.67	0.05
Ψ(stage)p(.)	5	1546.02	63.88	0.00
Ψ(stage)p(trail)	6	1546.26	64.12	0.00
Ψ(waterpa)p(trail)	5	1547.54	65.40	0.00
Ψ(stage)p(mass)	6	1547.89	65.74	0.00
Ψ(.)p(trail)	4	1548.59	66.45	0.00
Ψ(water)p(trail)	5	1549.45	67.30	0.00
Ψ(waterpa)p(.)	4	1549.82	67.67	0.00
Ψ(.)p(.)	3	1550.07	67.92	0.00
Ψ(physiog)p(trail)	5	1550.47	68.33	0.00
Ψ(water)p(.)	4	1551.56	69.41	0.00
Ψ(waterpa)p(mass)	5	1551.62	69.48	0.00
Ψ(physiog)p(.)	4	1551.84	69.70	0.00
Ψ(.)p(mass)	4	1551.92	69.78	0.00
Ψ(water)p(mass)	5	1553.39	71.25	0.00
Ψ(physiog)p(mass)	5	1553.70	71.56	0.00
Royle-Nichols model				
Ψ(stage)p(trophic)	8	1475.52	0.00	0.72
Ψ(waterpa)p(trophic)	7	1478.77	3.25	0.14
Ψ(.)p(trophic)	6	1480.15	4.63	0.07
Ψ(water)p(trophic)	7	1481.27	5.75	0.04
Ψ(physiog)p(trophic)	7	1482.01	6.49	0.03
Ψ(waterpa)p(trail)	5	1540.53	65.01	0.00
Ψ(stage)p(trail)	6	1541.60	66.08	0.00
Ψ(stage)p(.)	5	1542.15	66.62	0.00
Ψ(water)p(trail)	5	1542.95	67.43	0.00
Ψ(.)p(trail)	4	1543.18	67.66	0.00
Ψ(stage)p(mass)	6	1543.88	68.36	0.00
Ψ(waterpa)p(.)	4	1544.92	69.40	0.00
Ψ(physiog)p(trail)	5	1545.14	69.62	0.00
Ψ(.)p(.)	3	1545.89	70.37	0.00
Ψ(waterpa)p(mass)	5	1546.68	71.16	0.00
Ψ(water)p(.)	4	1547.03	71.51	0.00
Ψ(.)p(mass)	4	1547.64	72.12	0.00
Ψ(physiog)p(.)	4	1547.75	72.23	0.00
Ψ(water)p(mass)	5	1548.80	73.28	0.00
Ψ(physiog)p(mass)	5	1549.50	73.98	0.00

Ψ= occupancy; p= detection probability; K= number of parameters; QAICwt= QAIC weight. Refer to Table 1 for covariates codes.

Table S3: Full set of models for the species level occupancy modelling of large mammal at Veredas do Peruaçu State Park.

	K	AIC	ΔAIC	AICwt	cumwt
Giant anteater					
Ψ(waterpa)p(trail)	4	161.27	0.00	0.72	0.72
Ψ(.)p(trail)	3	165.40	4.13	0.09	0.81
Ψ(stage)p(trail)	5	166.56	5.29	0.05	0.86
Ψ(water)p(trail)	4	167.31	6.04	0.04	0.90
Ψ(stage)p(.)	4	167.39	6.12	0.03	0.93
Ψ(physiog)p(trail)	4	167.40	6.13	0.03	0.96
Ψ(waterpa)p(.)	3	169.21	7.94	0.01	0.98
Ψ(water)p(.)	3	169.59	8.33	0.01	0.99
Ψ(.)p(.)	2	169.96	8.69	0.01	1.00
Ψ(physiog)p(.)	3	171.96	10.69	0.00	1.00
Yellow armadillo					
Ψ(water)p(trail)	4	51.79	0.00	0.60	0.60
Ψ(water)p(.)	3	54.21	2.42	0.18	0.78
Ψ(.)p(trail)	3	56.16	4.37	0.07	0.85
Ψ(stage)p(trail)	5	57.10	5.31	0.04	0.89
Ψ(waterpa)p(trail)	4	57.29	5.51	0.04	0.93
Ψ(physiog)p(trail)	4	57.57	5.78	0.03	0.96
Ψ(stage)p(.)	4	58.78	6.99	0.02	0.98
Ψ(.)p(.)	2	60.39	8.60	0.01	0.99
Ψ(waterpa)p(.)	3	60.85	9.07	0.01	1.00
Ψ(physiog)p(.)	3	61.56	9.78	0.00	1.00
Maned wolf					
Ψ(physiog)p(trail)	4	79.13	0.00	0.27	0.27
Ψ(water)p(trail)	4	79.42	0.29	0.24	0.51
Ψ(waterpa)p(trail)	4	79.90	0.77	0.19	0.70
Ψ(.)p(trail)	3	79.98	0.85	0.18	0.87
Ψ(stage)p(trail)	5	82.40	3.27	0.05	0.93
Ψ(physiog)p(.)	3	83.57	4.44	0.03	0.96
Ψ(.)p(.)	2	84.32	5.19	0.02	0.98
Ψ(waterpa)p(.)	3	85.69	6.56	0.01	0.99
Ψ(water)p(.)	3	85.86	6.73	0.01	1.00
Ψ(stage)p(.)	4	87.98	8.85	0.00	1.00
Ocelot					
Ψ(.)p(trail)	3	61.31	0.00	0.15	0.15
Ψ(.)p(.)	2	61.39	0.09	0.15	0.30
Ψ(waterpa)p(trail)	4	61.61	0.30	0.13	0.43
Ψ(water)p(trail)	4	62.18	0.87	0.10	0.53
Ψ(waterpa)p(.)	3	62.39	1.08	0.09	0.62
Ψ(physiog)p(.)	3	62.42	1.11	0.09	0.71
Ψ(physiog)p(trail)	4	62.52	1.21	0.08	0.79
Ψ(stage)p(trail)	5	62.65	1.34	0.08	0.87
Ψ(water)p(.)	3	62.97	1.66	0.07	0.94
Ψ(stage)p(.)	4	63.12	1.81	0.06	1.00
Oncilla					
Ψ(physiog)p(trail)	4	196.13	0.00	0.57	0.57
Ψ(waterpa)p(trail)	4	197.99	1.87	0.22	0.79

Table S3 (cont.)	K	AIC	ΔAIC	AICwt	cumwt
Oncilla (cont.)					
Ψ(.)p(trail)	3	199.33	3.21	0.11	0.91
Ψ(water)p(trail)	4	201.26	5.13	0.04	0.95
Ψ(stage)p(trail)	5	201.53	5.40	0.04	0.99
Ψ(physiog)p(.)	3	204.82	8.69	0.01	1.00
Ψ(.)p(.)	2	208.58	12.46	0.00	1.00
Ψ(waterpa)p(.)	3	208.83	12.70	0.00	1.00
Ψ(stage)p(.)	4	209.51	13.39	0.00	1.00
Ψ(water)p(.)	3	210.58	14.45	0.00	1.00
Hog-nosed skunk					
Ψ(water)p(.)	3	99.39	0.00	0.51	0.51
Ψ(water)p(trail)	4	100.14	0.76	0.35	0.87
Ψ(waterpa)p(trail)	4	103.89	4.51	0.05	0.92
Ψ(waterpa)p(.)	3	105.13	5.75	0.03	0.95
Ψ(stage)p(.)	4	105.44	6.05	0.02	0.97
Ψ(stage)p(trail)	5	106.25	6.86	0.02	0.99
Ψ(.)p(trail)	3	109.15	9.76	0.00	0.99
Ψ(physiog)p(trail)	4	109.23	9.84	0.00	1.00
Ψ(physiog)p(.)	3	112.65	13.26	0.00	1.00
Ψ(.)p(.)	2	112.98	13.60	0.00	1.00
Tapir					
Ψ(waterpa)p(trail)	4	75.73	0.00	0.77	0.77
Ψ(waterpa)p(.)	3	79.53	3.80	0.12	0.89
Ψ(water)p(trail)	4	80.59	4.85	0.07	0.96
Ψ(water)p(.)	3	81.64	5.91	0.04	1.00
Ψ(stage)p(trail)	5	92.15	16.41	0.00	1.00
Ψ(stage)p(.)	4	92.77	17.03	0.00	1.00
Ψ(.)p(.)	2	101.97	26.24	0.00	1.00
Ψ(physiog)p(.)	3	102.17	26.44	0.00	1.00
Ψ(physiog)p(trail)	4	102.65	26.91	0.00	1.00
Ψ(.)p(trail)	3	102.76	27.03	0.00	1.00
Gray-brocket deer					
Ψ(water)p(.)	3	232.08	0.00	0.23	0.23
Ψ(.)p(.)	2	232.18	0.10	0.22	0.45
Ψ(.)p(trail)	3	233.28	1.20	0.13	0.57
Ψ(water)p(trail)	4	233.77	1.68	0.10	0.67
Ψ(waterpa)p(.)	3	234.05	1.97	0.09	0.75
Ψ(physiog)p(.)	3	234.16	2.07	0.08	0.83
Ψ(waterpa)p(trail)	4	235.25	3.16	0.05	0.88
Ψ(physiog)p(trail)	4	235.28	3.20	0.05	0.93
Ψ(stage)p(.)	4	235.36	3.27	0.04	0.97
Ψ(stage)p(trail)	5	236.29	4.21	0.03	1.00
White-lipped peccary					
Ψ(waterpa)p(.)	3	105.75	0.00	0.62	0.62
Ψ(waterpa)p(trail)	4	107.43	1.68	0.27	0.88
Ψ(water)p(.)	3	110.22	4.47	0.07	0.95
Ψ(water)p(trail)	4	111.64	5.89	0.03	0.98
Ψ(stage)p(.)	4	114.04	8.29	0.01	0.99
Ψ(stage)p(trail)	5	116.03	10.28	0.00	0.99
Ψ(.)p(.)	2	116.20	10.45	0.00	1.00
Ψ(.)p(trail)	3	118.17	12.42	0.00	1.00
Ψ(physiog)p(.)	3	118.19	12.44	0.00	1.00
Ψ(physiog)p(trail)	4	120.16	14.41	0.00	1.00

Table S3 (cont.)	K	AIC	ΔAIC	AICwt	cumwt
Azara's agouti					
Ψ(physiog)p(.)	3	255.53	0.00	0.50	0.50
Ψ(physiog)p(trail)	4	255.70	0.17	0.46	0.96
Ψ(.)p(.)	2	262.98	7.45	0.01	0.97
Ψ(.)p(trail)	3	263.49	7.96	0.01	0.98
Ψ(waterpa)p(.)	3	264.75	9.22	0.01	0.98
Ψ(water)p(.)	3	264.97	9.44	0.00	0.99
Ψ(waterpa)p(trail)	4	265.18	9.65	0.00	0.99
Ψ(water)p(trail)	4	265.44	9.91	0.00	1.00
Ψ(stage)p(.)	4	266.16	10.63	0.00	1.00
Ψ(stage)p(trail)	5	266.73	11.20	0.00	1.00
Ψ(stage)p(trail)	5	266.73	11.20	0.00	1.00

Ψ= occupancy; p= detection probability; K= number of parameters; AICwt= AIC weight; cumwt= cumulative AIC weight. Refer to Table 2.1 for covariates codes.

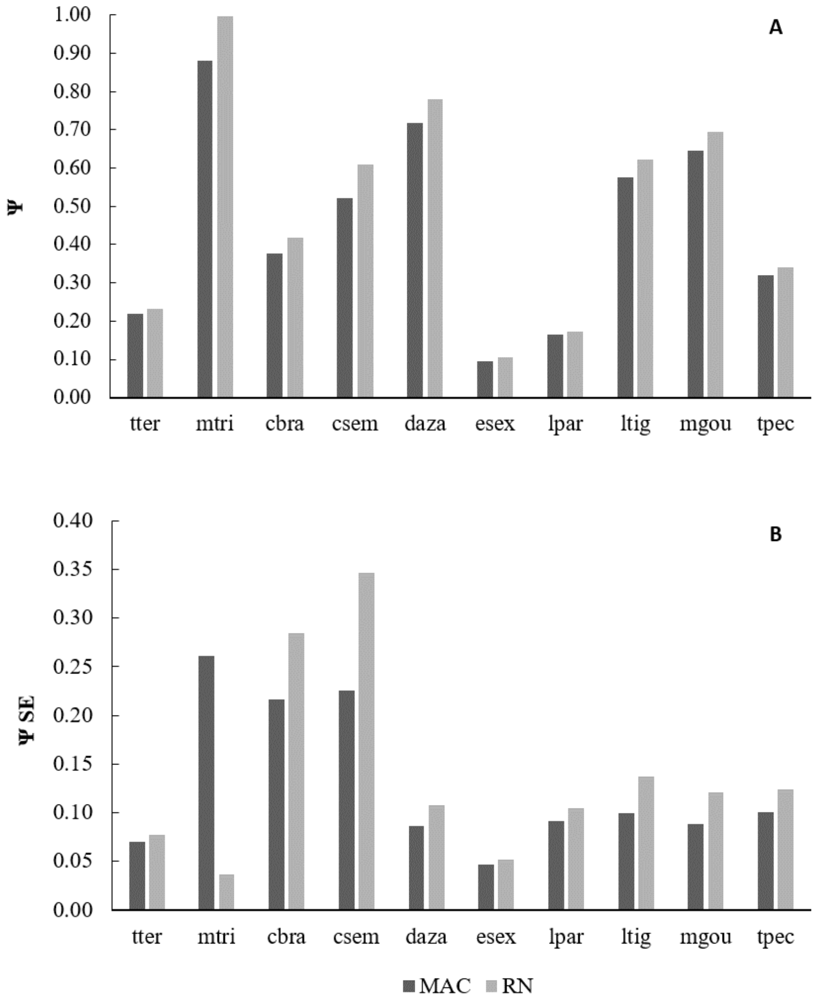


Figure S1: Comparison between regular (MAC) and Royle-Nichols (RN) occupancy models at the species level modelling. A) Occupancy estimates (Ψ); B) Standard errors of occupancy estimates (Ψ SE). Species codes composed of first letter of the genus and first three letters of the specific name (refer to Table S1 for species names). Note the differences on the vertical axis.

Chapter 3: Protected area effectiveness at safeguarding large threatened mammals in the Brazilian Cerrado

Veredas at Porto Cajueiro Private Reserve

3.1 Introduction

Measuring protected area (PA) performance is not a simple task. Due to the number of metrics that could be used and, most importantly, to the challenge of obtaining accurate data on these metrics there is a poor understanding of the extent to which PAs deliver positive biodiversity outcomes (Ferraro & Pattanayak 2006; Coetzee et al. 2014). Most PA performance evaluations have focused on Management Effectiveness assessments (usually questionnaire-based evaluations collecting data from PA managers; e.g. Coad et al. 2015) or on remote sensing data to estimate deforestation (e.g. Carranza et al. 2014a; Ament & Cumming 2016). While Management Effectiveness assessments may be useful in adaptive management, their subjective and ordinal nature does not allow for robust impact evaluation (Coad et al. 2015). On the other hand, avoided conversion of natural vegetation is clearly a direct conservation outcome and a valid measure of PA success (Geldmann et al. 2013).

Biodiversity loss, however, can still happen without a significant change in vegetation cover. Poaching and bushmeat hunting can severely deplete populations of vertebrates (Redford 1992; Peres 2001; Corlett 2007) and habitat degradation – an impact not easily detected by remote sensing – can have strong negative effects on biodiversity (Ribeiro et al. 2015; Barlow et al. 2016). Therefore reliable measures of conservation outcomes based on local biodiversity metrics are paramount to investigate PA effectiveness and could complement assessments quantifying habitat conversion. Despite the limited amount of data comparing sites under contrasting levels of protection, recent global studies have shown that PAs are to some extent effective in conserving biodiversity, supporting higher species richness and abundance (Coetzee et al. 2014; Gray et al. 2016). However, data available for such studies are not homogeneously distributed across the planet, resulting in poor geographic coverage of some regions. A case in point is the Brazilian Cerrado, a global biodiversity hotspot where little information exists about the effectiveness of PAs in conserving local biodiversity.

Given that half of the Cerrado has been converted to anthropogenic land uses (MMA 2014a) and only 3% is within strict PAs (MMA 2018), it is critical that we establish the role of these PAs in conserving local biodiversity, and that we obtain information allowing us to maximise their effectiveness in safeguarding species. However, except for a few assessments showing that Cerrado PAs are effective in avoiding land conversion (Carranza et al. 2014a; Françoso et al. 2015) virtually nothing else is known about the effect of habitat protection on this ecosystem. This paucity of evidence is a cause of concern in a time when the very existence of some Brazilian PAs is under threat (Bernard et al. 2014; Silveira et al. 2018) and there is a global trend of weakening the legal protection conferred to natural areas (Mascia & Pailler 2011).

Here we use data gathered from a network of camera traps deployed in five strict and two large multiple-use PAs to conduct the first assessment of PA effectiveness at safeguarding local biodiversity in the Brazilian Cerrado. Our study was specifically designed to answer the question: Do strict PAs support higher levels of mammal diversity in the Cerrado? We adopted a multi-species occupancy framework that allowed us to estimate species' probability of occupancy and species richness in the two contrasting types of PA while controlling for confounding factors that are not directly related to protection level. We expected an overall positive effect of strict PAs over species richness, although we anticipated variation in species' response due to differences in their biology, natural history and conservation status. More specifically, we predicted that larger and threatened species would tend to benefit from stricter protection, whereas non-threatened and smaller species would generally show a neutral response, with similar occupancy probability in both PA types.

3.2 Material and methods

3.2.1 Study area

We conducted our study at a mosaic of protected areas located in northern Minas Gerais state, south-eastern Brazil. The Sertão Veredas-Peruaçu mosaic (SVP; Fig. 3.1) extends over approximately 18,000 km^2 in a transitional area between Cerrado – a tropical savanna ecosystem – and Caatinga – a complex of thorn scrub and seasonally dry forests associated with semi-arid climate. SVP is formed of 14 PAs – eight strict (IUCN categories I-IV) and six multiple-use PAs (IUCN categories V-VI) – and two indigenous lands. The region is a high priority area for conservation (WWF-Brasil & MMA 2015) and harbours 80% of all mammals >1 kg found in the Cerrado (Ferreira & Oliveira 2014). In this study, we surveyed seven of SVP's PAs: four national/state parks, one Natural Heritage Private Reserve (RPPN in Portuguese) and two Environmental Protection Areas (APA in Portuguese) (Table 3.1).

Parks (IUCN category II) and private reserves (IUCN category IV) have strict and similar regulations with conservation as their ultimate goal (Brasil 2000), conferring the same level of habitat protection and allowing us to treat them as a single group defined as 'strict PAs'. Conversely, APAs (IUCN category V) are the least restrictive category of multiple-use PA in Brazil, where human settlements and some degree of land conversion are allowed (Brasil 2000). For this reason, they are not as effective at avoiding Cerrado deforestation (Françoso et al. 2015) and have been described as being closer to a land-management scheme than an actual PA (Rylands & Brandon 2005). The two APAs assessed in this study are characterised by low human density distributed across scattered villages and one small town connected by unpaved roads. Despite human occupation and use (mostly small-scale agriculture and cattle ranching), these APAs have at least 60% of their area covered with natural vegetation (WWF-Brasil 2011).

Due to its location in an ecotone between two major biomes, several vegetation types are found at SVP, ranging from gallery and dry forests to palm swamps (locally known as *veredas*) and savannas. In fact, savannas (a broad term encompassing vegetation types with a wide range of tree and shrub density), dominate the landscape covering at least 50% of the region (data from SEMAD 2017), while pasture and agriculture cover approximately 10% (WWF-Brasil 2011). The climate is markedly seasonal, with well-defined wet and dry seasons, each one lasting for roughly six months; mean annual rainfall ranges from 800 to 1,400 mm and mean temperature is approximately 24 ^{0}C (MMA/IBAMA/Funatura 2003; MMA/IBAMA/Geoclock 2005).

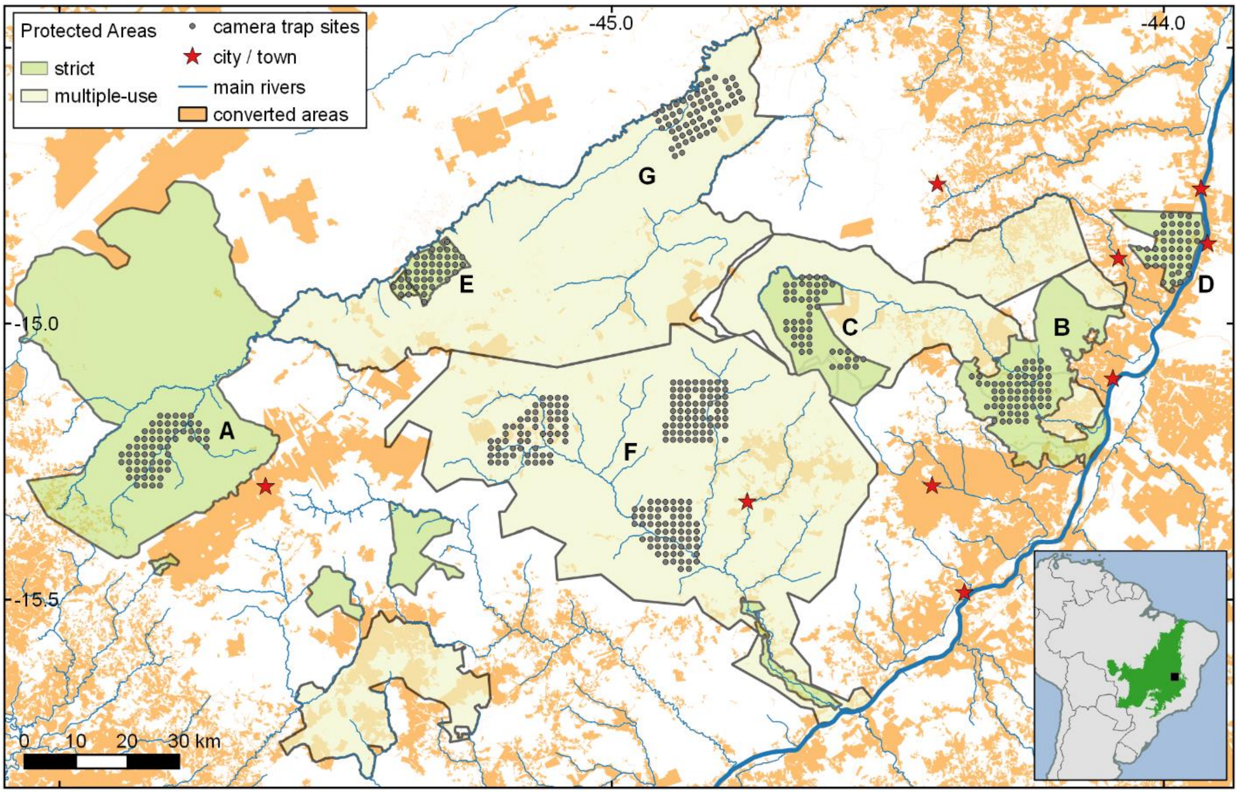


Figure 3.1: Location of camera trap sites surveyed at the Sertão Veredas-Peruaçu mosaic, Brazil. See Table 3.1 for names and characteristics of protected areas surveyed.

Table 3.1: Protected areas surveyed at Sertão Veredas-Peruaçu mosaic in the Brazilian Cerrado.

Protected Area	IUCN category	Area (km^2)	Year created	Camera trap sites/effort (camera days)	Human density at CT array [a]	Year surveyed
Strict protected areas						
Grande Sertão Veredas National Park (A)	II	2,300	1989	65/3,767	0	2017
Cavernas do Peruaçu National Park (B)	II	568	1999	60/2,939	0.03	2014
Veredas do Peruaçu State Park (C)	II	312	1994	50/1,826	0	2012
Mata Seca State Park (D)	II	136	2000	46/2,085	0	2013
Porto Cajueiro Private Reserve (E)	IV	90	2004	43/2,048	0	2015
Multiple-use protected areas						
Rio Pandeiros Environmental Protection Area (F)	V	3,801	1995	193/10,916[b]	1.14, 2.31, 4.33	2015, 2016
Cochá Gibão Environmental Protection Area (G)	V	2,844	2004	60/2,786	4.59	2017

Letters inside the parenthesis indicate protected areas location at Fig. 3.1. [a] Density at the camera trap array (in people/km^2; see Fig. S2); [b] Divided in three independent arrays of 60, 63 and 70 camera trap sites.

3.2.2 Survey design and data collection

A robust PA impact evaluation should use a counterfactual that on average is similar to the area being protected, except for the protection status (Mascia et al. 2017). Therefore, contextual factors that affect the outcome of interest but are not directly related to protection need to be controlled when assessing PA performance. We accounted for those factors as far as possible through study design, and additionally through statistical control for confounding variables. The contextual factors we controlled for have a considerable overlap with the ones used by Carranza et al. (2014a) in a matching process to investigate PA effectiveness in avoiding Cerrado deforestation, and they are also known to influence the occurrence of Neotropical mammals (Pinho et al. 2017; Ferreira et al. 2017a; Nagy-Reis et al. 2017). In this study, we treated strict PAs as the intervention and APAs as the counterfactual. Although APAs (herein referred to simply as multiple-use PAs) have legal protection status, the levels of restrictions and management implemented make them an adequate counterfactual to test the effect of strict protection in Brazil.

We adapted a standardized camera trapping protocol (TEAM Network 2011) to survey the mammal community in 517 sampling sites distributed across nine arrays (five in strict PAs and four in multiple-use PAs) – covering an area of approximately 1,000 km^2 and totalling 26,367 survey days (Table 3.1; Fig. 3.1). Because strict PAs are more likely to be found further away from cities and towns (Joppa & Pfaff 2009) and this may influence local biodiversity, arrays within multiple-use PAs were at least 10 km from any town. Additionally, to avoid eventual spill-over of wildlife from strict PAs, arrays within multiple-use areas were again at least 10 km from the border of strict PAs. Finally, to ensure a large spatial cover of our sampling and to minimize problems of spatial non-independence, the shortest distance between neighbouring arrays was 12 km (average: 24.7; range: 12-46). Other environmental and landscape characteristics were accounted for within the data analysis.

Each camera trap array consisted of 43-70 sampling sites systematically distributed at intervals of 1.5 km (Fig. 3.1). We deployed most camera trap units (Bushnell TrophyCam and Bushnell Agressor) within a 50-m buffer of the sampling sites' pre-determined coordinates, aiming to select locations that we deemed most likely to record mammals (ca. 3% were 100-200 m away from the pre-determined coordinates due to access issues). Because we followed a systematic design with evenly spaced sampling sites, our survey represents elements of the landscape roughly at the same proportion as they occur at the camera trap array, ensuring our sampling sites were not biased towards specific vegetation types or human trails and roads. To minimize variation in camera trap deployment, equipment at all 517 sites were deployed by only four different researchers with large experience setting up camera traps in the Cerrado, and usually working in pairs between them. Cameras were always deployed in natural vegetation areas and at least 200 m from smaller settlements or isolated houses. Each camera trap site was surveyed for no more than 74 days (average: 50.8) and only during the dry season (mid-April to mid-October) between 2012 and 2017. Camera traps sensitivity was set to 'normal', a 30-

seconds interval between sequential triggers was observed and no bait was used to attract animals.

3.2.3 Data analysis

After accounting for malfunctioning and theft, we divided the survey period into 6-day intervals (sampling occasions) and assembled detection/non-detection matrices at 501 camera trap sites for 27 mammal species >1 kg (*Dasypus novemcinctus* and *D. septemcinctus* were joined under *Dasypus* spp. because they were difficult to distinguish in many images). We used a data augmentation procedure to estimate species richness (Dorazio et al. 2006), adding all-zero detection histories for seven mammal species >1 kg that occur at SVP (Ferreira & Oliveira 2014) but were not detected during our survey. We joined these matrices together resulting in a large array of 501 sites, 12 6-day survey occasions and 34 species.

We used a hierarchical multi-species occupancy framework that allows us to estimate species richness based on a model of species occurrence while accounting for imperfect detection during surveys (Dorazio et al. 2006). The modelling approach assumes that detection and occupancy parameters for each species are drawn from a common distribution governed by hyper-parameters representing the mean effect of covariates over the whole community (Kery & Royle 2016). This community component improves precision of individual species estimates, ensuring efficient use of the dataset (Zipkin et al. 2009). Following Zipkin's et al. (2010) approach, we modelled species-level occupancy probabilities in each PA type (strict and multiple-use) independently while accounting for the following potential confounding variables: distance from main roads, distance from water sources, and mean Normalized Difference Vegetation Index (NDVI) of a 500-m buffer around the camera trap site (details on the modelling approach and on the process of obtaining variables for analysis are described in Supporting information 1). A variable representing human presence at the survey area (e.g. distance from village or house) was not included because human occupation is the main legal difference between multiple-use and strict PAs in Brazil and, therefore, directly related to management regime. Moreover, distance from towns was accounted for in the survey design.

We assessed the effect of strict protection on 21 species with at least 15 records by taking the difference in occupancy estimates between strict and multiple-use PAs (both on logit scale) at each iteration of the Bayesian sampling process, where positive values indicate the species had higher occupancy in strict PAs and negative values indicate higher occupancy in multiple-use PAs. We follow recommendations from MacKenzie et al. (2006) and interpret occupancy estimates as the species' probability of occurring or using the area sampled by a camera trap during our survey period, an approach commonly adopted in similar studies (e.g. Tobler et al. 2015; Rich et al. 2016). Occupancy modelling explicitly accommodates imperfect detection – when a species was present but not recorded – through an additional hierarchical component of the model (Kery & Royle 2016). In our study, we modelled detection probability as a function of camera trap location in relation to trail (on or off trail) and camera trap model (based on production year).

To investigate the influence of body size and threat status on the effect of strict protection we constructed two additional models that included distinct hyper-parameters for groups of species according to these two factors (size and threat). In the first model, species were divided into two groups according to body size (larger: ≥15 kg; smaller: <15 kg) and two distinct hyper-parameters governing each of these groups were specified. In the second model, species were again divided into two groups with distinct hyper-parameters governing each group of species, but this time grouping was based on threat status, with nationally threatened species (vulnerable, endangered or critically endangered; MMA 2014b) forming one group and non-threatened species forming the other group. We constructed these additional models using the same formulation and variables as in the model used to obtain species-level estimates. The only difference is that instead of having a single hyper-parameter governing the response of all species in the community we have two hyper-parameters governing the response of species according to the group they belong (Kery & Royle 2016; Rich et al. 2016). Therefore, the estimated values for the hyper-parameters in these additional models represent the mean effect of covariates on a given group of species (i.e. larger vs smaller and threatened vs non-threatened). We used results from these additional models only to investigate the effect of protection on occupancy estimates of species groups and decided to use the model with a single hyper-parameter governing the whole community for species-level inferences because we considered it to be more conservative regarding our predictions.

In multi-species occupancy models, species richness per sampling site (herein site species richness) emerges naturally at each iteration of the Bayesian sampling process as the sum of species occurring at a site (Dorazio et al. 2006). We used the single hyper-parameter model (used to obtain species-level occupancy probability) to estimate mean site species richness at each PA type for all mammal species >1 kg (overall species richness) and for five subsets of the community: globally threatened species (vulnerable, endangered or critically endangered), nationally threatened species (vulnerable, endangered or critically endangered), non-threatened species (not present in the national Red List), larger species (mean weight ≥15 kg), and smaller species (mean weight <15 kg). Global and national threat status follows IUCN (2017) and MMA (2014b), respectively, whereas species' mean weight was obtained from Marinho-Filho et al. (2002) and Paglia et al. (2012).

We adopted a Bayesian approach to implement all models in JAGS (Plummer 2013) through R (R Development Core Team 2015) using the package JagsUI (Kellner 2017). After a burn-in of 30,000 iterations, we ran three chains of 90,000 iterations with a thinning rate of 10, and assessed convergence with R-hat statistic (Supporting information 1). We used vague priors for all parameters estimated and conducted a prior sensitivity analysis, as well as an assessment of model fit (Supporting information 1; Table S3). All inferences are based on posterior means and 95% credible intervals. R code used to implement the model with a single-hyper parameter is available as Supporting information 2.

3.3 Results

3.3.1 Species occupancy

PA type had a strong effect on almost half of the species assessed (10 of 21), of which nine had higher occupancy in strict PAs and one in multiple-use PAs (Fig. 3.2 top panel; Table S4). As predicted, our results show that larger and threatened species tend to benefit from strict protection: seven of the eight largest species, 75% of the globally threatened and 66% of the nationally threatened species assessed had higher occupancy probability in strict PAs. It is striking that occupancy probability of large and functionally important species such as puma (*Puma concolor*), maned wolf (*Chrysocyon brachyurus*), tapir (*Tapirus terrestris*), peccaries (*Pecari tajacu* and *Tayassu pecari*) and giant anteater (*Myrmecophaga tridactyla*) was at least five times higher in SVP's strict PAs - for some the difference was tenfold (Table S4).

Conversely, hoary fox (*Lycalopex vetulus*) – a small-sized canid nationally listed as vulnerable – was the only species with higher probability of occupancy in multiple-use PAs. For another 11 species, PA type did not seem to have a strong effect – although the crab-eating fox (*Cerdocyon thous*) and hog-nosed skunk (*Conepatus semistriatus*) tended to favour multiple-use and ocelot strict PAs (but credible intervals overlapped 0). As predicted, species that did not respond to PA type were generally smaller (only one species >15 kg; grey brocket deer *Mazama gouazoubira*) and non-threatened (only three threatened species, all of them small felids: Pampas cat *Leopardus colocolo*, oncilla *L. trigrinus* and jaguarundi *Herpailurus yagouaroundi*). Confirming the patterns observed for individual species, the additional models with distinct hyper-parameters for species groups indicated that, on average, larger and threatened species benefit more from strict protection than smaller and non-threatened species (Fig 3.2 bottom panel).

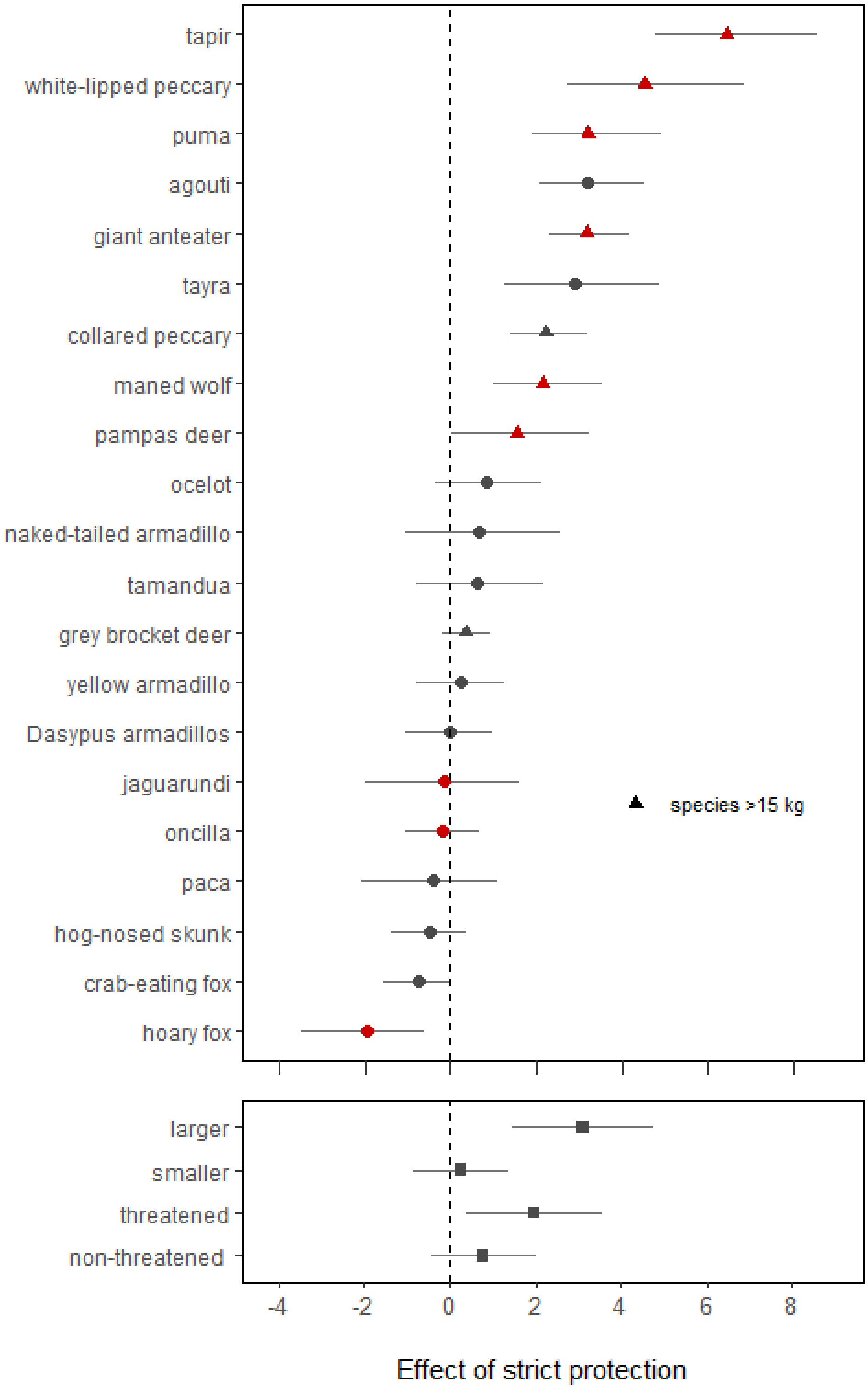


Figure 3.2: Effect of strict protection on the mammal community at Sertão Veredas-Peruaçu mosaic. The effect is the difference in probability of occupancy (logit scale) between strict and multiple-use protected areas, with positive values indicating higher occupancy in strict protected areas. Top panel displays species-level estimates obtained from a multi-species occupancy model with a single hyper-parameter specification and the bottom panel displays group-level estimates from models with distinct hyper-parameters for each group (see Data

analysis). Symbols represent the posterior means and lines the 95% credible interval; red symbols denote nationally threatened species. Refer to Table S4 for species' Latin names and probability of occupancy at each protected area type.

3.3.2 Species richness

Mean site species richness was greater in strict PAs, with nearly twice as many species as in multiple-use PAs (Fig. 3.3; overall). The same pattern was observed for subsets of the community, with greater richness in strict PAs regardless of body size or threat level (Fig 3.3). However, the difference between PA types was even greater for larger (>15 kg) and globally threatened species richness, with 2.7 and 2.4 times more species per site in strict than in multiple-use PAs, respectively. On the other hand, the effect of stricter protection levels on smaller species richness was more moderate, with only 1.3 times more species in strict PAs. The spatial distribution of species richness was also largely driven by PA type, with 'very low' species richness sites highly concentrated in multiple-use PAs and 'very high' richness sites mostly found in strict PAs (Fig 3.4) – a pattern also found for the spatial distribution of species richness of subsets of the mammal community (Figure S1).

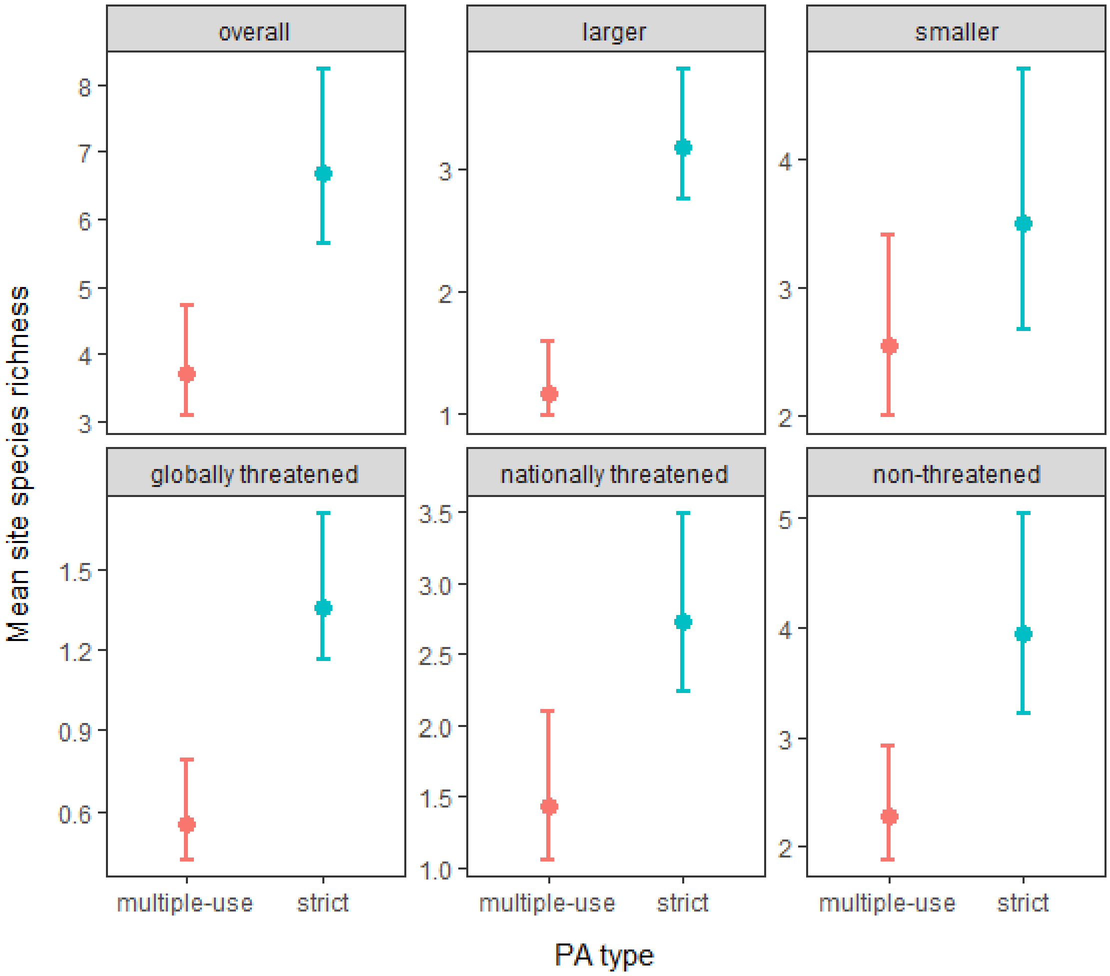


Figure 3.3: Mean camera trap site species richness for the mammal community (overall) and five subsets in each protected area type. Points are posterior means and lines indicate 95% credible intervals. Larger species are mammals with mean weight >15 kg, whereas smaller species have mean weight <15 kg.

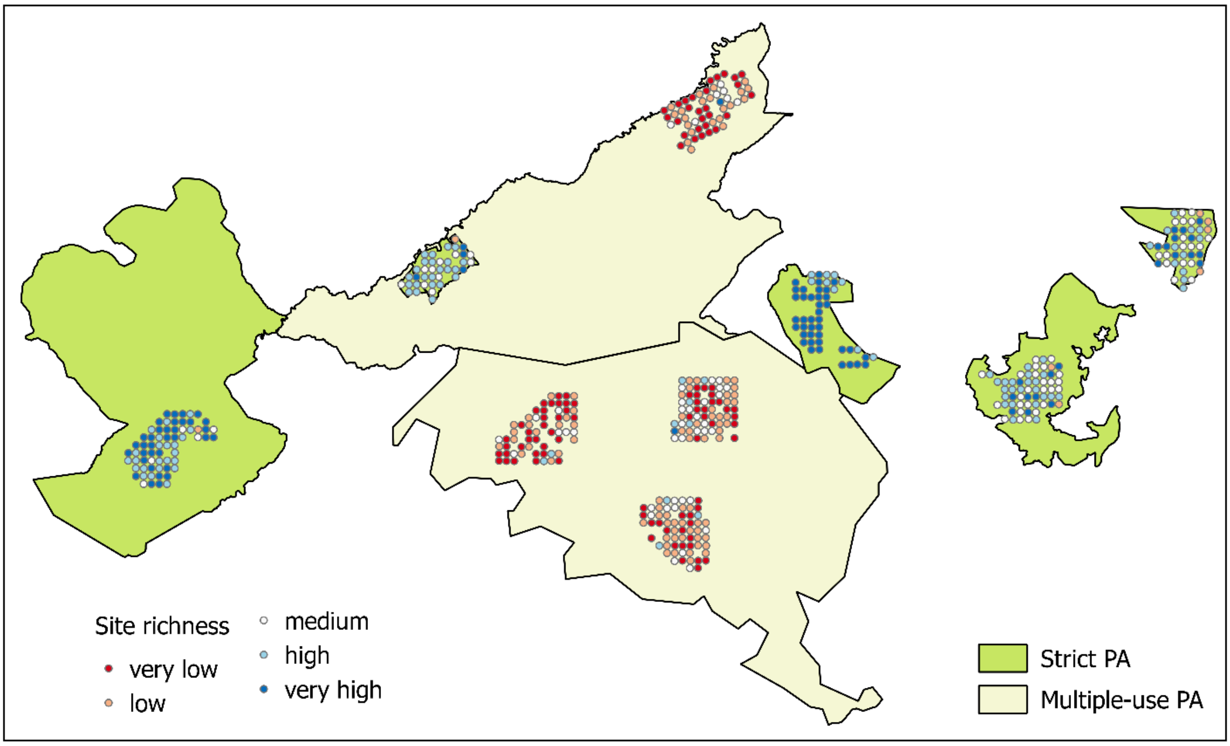


Figure 3.4: Spatial distribution of mammal species richness per camera trap site at Sertão Veredas-Peruaçu mosaic. Assignment to groups followed the 20th, 40th, 60th, and 80th percentile of species richness (from 'very low' to 'very high', respectively). Only Protected Areas (PA) surveyed are shown in the map. See Fig. S1 for results on subsets of the mammal community.

3.4 Discussion

3.4.1 Biodiversity patterns in contrasting levels of protection

Using a counterfactual analysis, we provide empirical evidence that strict PAs in the Cerrado support higher levels of mammal diversity than similar areas under less restrictive management. To our knowledge this is the first systematic assessment of PA performance regarding local terrestrial biodiversity in the Cerrado, and one of the few in Brazil (see Coetzee et al. 2014 and Gray et al. 2016 for global assessments including data from Brazil, and Xavier da Silva et al. 2018 for a longitudinal evaluation of Iguaçu National Park). Our results are consistent with similar studies in Africa that found areas with stricter protection to support greater mammal diversity (Kinnaird & O'brien 2012; Rich et al. 2016) and with research showing negative effects of anthropogenic pressure on some Neotropical mammals (Michalski & Peres 2005; Nagy-Reis et al. 2017; Cruz et al. 2018).

We also demonstrated a strong positive impact of strict PAs on larger and threatened mammals in the study region, which seems to be part of a broader trend of large-bodied species benefitting more from stricter PAs than smaller species (Kinnaird & O'brien 2012; Rich et al. 2016; Velho et al. 2016). Interestingly, size seems to have even greater influence on the effect of strict protection than threat status in the mammal community studied. The difference in occupancy between the two PA types assessed was much greater for the larger vs smaller comparison than for the threatened vs non-threatened comparison (Fig. 3.2 bottom panel). Similarly, we observed a greater difference in species richness at each PA type for larger than smaller species, whereas the difference between PA types was more stable among threatened and non-threatened species – although still larger for globally threatened species (Fig. 3.3).

Our analyses suggest that top predators, large insectivores and large herbivores/frugivores are extremely rare in the areas surveyed within multiple-use PAs, as none of them had a probability of occupancy greater than 10% (Table S4). Moreover, larger species richness in multiple-use PAs only reached one-third of that in strict PAs. The absence of these large and functionally important animals in significant parts of the multiple-use areas, combined with the low occupancy of the seed-disperser agouti, is likely to have profound impacts on the ecosystem, affecting the plant community, nutrient cycling and even carbon storage (Terborgh et al. 2001; Dirzo et al. 2014; Bello et al. 2015). On the other hand, a subset of the local mammal community seems to thrive in SVP's less restrictive areas. This group of species, however, is mainly composed by smaller, non-threatened mammals, known to tolerate or favour degraded habitats, but also includes the globally threatened oncilla and two nationally vulnerable small carnivores.

Our findings are extremely unlikely to reflect natural patterns of species occurrence that existed before the PAs were created, instead there is strong evidence that the patterns reported here reflect levels of protection. Firstly, spatially explicit biodiversity metrics were not available (and are still scarce) when SVP's parks and private reserves were created; their establishment was mainly driven by a mix of opportunity, scenic beauty and an attempt to protect large tracts of remaining natural vegetation. Additionally, we accounted for important confounding factors – both in study design and analysis – that could influence the occurrence of mammals in the region. In fact, we believe the pattern observed here is likely to be the case for broad parts of the Cerrado, as the surveyed areas within multiple-use PAs have lower human density than the average PA in the same category (Fig. S2) and SVP's natural vegetation cover of 80% (WWF-Brasil 2011) is higher than at the biome level. However, our study has the limitation of not providing information on population trends. Because declines can occur inside PAs (Craigie et al. 2010) long term monitoring of strict PAs in the Cerrado is necessary to ensure they are operating at their maximum effectiveness. The survey and analytical approach adopted here if implemented over the years is suitable for such monitoring in the Cerrado (Ferreira et al. 2017a) and is being successfully used to monitor trends of tropical forest vertebrates across the globe (Beaudrot et al. 2016, 2019b).

3.4.2 Conservation and policy implications

Our results combined with Cerrado-wide assessments of PA effectiveness in avoiding deforestation (Carranza et al. 2014a; Françoso et al. 2015) are strong arguments against attempts to downgrade or downsize PAs in Brazil (e.g. de Marques & Peres 2014; Bernard et al. 2014) and they give much needed scientific evidence for increasing strict PA coverage in the biome, currently at only 3% (MMA 2018). Considering that the main difference between the two types of PA surveyed – in practical and legal terms – is human use and occupation, it is reasonable to assume this is one of the main drivers of our results. Locally, small human settlements are known to negatively affect occupancy of a mammal species favoured by poachers (Ferreira 2018). Therefore, we suggest that solving land tenure issues in strict PAs and adopting strategies to reduce anthropogenic pressure within these reserves should be a priority for agencies and managers. This is echoed by Françoso et al. (2015) who showed deforestation rates to be higher in Cerrado PAs with unsolved land tenure problems. Indeed, adequate implementation and management of PAs, as well as increase in PA coverage, are strategic goals of the Cerrado national action plan (MMA 2014a), one of the key conservation policies for the biome.

Probably, because APAs are the least restrictive category of PA in Brazil and, consequently have low political and financial costs of implementation, PA creation policy in the Cerrado has largely focused on this category, which currently represents more than 60% of the area protected in the biome and 97% of the area under multiple-use PAs (MMA 2018). We argue this trend needs to be readdressed if a functional and diverse mammal community is to exist in the future. Without careful consideration of what is feasible to achieve with each PA category and an adequate balance between strict protection and multiple-use, we risk losing an important portion of Cerrado's biodiversity, even in the event of reaching 17% of the biome under legal protection (Aichi Target 11) – which is unlikely to be achieved by 2020 (Pacheco et al. 2018; Sano et al. 2019) or in the near future. As a complementary approach, a sound zoning system (e.g. establishment of core areas and corridors) informed by the understanding of factors driving threatened mammal occurrence, has the potential to improve the effectiveness of multiple-use PAs. Such measures are difficult to implement on the ground, but they could be more successful if focused on large rural properties (Stefanes et al. 2018). Agencies issuing permits to convert natural vegetation within such properties should work together with PAs managers and land owners to indicate the best location for the compulsory legal reserves (proportion of land that cannot be converted according to Brazil's forest code) and to negotiate compensations, such as the establishment of private PAs (RPPNs).

We acknowledge that strict protection is not the only way forward and that a mix of management regimes and strategies are necessary to promote Cerrado conservation while accommodating the needs of human populations and agriculture production (MMA 2014a;

Strassburg et al. 2017). Indeed some types of economically productive landscapes have been shown to provide habitat for a range of threatened species in other settings (Wearn et al. 2017). However, our work supports the conclusion that strict PAs play a vital role in maintaining Cerrado wildlife and without them the conservation of larger and threatened mammal species would be compromised. We argue that a shift in PA policy is needed in the Cerrado, with a focus on increasing the scant coverage of strict PAs, strengthening the management capacity of existing parks and reserves, as well as on concrete measures to improve performance of multiple-use PAs. Otherwise iconic animals such as maned wolves and giant anteaters will have trouble persisting in large parts of the Brazilian savanna.

3.5 Supporting information

3.5.1 Supporting information 1

Additional details on data analysis

Detection/no-detection matrix and variables for analysis

When assembling each species' detection/no-detection matrix, camera trap sites where survey effort was not a multiple of six had the remaining survey days and eventual records discarded. This is because our survey occasion was defined as each six days of sampling and it was necessary to ensure the sampling effort aggregated at each occasion was exactly the same. Additionally, to produce all matrices with the same dimensions, we attributed 'NA' whenever a camera trap site was not surveyed during an occasion (usually due to malfunctioning or to the time gap between setting up the first and last few cameras). All camera trap records of mammals >1 kg and a sample of the records tagged as not having any animal were double-checked to ensure detections were attributed to the correct species.

We used the software QGIS (v. 2.14.0) to extract spatial variables used in the analysis and downloaded data on river system and roads from SEMAD (2017) and Landsat satellite images from USGS (2018). The layer 'water sources' was produced by joining all streams and rivers above first order (i.e. from second-order onwards) in the western portion of Sertão Veredas-Peruaçu Mosaic - SVP (Grande Sertão Veredas National Park, Porto Cajueiro Private Reserve, Cochá Gibão and Rio Pandeiros Environmental Protection Areas), all streams and rivers above second order (i.e. from third-order onwards) in the eastern portion of SVP (Cavernas do Peruaçu National Park, Veredas do Peruaçu and Mata Seca State Parks) and data on large permanent lakes produced manually using our knowledge of the study region and Google Earth Pro. The use of distinct stream/river orders is due to water availability in the dry season (when we conducted our surveys); the greater the order, the more likely it is to be a permanent waterbody. In eastern SVP second-order streams do not hold water during the dry season, whereas in the western part of the mosaic they do. The final resulting layer matches closely what we observed in the field. The ‘main roads’ layer was produced by selecting only the roads, either paved or unpaved, directly connecting cities and towns in the region, and complementing it with GPS data collected in the field (because portions of some main roads were not available in the online database). Therefore, this layer does not represent all the roads in the region, but it represents all paved and the main unpaved roads that concentrate the vast majority of vehicle traffic. From these two layers we extracted the Euclidean distance from each camera trap site to the nearest water source and main road.

Normalized Difference Vegetation Index (NDVI) is related to vegetation productivity (Pettorelli et al. 2005), and in the Cerrado it represents well landscape green cover as well as the distinct vegetation types (Ferreira et al. 2003). We calculated NDVI from the red (R) and near infrared (NIR) bands of Landsat 8 images with the highest geodetic precision (Level 1 TP) and <10% cloud cover using the formula: NDVI = (NIR-R)/(NIR+R) (Pettorelli et al. 2018). We downloaded satellite images available at Earth Explorer (https://earthexplorer.usgs.gov/) from the final months of the rainy season (January-March), just before the camera trap survey was conducted in each area (Table S1). We decided to use images from the rainy season because exploratory analysis showed that in this period NDVI reflects better the structural difference between dry forests and savannas in the study area. For two areas surveyed before 2014 there is no Landsat 8 image available and we used scenes from this satellite obtained after the camera trap survey (Table S1). This is unlikely to be a problem because they are both located within strict PAs where vegetation cover does not change significantly over a period of only two years (a test with a sample of 120 camera trap sites showed that NDVI values obtained in the end of the wet season from two distinct years were highly correlated: 0.97). We overlaid a shape file containing all camera trap sites with the satellite images and produced a 500-m buffer around each site encompassing approximately 870 pixels of the Landsat image. The mean value of the pixels within each buffer gave us the mean NDVI value of the camera trap site used in the analysis. In a few cases we had to edit pixel values inside buffers overlapping large rivers or lakes, and with some cloud cover. Pixels over water were set to have no value (i.e. they did not contribute to the mean) and values for pixels with clouds cover were set to have the same value as the closest neighbouring pixel without cloud cover. These modifications were conducted in <2% of all buffers produced, and for the buffers modified less than 30 pixels of the approximately 870 within the 500-m buffer had their values changed. We also obtained mean NDVI values from 50-m and 2-km buffers around the camera trap site, but the values were highly correlated (> 0.9) with values from the 500-m buffer. All variables used in the model were scaled (centring at 0 and dividing by the variable's standard deviation) and checked for collinearity before the analysis (Table S2).

Table S1: Details of Landsat 8 images used to obtain mean NDVI for camera trap sites.

Protected Area	Scene identification	Date	Before survey
Veredas do Peruaçu State Park	219070	12/03/14	N
Mata Seca State Park	219070	12/03/14	N
Cavernas do Peruaçu National Park	219070	12/03/14	Y
Rio Pandeiros Environmental Protection Area (south)	219071	10/01/15	Y
Porto Cajueiro Private Reserve	219070	10/01/15	Y
Rio Pandeiros Environmental Protection Area (east and west)	219071	01/03/16	Y
Grande Sertão Veredas National Park	220070	23/02/17	Y
Cochá Gibão Environmental Protection Area	219070	20/03/17	Y

Table S2: Correlation among the variables used in the multi-species occupancy model.

	Dist_road	Dist_water	NDVI
Dist_road	1	-0.09	-0.43
Dist_water	-0.09	1	0.21
NDVI	-0.43	0.21	1

Modelling approach

Multi-species occupancy model can be understood simply as a community-occupancy model (Kery & Royle 2016). This modelling approach is similar to joining together a number of single-species occupancy models (MacKenzie et al. 2002), where the parameters estimated for each species are treated as random effects governed by a common distribution (Kery & Royle 2016).

Our multi-species occupancy modelling framework and script follows Zipkin et al. (2010), with adaptations based on Kery & Royle (2016). The occupancy component of the model was specified as:

$$\text{logit}(\psi[j,i]) =$$

$$\psi\text{Multiple-use}[i]*(1-\text{PAtype}[j]) + \psi\text{Strict}[i]*\text{PAtype}[j] + \alpha1[i]*\text{Dist\_road}[j] + \alpha2[i]*\text{Dist\_water}[j] + \alpha3[i]*\text{NDVI}[j]$$

Where $\text{logit}(\psi[j,i])$ is the probability, on the logit scale, that species *i* occurs at site *j*. In this model $\psi\text{Multiple-use}[i]$ and $\psi\text{StrictPA}[i]$ are the occupancy probability of species *i* at each PA type when the other variables (Dist_road, Dist_water and NDVI) are at their average value (i.e. 0).

Occupancy modelling takes advantage of repeated surveys at each sampling site and has an additional hierarchical component to model the probability of detecting a species at the site surveyed, which can be modelled as a function of methodological or environmental features (MacKenzie et al. 2002; Kery & Royle 2016). The detection component of our model was specified as follows:

$$\text{logit}(p[i,j,k]) =$$

$$\beta1[i] + \beta2[i]*\text{trail}[j] + \beta3[i]*\text{CT\_code}[j]$$

Where logit(p[i,j,k]) is the probability, on the logit scale, of detecting species *i* at site *j* during survey occasion *k*. In practice, there were two parameters estimated for 'CT_code' because this is a categorical variable with three levels indicating camera trap model (see Supporting information 2 for details in the R script).

Although the model we implemented used a data augmentation procedure (Dorazio et al. 2006), in preliminary versions we investigated the effect of adding the all-zero detection histories to our estimates. We ran two alternative models: with no data augmentation and adding 30 all-zero species. In both cases we obtained estimates of species richness similar to the values obtained in the adopted model (with 7 all-zero species), and therefore concluded that data augmentation did not inflate our estimates. We decided to proceed with data augmentation of 7 all-zero species because it is biologically reasonable (Ferreira & Oliveira 2014) and is a common approach on multi-species occupancy modelling (Dorazio et al. 2006; Zipkin et al. 2010; Kery & Royle 2016).

Model fit and prior sensitivity analysis

We used the Gelman-Rubin diagnostic for convergence of the Markov Chain, R-hat, to check for parameter convergence (Gelman & Hill 2006). Average R-hat values for estimated parameters was 1.0 in all three models used for inference (maximum R-hat value in any model was 1.01), indicating adequate convergence. To assess model fit, we followed recommendations from Kery & Royle (2016) and obtained posterior probabilities of Bayesian p-value and c-hat based on simulated data from the model. Bayesian p-values close to 0.5 and c-hat values close to 1 are indicative of adequate fit (Kery & Royle 2016). The posterior means indicated the model with one hyper-parameter had adequate fit: Bayesian p-values (both for each species and overall) ranged between 0.38-0.66, overall c-hat was 1.01, and average c-hat values for species with >5 records was 1.05 (range: 0.95-1.19). Expectedly, six species with <5 records had very high c-hat values due to scarce data, and no inference was made about them. Similarly, models with two distinct hyper-parameters had overall c-hat of 1.01 (both threat and size models) and range of c-hat values for species with >5 records for both models combined was 0.96 and 1.25. Bayesian p-values for threat and size models also did not reach extreme values and ranged between 0.32-0.67 and 0.36-0.63, respectively.

We also conducted a prior sensitivity analysis by running the model used for species-level inference with four variations of prior specification for the hyper-parameters (common distribution governing the species-specific effects). The posteriors obtained in our sensitivity analysis were very similar among all four models (Table S3), therefore, we considered prior specification to have little influence over the results obtained. Due to the long time needed to run each model, the similarities in model specification and in the results obtained from models with single and two hyper-parameters, we did not conduct a prior sensitivity analysis for the models with two distinct hyper-parameters.

The type of distribution adopted (either normal or uniform) and values used (mean and precision) to specify the distinct priors in the sensitivity analysis are based on examples from Kery & Royle (2016) and are given below:

- Model 1 (used for species-level inference): Mean ~ normal (0,0.001); Precision = $(sd)^{-2}$; Standard deviation ~ uniform (0,2).
- Model 2: Mean ~ normal (0,0.001); Precision ~ gamma (0.1,0.1)
- Model 3: Mean ~ uniform (-20,20); Precision ~ gamma (0.1,0.1)
- Model 4: Mean ~ uniform (-20,20); Precision = $(sd)^{-2}$; Standard deviation ~ uniform (0,2).

Table S3: Posterior means (logit scale) and standard deviations (sd) of hyper-parameters for models with distinct prior specifications.

	model 1		model 2		model 3		model 4	
	mean	sd	mean	sd	mean	sd	mean	sd
mu.Multi	-3.01	0.41	-2.91	0.50	-3.16	0.53	-3.00	0.41
mu.Strict	-1.75	0.37	-1.66	0.38	-1.81	0.41	-1.75	0.37
mu.alphaRoad	0.15	0.13	0.15	0.13	0.15	0.13	0.15	0.13
mu.alphaWat	0.00	0.14	0.00	0.14	-0.01	0.14	-0.01	0.14
mu.alphaNDVI	-0.10	0.17	-0.09	0.16	-0.09	0.16	-0.09	0.16
mu.betaNtrail	-2.97	0.36	-3.02	0.42	-2.94	0.39	-2.99	0.37
mu.betaYtrail	0.21	0.17	0.21	0.16	0.21	0.16	0.21	0.17
mu.betaCT2	-0.06	0.20	-0.08	0.21	-0.08	0.21	-0.06	0.20
mu.betaCT3	-0.15	0.31	-0.13	0.29	-0.13	0.29	-0.14	0.30

3.5.2 Supporting information 2

R script with data preparation and specification of the model used for inference in BUGS language

```
# Multi-species occupancy model to investigate effect of protected area type on mammal species in the Brazilian Cerrado
# Implemented in JAGS through R and using the package JagsUI
# Model and script largely based on Zipkin et al (2010) and Kery & Royle (2016)
# The latter reference has detailed guidance on how to run a multi-species occupancy model (chapter 11)
##### Step 1 - loading and preparing data #####
X <- abind(Mtxlist, along=3)     # 3D array of 501 camera trap sites (rows) 12 survey occasions (collumns) and 34 species (3rd dimension)
n <- dim(X)[3]-7              # number of observed spp (total species minus the all-zero species)
nzeroes <- dim(X)[3]-27 # number of augmented (all-zero) species in the data set
J <- dim(X)[1]     # number of CT sites
K <- read.csv("validOccasions_VECTOR_NAiflessThan6d.csv")      # number of occasions at each CT site
# covariates data
covs <- read.csv("Scaled_SVP_sitecovs_501sites.csv", header=T) # continuous variables are scaled
pa_type <- covs$pa_type            # one PA type must be 0 to eliminate its term in the equation
NDVI <- covs$NDVImean_500m
trail <- covs$trail
Dist_road <- covs$Dist_road
Dist_water <- covs$Dist_water
CTcode2 <- as.numeric(covs$CTcode2)


##### Step 2 - Bundle and summarize data #####
str(sp.data <- list(n = n, nzeroes = nzeroes, J = J, K = K, X = X,
            pa_type = pa_type,
            Dist_road = Dist_road, Dist_water = Dist_water, NDVI = NDVI,
            trail = trail, CTcode2 = CTcode2) )
```

```
#### Step 3 - Defining initial values for MCMC ####
# wst and zst are as suggested by Kery & Royle 2016
wst <- rep(1, n+nzeroes)                  # set all species as occurring
zst <- array(1, dim = c(J, n+nzeroes))        # same as above

sp.inits <- function() {
  omegaGuess = runif(1, n/(n+nzeroes), 1)
  psi.meanGuess = runif(1, .25,1)
  list(omega=omegaGuess, Z = zst, w = wst,
       psiMulti = rnorm(n = n+nzeroes), psiStrict = rnorm(n = n+nzeroes),
       alphaRoad = rnorm(n = n+nzeroes),
       alphaWat = rnorm(n = n+nzeroes), alphaNDVI = rnorm(n = n+nzeroes),
       betaNtrail = rnorm(n = n+nzeroes), betalYtrail = rnorm(n = n+nzeroes),
       betalCT2 = rnorm(n = n+nzeroes), betalCT3 = rnorm(n = n+nzeroes))
}

##### Step 4 - specify the model in BUGS language ####
Model 1
sink("model.txt")
cat("
    model {
    # Prior distribution for community-level parameters – ‘hyperpriors’
    omega ~ dunif(0,1)
    mu.Multi  ~ dnorm(0, 0.001)
    mu.Strict ~ dnorm(0, 0.001)
    mu.alphaRoad ~ dnorm(0, 0.001)
    mu.alphaWat ~ dnorm(0, 0.001)
    mu.alphaNDVI ~ dnorm(0, 0.001)
    mu.betaNtrail ~ dnorm(0, 0.001)
    mu.betaYtrail ~ dnorm(0, 0.001)
    mu.betaCT2 ~ dnorm(0, 0.001)
```

```
    mu.betaCT3 ~ dnorm(0, 0.001)


    # precision
    tau.Multi <- pow(sd.Multi,-2)
    tau.Strict <- pow(sd.Strict,-2)
    tau.alphaRoad <- pow(sd.alphaRoad,-2)
    tau.alphaWat <- pow(sd.alphaWat,-2)
    tau.alphaNDVI <- pow(sd.alphaNDVI,-2)
    tau.betaNtrail <- pow(sd.betaNtrail,-2)
    tau.betaYtrail <- pow(sd.betaYtrail,-2)
    tau.betaCT2 <- pow(sd.betaCT2,-2)
    tau.betaCT3 <- pow(sd.betaCT3,-2)


# sd
    sd.Multi ~ dunif(0,2)
    sd.Strict ~ dunif(0,2)
    sd.alphaRoad ~ dunif(0,2)
    sd.alphaWat ~ dunif(0,2)
    sd.alphaNDVI ~ dunif(0,2)
    sd.betaNtrail ~ dunif(0,2)
    sd.betaYtrail ~ dunif(0,2)
    sd.betaCT2 ~ dunif(0,2)
    sd.betaCT3 ~ dunif(0,2)
   # specify species-level priors for species i (out of 34); governed by community-level hyper-parameters
    for (i in 1:(n+nzeroes)) {
    w[i] ~ dbern(omega)
    psiMulti[i] ~ dnorm(mu.Multi, tau.Multi)
    psiStrict[i] ~ dnorm(mu.Strict, tau.Strict)
    alphaRoad[i] ~ dnorm(mu.alphaRoad, tau.alphaRoad)
    alphaWat[i] ~ dnorm(mu.alphaWat, tau.alphaWat)
    alphaNDVI[i] ~ dnorm(mu.alphaNDVI, tau.alphaNDVI)
```

```
betaNtrail[i] ~ dnorm(mu.betaNtrail, tau.betaNtrail)

betaYtrail[i] ~ dnorm(mu.betaYtrail, tau.betaYtrail)

betaCT2[i] ~ dnorm(mu.betaCT2, tau.betaCT2)

betaCT3[i] ~ dnorm(mu.betaCT3, tau.betaCT3)


  # Ecological model for latent occurrence (process model; occupancy component) of spp i at site j

# loop to define Z-matrix ('true' matrix of 1-0)

for (j in 1:J) {

logit(psi[j,i]) <- psiMulti[i]*(1 - pa_type[j]) + psiStrict[i]*pa_type[j] +

alphaRoad[i]*Dist_road[j] + alphaWat[i]*Dist_water[j] + alphaNDVI[i]*NDVI[j]


mu.psi[j,i] <- psi[j,i] * w[i]

Z[j,i] ~ dbern(mu.psi[j,i])


# Observation model for replicated detection/no-detection observations

# observed 1-0 matrix (from field data)

# detection of species i at site j for survey occasion k (detection component)

for (k in 1:K[j]) {

logit(p[j,k,i]) <- betaNtrail[i] + betaYtrail[i] * trail[j] +

betaCT2[i] * equals(CTcode2[j],2) + betaCT3[i] * equals(CTcode2[j],3)


mu.p[j,k,i] <- p[j,k,i] * Z[j,i]

X[j,k,i] ~ dbern(mu.p[j,k,i])

Xnew[j,k,i] ~ dbern(mu.p[j,k,i])  # replicate data


# assessing model fit

# Observed dataset

chi2.actual[j,k,i] <- pow(X[j,k,i] - mu.p[j,k,i], 2)/ (mu.p[j,k,i] + 0.0001)  # Add small value to denominator to prevent division by zero

# Expected dataset

chi2.sim[j,k,i] <- pow(Xnew[j,k,i] - mu.p[j,k,i], 2)/ (mu.p[j,k,i] + 0.0001)  # same as above

}
```

```
   chi2.actual.sum[j,i] <- sum(chi2.actual[j,1:K[j],i])
   chi2.sim.sum[j,i] <- sum(chi2.sim[j,1:K[j],i])
   }
   }
    ###### Derived quantities ########
   # calculating effect of protection: psi in strict PA - psi in multi PA (logit scale)
   for(u in 1:n){
   PAeffect[u] <- psiStrict[u] - psiMulti[u]
   }


# Site species richness overall, large (>15kg), nationally-threatened (MMA 2014) and globally-threatened (IUCN 2017)
      for (s in 1:J){
   Nsite[s] <- sum(Z[s,])         # Number of occurring species at each site
   Nsite.large[s] <- sum(Z[s,c(1,11,16,17,19,21,22,25,26,29,30,32,33)])      # Number of  spp >15kg at each site
   Nsite.threat[s] <- sum(Z[s,c(1,12,14,15,17,19,21,23,24,25,26,28,29,30,32,34)]) # Number of nationally-threatened spp at each site
   Nsite.Glob.threat[s] <- sum(Z[s,c(14,17,25,26,28,29,32)]) # Number of globally threatened spp at each site
   }
    #### Mean site spp richness for each type of PA
   # Overall
   Nsite.strict <- Nsite[c(1:38,108:166,224:331,454:501)]    # sp richness per site for strict PA; no need to monitor
   Nsite.multi <-Nsite[c(39:107,167:223,332:453)]         # sp richness per site for multi-use PA; no need to monitor
   mean.Nsite.strict <- mean(Nsite.strict) # mean sp richness per site for strict PAs, param to be monitored
   mean.Nsite.multi <- mean(Nsite.multi)   # mean sp richness per site for multi-use PAs, param to be monitored


   # Larger species (> 15kg)
   Nlarge.strict <- Nsite.large[c(1:38,108:166,224:331,454:501)]    # larger sp richness per site for strict PA; no need to monitor
```

```
   Nlarge.multi <-Nsite.large[c(39:107,167:223,332:453)]        # larger sp richness per site for multi-use PA; no need to monitor


  mean.Nlarge.strict <- mean(Nlarge.strict) # mean larger sp richness per site for strict PAs, param to be monitored

   mean.Nlarge.multi <- mean(Nlarge.multi)   # mean larger sp richness per site for multi-use PAs, param to be monitored


   # Nationally-threatened species (MMA 2014)

   Nthreat.strict <- Nsite.threat[c(1:38,108:166,224:331,454:501)]    # threatened sp richness per site for strict PA; no need to monitor

   Nthreat.multi <-Nsite.threat[c(39:107,167:223,332:453)]        # threatened sp richness per site for multi-use PA; no need to monitor


   mean.Nthreat.strict <- mean(Nthreat.strict) # mean threat sp richness per site for strict PAs, param to be monitored

   mean.Nthreat.multi <- mean(Nthreat.multi)   # mean threat sp richness per site for multi-use PAs, param to be monitored


   # Globally threatened species (IUCN 2017)

   NGlobthreat.strict <- Nsite.Glob.threat[c(1:38,108:166,224:331,454:501)]    # glob-threat sp richness per site for strict PA; no need to monitor

   NGlobthreat.multi <-Nsite.Glob.threat[c(39:107,167:223,332:453)]        # glob-threat sp richness per site for multi-use PA; no need to monitor


   mean.NGlobthreat.strict <- mean(NGlobthreat.strict) # mean glob-threat sp richness per site for strict PAs, param to be monitored

   mean.NGlobthreat.multi <- mean(NGlobthreat.multi)   # mean glob-threat sp richness per site for multi-use PAs, param to be monitored


   }

   ",fill = TRUE)

sink()

# end of model in BUGS language

# parameters to monitor
```

```
params1 <- c("omega", "mu.Multi", "mu.Strict", "mu.alphaRoad", "mu.alphaWat",
"mu.alphaNDVI", "mu.betaNtrail", "mu.betaYtrail", "mu.betaCT2", "mu.betaCT3",
"psiMulti", "psiStrict", "alphaRoad", "alphaWat", "alphaNDVI", "betaNtrail", "betaYtrail",
"betaCT2", "betaCT3", "PAeffect”)

# MCMC settings

ni <- 120000   ;   nt <- 10   ;   nb <- 30000   ;   nc <- 3


# Run the model in JAGS

library(jagsUI)

out1 <- jags(sp.data, sp.inits, params1, "model1.txt",

          n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE)
```

3.5.3 Supporting information 3

Supporting table and figures

Table S4: Occupancy probability at each protected area type for 27 mammal species recorded at Sertão Veredas-Peruaçu mosaic (ranked by body mass).

		multiple-use PA			strict PA							
Species[1]	Common name	occupancy	LCI	UCI	occupancy	LCI	UCI	number of records	body mass (kg)[2,3]	larger species (>15kg)	nationally threatened[4]	globally threatened[1]
Tapirus terrestris	lowland tapir	0.00	0.00	0.00	0.39	0.28	0.52	138	225	Y	Y	Y
Puma concolor	puma	0.07	0.03	0.18	0.67	0.41	0.92	68	75	Y	Y	N
Hydrochoerus hydrochaeris	capybara	0.04	0.00	0.48	0.06	0.00	0.51	2	50	Y	N	N
Tayassu pecari	white-lipped peccary	0.00	0.00	0.01	0.13	0.06	0.24	28	32.5	Y	Y	Y
Ozotoceros bezoarticus	Pampas deer	0.02	0.00	0.06	0.07	0.02	0.21	23	31.5	Y	Y	N
Mymercophaga tridactyla	giant anteater	0.04	0.02	0.07	0.47	0.35	0.62	119	31	Y	Y	Y
Chrysocyon brachyurus	maned wolf	0.06	0.02	0.15	0.34	0.16	0.66	39	25	Y	Y	N
Pecari tajacu	collared peccary	0.09	0.05	0.15	0.48	0.34	0.66	150	23.5	Y	N	N
Mazama gouazoubira	grey brocket deer	0.62	0.53	0.71	0.70	0.61	0.78	661	18	Y	N	N
Leopardus pardalis	ocelot	0.05	0.02	0.11	0.10	0.05	0.19	51	11.5	N	N	N
Cuniculus paca	paca	0.02	0.01	0.05	0.01	0.00	0.04	23	9	N	N	N
Herpailurus yagouaroundi	jaguarundi	0.08	0.02	0.31	0.07	0.02	0.30	15	6.5	N	Y	N
Cerdocyon thous	crab-eating fox	0.34	0.24	0.46	0.19	0.12	0.29	145	6.5	N	N	N
Tamandua tetradactyla	tamandua	0.20	0.07	0.54	0.32	0.11	0.75	33	6	N	N	N
Speothos venaticus	bush dog	0.01	0.00	0.17	0.06	0.00	0.54	1	6	N	Y	N
Procyon cancrivorus	crab-eating racoon	0.01	0.00	0.12	0.05	0.00	0.40	3	5.5	N	N	N
Nasua nasua	South American coati	0.01	0.00	0.19	0.07	0.01	0.62	2	5.1	N	N	N
Euphractus sexcinctus	yellow armadillo	0.14	0.07	0.29	0.17	0.08	0.35	49	5	N	N	N
Eira barbara	tayra	0.01	0.00	0.05	0.17	0.08	0.36	34	4.85	N	N	N
Dasypus spp.	nine- and seven-banded armadillo	0.09	0.05	0.18	0.09	0.05	0.18	46	4.4	N	N	N
Lycalopex vetulus	hoary fox	0.14	0.07	0.25	0.02	0.01	0.07	76	3.75	N	Y	N
Cabassous unicinctus	southern naked-tailed armadillo	0.20	0.04	0.80	0.30	0.07	0.81	17	3.25	N	N	N
Leopardus colocolo	Pampas cat	0.20	0.02	0.90	0.03	0.00	0.35	4	3	N	Y	N
Dasyprocta azarae	agouti	0.01	0.00	0.03	0.23	0.16	0.32	179	2.85	N	N	N
Conepatus semistriatus	striped hog-nosed skunk	0.32	0.20	0.47	0.22	0.13	0.34	99	2.5	N	N	N
Leopardus tigrinus	oncilla	0.49	0.34	0.69	0.44	0.30	0.62	151	2.15	N	Y	Y
Galicts cuja	lesser grison	0.01	0.00	0.22	0.09	0.01	0.65	2	1.75	N	N	N

1: IUCN (2017); 2: Marinho-Filho et al. (2002); 3: Paglia et al. (2012); 4: MMA (2014) . LCI= Lower Credible Interval; UCI= Upper Credible Interval. Number of records: maximum 1 per 6 survey-days/site.

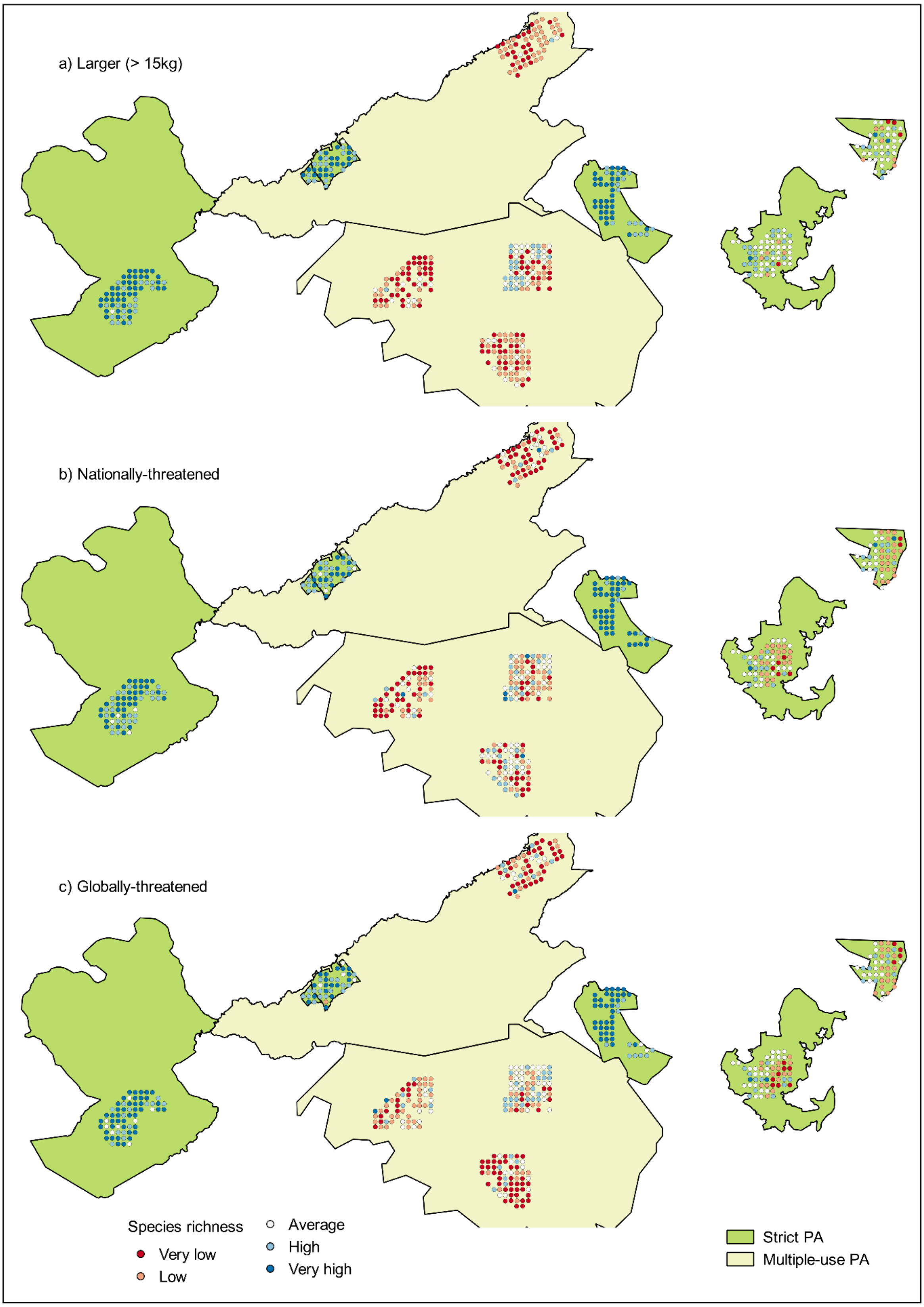
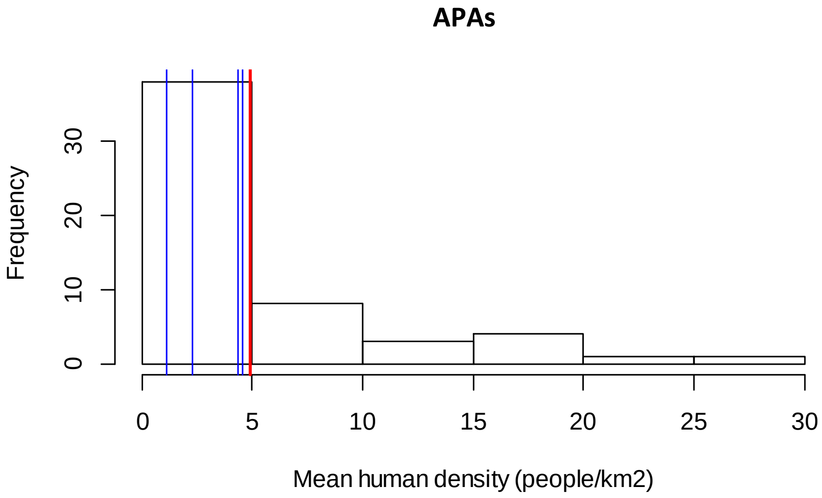


Figure S1: Spatial distribution of mammal species richness per camera trap site at Sertão Veredas-Peruaçu Mosaic for subsets of the community (a-c). Assignment to groups followed the 20th, 40th, 60th, and 80th percentile of species richness (from 'very low' to 'very high', respectively). Only protected areas (PA) assessed are shown.



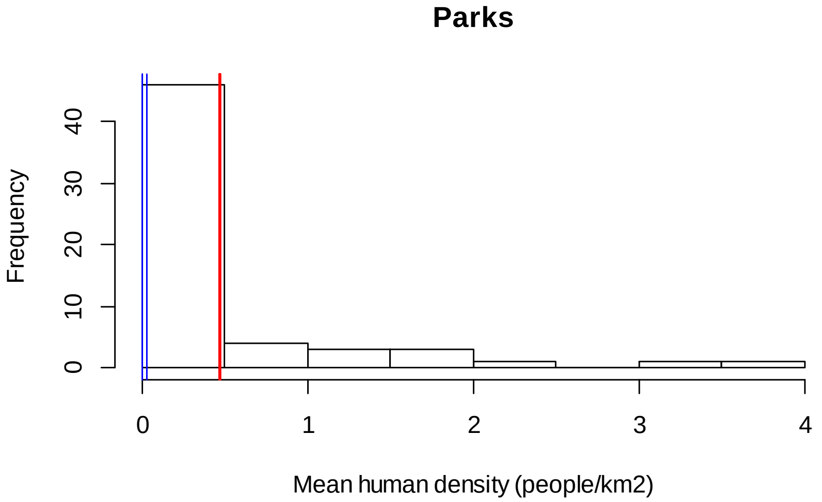


Figure S2: Distribution of human density at Cerrado's Environmental Protection Areas - APAs (multiple-use PA, IUCN category V) and Parks (strict PA, IUCN category II). Red lines indicate mean human density across the whole biome for all PAs in that category and blue lines indicate the mean at each camera trap array at SVP. Four of the arrays in strict PAs had mean density of 0 and are represented by a single blue line. We used QGIS to calculate mean human density at each PA by clipping a raster layer with human density in Brazil in 2010 at 1 km^2 resolution (IBGE 2017) with the limits of Cerrado's state and federal PAs from Brazil's Environmental Ministry (http://mapas.mma.gov.br/i3geo/datadownload.htm). Four parks and four EPAs (probably peri-urban PAs) from the governmental database were excluded before calculating the mean due to extremely high human densities. The bottom graph does not include private reserves (RPPNs) because there is no consolidated database with their polygons and location.

Chapter 4: Little evidence of anthropogenic pressure affecting mammal species activity patterns in a mosaic of protected areas

Xeric vegetation at Mata Seca State Park

4.1 Introduction

Anthropogenic pressure has well-documented effects on the spatial distribution of biodiversity (Ceballos & Ehrlich 2002; Di Marco & Santini 2015; Barlow et al. 2016), often reducing animal abundance and species richness (Newbold et al. 2015). However, human presence and activities can also have more subtle effects on wildlife influencing the time of the day (e.g. Gaynor et al. 2018) and for how long animals are active (e.g. Ciuti et al. 2012; Clinchy et al. 2016). These temporal effects have not received much attention from the scientific and conservation community (Frey et al. 2017), despite activity being intrinsically related to crucial aspects in an animal's life such as acquiring food and avoiding predators (e.g. Creel & Christianson 2008; Shamoon et al. 2018), thus potentially affecting its reproductive and survival rate. In addition to demographic effects, the period of the day a species is active may also drive rapid evolutionary changes of whole taxonomic branches (Baker & Venditti 2019), suggesting that in extreme cases human-driven alterations in activity patterns could even have long-lasting consequences for biodiversity.

A recent global analysis revealed that human disturbance has increased nocturnal activity in a wide-range of mammal species across the globe (Gaynor et al. 2018). In fact, change in activity patterns, particularly an increase in nocturnality, has been revealed as a response to very distinct impacts such as hunting (Di Bitetti et al. 2008; van Doormaal et al. 2015), agriculture (Ramesh & Downs 2013; Shamoon et al. 2018) and outdoor recreation (Reilly et al. 2017; Oberosler et al. 2017). However, despite their potential negative effects, such shifts are not necessarily always detrimental to species. When change in activity pattern does not have a substantial impact on demographic rates, it may be an effective strategy allowing the use of areas under anthropogenic influence that otherwise would be unsuitable. For instance, it has been argued that a shift from diurnal to more nocturnal activity in tigers enables co-occurrence with humans even under relatively high human densities (Carter et al. 2012).

In the Neotropics, the effect of human pressure on mammal activity has been assessed using camera traps in a handful of studies, revealing a shifting in the period of activity for some species, but not across all species or regions assessed. In the Andean mountains, three of seven species investigated altered their activity patterns in response to the presence of domestic dogs (Zapata-Ríos & Branch 2016). In the Atlantic forest of Argentina red brocket deer (*Mazama americana*), southern tiger cat (*Leopardus guttulus*) and puma (*Puma concolor*) seemed to increase nocturnal activity in response to higher levels of poaching and easier access to humans, but dwarf brocket deer (*Mazama nana*), jaguarundi (*Herpailurus yagouaroundi*) and margay (*Leopardus wiedii*) did not show a shift in activity (Di Bitetti et al. 2008; Paviolo et al. 2009; Cruz et al. 2018). Human disturbance increased nocturnal activity in ocelot (*Leopardus pardalis*) in the Brazilian Atlantic forest (Massara et al. 2018), whereas it did not change the species activity in the Peruvian Amazon (Kolowski & Alonso 2010). Finally, forest fragmentation has been shown to reduce diurnal activity in nine-banded armadillo (*Dasypus novemcinctus*), but not in opossum (*Didelphis marsupialis*) and agouti (*Dasyprocta leporina*) (Norris et al. 2010).

Although the last decade saw an improvement in the knowledge of human impacts on Netropical mammals' activity pattern, most studies focused on forest ecosystems and on a few species in each locality. Furthermore, despite the establishment of protected areas (PAs) being one of the most popular interventions to minimise anthropogenic pressure on biodiversity (Watson et al. 2014), seldom was the effect of habitat protection on activity patterns explicitly investigated in South America (but see Paviolo et al. 2009). In this paper we use data from a large-scale camera trap survey to investigate the effect of protected area type and distance to households on activity of 15 mammal species occurring in the Brazilian Cerrado. We rely on those indicators of anthropogenic pressure because they are known to influence the spatial distribution of mammals in the region (Chapter 3; Ferreira 2018) and we focus our assessment on three metrics of activity: proportion of time active, daily activity pattern and probability of diurnal activity. As activity patterns in regions with high temperatures can also be influenced by environmental conditions (Penido et al. 2017; Attias et al. 2018), our analysis of the probability of diurnal activity includes not only variables indicating pressure but also vegetation cover and distance from water, factors that may help animals cope with high daytime temperatures found in our study area. Given the seemingly widespread increase in nocturnality in response to human disturbances (e.g. Ramesh and Downs 2013; Carter et al. 2015; Gaynor et al. 2018; Shamoon et al. 2018), our hypothesis is that greater anthropogenic pressure causes a shift in daily activity patterns towards the night in our study region, with animals decreasing the amount of activity between 06:00 and 18:00hs in multiple-use PAs and closer to households.

However, the studies conducted so far in other parts of the Neotropics do not allow us to pinpoint the characteristics of species most likely to change their activity due to human disturbance, making species-specific predictions difficult. One could argue that threatened species and animals frequently targeted by poachers would present a greater shift to nocturnality (e.g. Di Bitetti et al. 2008; Paviolo et al. 2009; Ohashi et al. 2013; van Doormaal et al. 2015). Nonetheless, we previously demonstrated that most large and threatened species in the study region showed a strong and positive spatial response to increased levels of habitat protection (Chapter 3), which could potentially minimise the need of a temporal response in some species. Alternatively, one could argue that the species more likely to overlap spatially with humans – in our study region those are usually the ones regarded as less sensitive – would show a temporal response to anthropogenic pressure, whereby they would shift activity towards the night to minimise encounters (e.g. Ramesh and Downs 2013; Oberosler et al. 2017; Reilly et al. 2017). Finally, although reduction of activity level in face of human disturbance has been reported (Ciuti et al. 2012; Clinchy et al. 2016), we do not expect large differences in the proportion of time species were active in each type of PA because temporal shifts in daily activity patterns would allow them to maintain roughly the same overall level of activity.

4.2 Material and methods

4.2.1 Study area

We conducted our study at a mosaic of protected areas in northern Minas Gerais state, in a region located within the Brazilian Cerrado but also encompassing part of the southern limit of the Caatinga. Sertão Veredas-Peruaçu mosaic (SVP) extends over approximately 18,000 km^2 and is formed of 14 PAs of distinct management categories and two indigenous lands (see detailed description of SVP in Chapter 1). For this research we surveyed seven of SVP's PAs, five strict and two large multiple-use PAs (Fig. 4.1; detailed characteristics of PAs are available in Chapter 3). In short, strict PAs have biodiversity conservation as their main goal and do not allow human occupation or direct use of natural resources (Brasil 2000), whereas the multiple-use PAs surveyed represent the least restrictive category of PA in Brazil where human settlements and some level of land conversion is permitted (Brasil 2000; Rylands & Brandon 2005). Despite the low level of restrictions, the two multiple-use PAs surveyed at SVP still have most of their natural vegetation cover (WWF-Brasil 2011) and human density is low (2.24 and 1.14 people/km^2), with the population concentrated in small scattered rural villages and one small town with less than 3,000 inhabitants (IBGE 2019).

The climate in northern Minas Gerais is markedly seasonal with a dry season between April and mid-October and a wet season from mid-October to March. Mean average temperature during the core survey period (April to August) recorded at the two long-running weather stations in the region was 23.8 and 21.2 ^{o}C, whereas the mean maximum temperature was 32.2 and 29.9 ^{o}C. These mean temperatures were calculated from data collected between 2012 and 2017 at Januária (eastern portion of SVP) and between 2012 and 2015 at Formoso (western portion of SVP) – raw data available from the Brazilian Institute of Meteorology (INMET; www. inmet.gov.br).

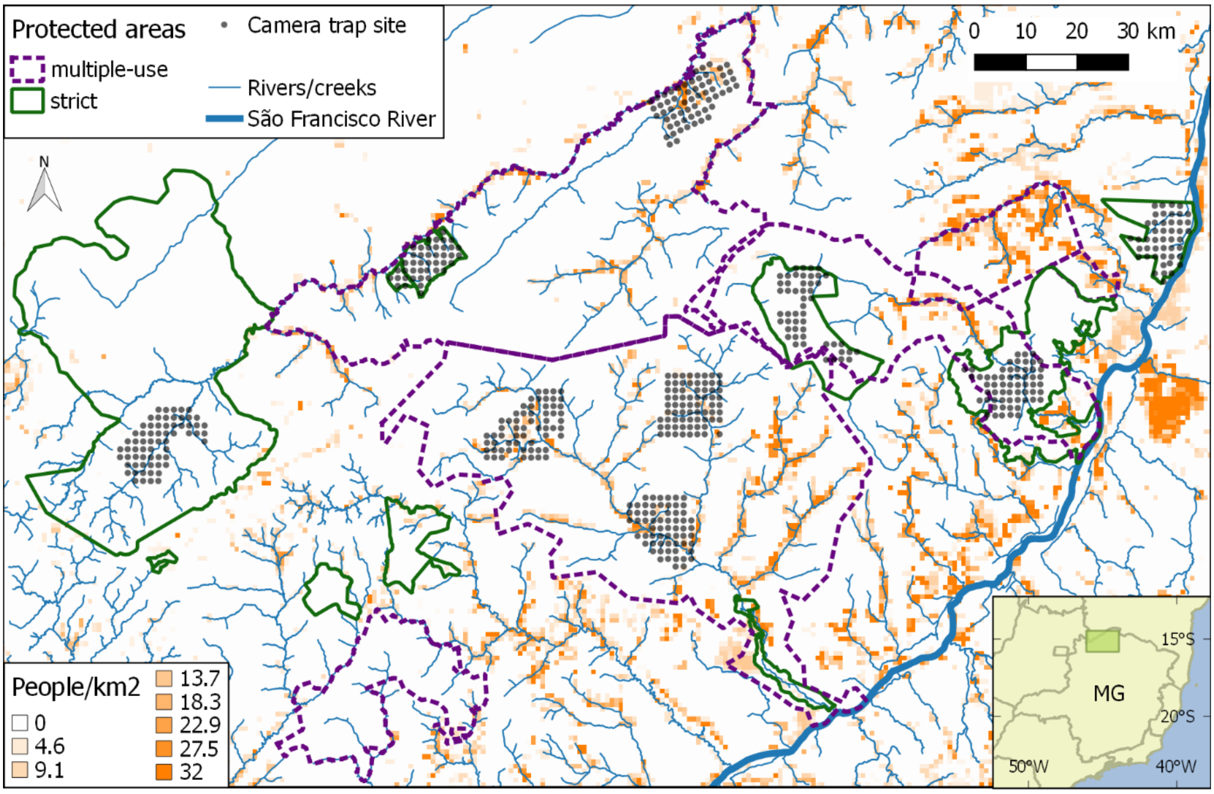


Figure 4.1: Location of camera trap sites and arrays relative to the distribution of human density at Sertão Veredas-Peruaçu mosaic.

4.2.2 Camera trapping

As the data collection procedures and camera trap dataset of this chapter are the same as in Chapter 3, we provide only a brief description of the survey design and camera trapping protocol, which are described in detail in the previous chapter. We deployed camera traps (Bushnell TrophyCam and Bushnell Agressor) to survey five arrays in strict PAs and four arrays in multiple-use PAs distributed across SVP (Fig. 4.1). Arrays within multiple-use PAs were always located at least 10 km away from towns and from strict PAs to minimize peri-urban effects on biodiversity and potential spill-over of animals from areas with higher protection, respectively. Additionally, we kept at least 12 km between pairs of camera trap arrays to cover a larger geographic area and minimize issues of spatial non-independence. Each array was composed of 43-70 sampling sites systematically distributed in grids at a distance of 1.5 km between sites, in which camera traps were deployed for no more than 74 days. We determined a 50-m buffer around the geographic coordinates of these sampling sites where we could select the location deemed most adequate to set up camera trap units. Overall we deployed camera traps at 517 sampling sites and only 8% of them were established outside the 50-m buffer due to challenging access conditions (but never more than 200 m away from the pre-determined coordinates). We retained data from 506 sites where camera traps worked adequately for more than five days (average effort per site 52 days; range 6-74; 90% of sites surveyed for at least 30 days; total effort >26,000 survey days). Surveys were conducted between 2012 and 2017, always during the dry season, and no bait or lure was used to attract animals.

4.2.3 Data analysis

Before conducting analysis we eliminated non-independent records from the raw camera trap data, which we defined as sequential records of a species at a single camera trap site with less than one minute interval between them. For example, if two records of a tapir (*Tapirus terrestris*) were obtained at the same camera trap site at 22:15 and 22:16, only one of these records would be considered for analysis. This is to minimise the impact of occasions when animals were standing still in front of the camera performing very little movement. We also joined nine-banded armadillo (*Dasypus novemcintus*) and seven-banded armadillo (*D. septemcinctus*) into *Dasypus* spp. because we could not confidently identify them to species level in all records.

To assess the effect of habitat protection on species activity, we compared the proportion of time active (activity level) and daily activity patterns between strict and multiple-use PAs for species with at least 25 independent records in each PA type (Table S1). This cut-off point in the number of records is needed to avoid large biases in estimates (Rowcliffe et al. 2014). We used the 'activity' package to fit a flexible circular kernel distribution to time-of-detection data and estimated the proportion of time species were active (Rowcliffe et al. 2014). Circular kernel density estimators are non-parametric methods that have been used in camera trap studies to estimate density of records across the 24 hours of the day, from which various activity metrics can be derived (Ridout & Linkie 2009; Oliveira-Santos et al. 2013). We implemented a Wald test to check whether the difference between estimates of activity level from strict and multiple-use PAs was significantly different from 0 and calculated 95% confidence intervals (CIs) by resampling the data via bootstrap (Rowcliffe et al. 2014). Exploratory analysis showed that the choice of bootstrap method (either resampling the data or the probability density distribution generated by the model) shifted slightly the 95% CIs obtained for some species, but did not change the interpretation of results.

To assess the amount of overlap between daily activity patterns of the same species in each PA type, we estimated a coefficient of overlap using the package 'overlap' (Meredith & Ridout 2014). This package uses circular kernel density estimation to calculate a coefficient that ranges from 0 to 1 (Ridout & Linkie 2009), where 0 indicates completely distinct activity patterns and 1 represents identical patterns. Ridout & Linkie (2009) tested the performance of three variations of the overlap coefficients (Dhat1, Dhat4, and Dhat5) and we followed their recommendation of adopting Dhat1 when the smallest sample size of the pair-wise comparison (i.e. strict vs multiple-use) was <50 records and Dhat4 for samples >50 independent records. We then used the package 'circular' (Agostinelli & Lund 2017) to conduct a Watson's two-sample test and determine whether species' daily activity patterns in strict and in multiple-use PAs were significantly different from each other (Jammalamadaka & SenGupta 2001; Oliveira-Santos et al. 2013). For these analyses all independent records of the species were aggregated according to PA type and clock time of these records were transformed into radians.

A third metric we used to investigate the effect of human pressure on species activity was the probability of diurnal activity. To estimate this probability we built a matrix with the number of independent diurnal (06:00-17:59) and nocturnal (18:00-05:59) records per camera trap site for each species. We then used these matrices as the response variable in generalised linear mixed effects models (GLMMs) with binomial distribution implemented via the package ‘lme4’ (Bates et al. 2014). We modelled the probability of diurnal activity for each species as a function of PA type (either strict or multiple-use), distance to the nearest household, distance to water sources and NDVI, while accounting for variation among camera trap arrays (a variable with nine levels determining random intercepts in the model – Zuur et al. 2009). Due to the study region location, the little latitudinal variation among camera trap arrays, and because surveys were concentrated in the same 6-month period every year, variation in sunset and sunrise during our data collection was minimum (https://www.esrl.noaa.gov/gmd/grad/solcalc/), and unlikely to influence results of this analysis.

In our global model, PA type and distance to households indicated the level of anthropogenic pressure at the camera trap site, whereas NDVI and distance to water sources were used to account for variation in environmental factors that may reduce the thermal stress related to daytime activity in animals, potentially enabling higher levels of diurnal activity (Owen-Smith 1998; Camilo-Alves & Mourão 2006; Cain et al. 2008; Attias et al. 2018). We could not account for variation in daily temperature, because our analysis needed data to be aggregated over the camera trap site during the whole survey period. However, all camera trap surveys were conducted during the dry season only, controlling for at least part of the variation in weather conditions.

We used Landsat 8 images to calculate mean NDVI (an index representing vegetation cover and related to vegetation structure in the Brazilian Cerrado – Ferreira et al. 2004) of a 500-m buffer around each camera trap site and measured distance to water sources based on a spatial layer of rivers, creeks and lakes (SEMAD 2017). Detailed procedures to calculate NDVI and distance to water sources for each camera trap site are available in Chapter 3. To calculate distance between camera trap sites and households, we used a spatial layer with human density in Brazil in 2010 (IBGE 2017) to extract the centroid of each 1 km^2 cell with density ≥ 1 person/km^2 – representing cells with human occupation. We then measured the shortest

Euclidian distance between each camera trap site and the extracted centroids. Because we extracted the centroid of 1 km^2 occupied cells, the geographic coordinates obtained do not represent the exact location of each household and may have caused some imprecision in the measurement of short distances (<750 m). Nonetheless, this approach still gives an adequate representation of distance from potential sources of anthropogenic pressure and is the most refined measurement we could obtain, given that there is no database with geographical coordinates of households at SVP. Using human density directly as a variable was not an option due to the large number of camera trap sites located in cells with no human occupation, which generated convergence problem in exploratory models. Similarly, we could not use number of human records in camera traps as a measure of pressure (e.g. Reilly et al. 2017; Oberosler et al. 2017; Shamoon et al. 2018) because most of our cameras were not deployed on human trails, resulting in very few images of people. All spatial analyses were performed in QGIS (QGIS Development Team 2017).

We restricted our analysis of probability of diurnal activity to 15 species recorded in more than 30 camera trap sites to ensure an adequate sample size (Table S1). We started the modelling approach by building a global model with the four explanatory variables and one variable determining random intercepts (prob. diurnal activity ~ PA type + Dist. household + Dist. water + NDVI + [1|camera trap array]). We first implemented this global model for each species to check estimates of the random component of the model. We did this because mixed-effects models may be unstable or unable to estimate the among-population variance if the random variable has less than five levels or if there is a large imbalance in sample sizes between these levels (Harrison et al. 2018). Although our random variable can have up to nine levels (one for each camera trap array), the actual number of levels varied among species, depending on the number of camera trap arrays where each species had been recorded (Table S1). For 10 of the 15 species, estimated variance between camera trap arrays was 0, indicating there was not enough data to account for variance. In these cases, the model does not estimate random intercepts and performs in the same way as a regular binomial GLM (Harrison et al. 2018).

We also checked this initial global model for convergence, and noticed that models for tapir, hoary fox (*Lycalopex vetulus*), yellow armadillo (*Euphractus sexcinctus*) and tamandua (*Tamandua tetradactyla*) had convergence problems. For these four species, eliminating the categorical variable (PA type) from the model solved the problem. This was due to very low number of records in one of the PA types (hoary fox and tapir) or because records at each camera trap site were either 100% at night or 100% at daytime (yellow armadillo and tamandua). After making these adaptations, we constructed alternative models representing all possible combinations (without interactions) of explanatory variables present in the global model, including the null model. The total number of models implemented for each species was either 16 or 8 depending on the inclusion of PA type in the global model. We conducted a model selection procedure based on Akaike Information Criteria corrected for small sample sizes (AICc) and selected a top model set for each species that included all models up to a summed AIC weight of 0.95 (Burnham & Anderson 2002). We then used the package 'MuMIn' (Barton 2018) to obtain averaged estimates of parameters and their precision from this 95% top model set. We adopted the more conservative approach of averaging estimates across all models (zero method or full average), which assumes a coefficient value of 0 for a variable that is not present in one or more models among the 95% top set (Burnham & Anderson 2002). All numerical variables were scaled (centring at 0 and dividing by the variable's standard deviation) and checked for collinearity before running the models.

We also implemented all the modelling procedures described above to estimate the probability of animals being active in a more restricted period of the day, between 07:00-16:00hs (defined as core diurnal activity), when encounters with people would be more likely. As the conclusions reached from these models are not different from the previous models estimating probability of diurnal activity between 06:00 and 18:00hs, we only present a synthesis of these new results as supporting information (Fig. S1). All statistical analyses for this chapter were conducted in R (R Development Core Team 2015).

4.3. Results

4.3.1 Effect of protected area type on activity

Confirming our predictions, PA type did not have great influence over the proportion of time species were active (Fig. 4.2). Only for oncilla (*Leopardus tigrinus*) was there evidence that activity level was higher in strict PAs than in multiple-use PAs (difference: 0.19; Wald test: 4.15; p-value: 0.04). For the other seven species investigated, difference between estimates of activity level in contrasting management regimes was not significant. In fact, species such as collared peccary (*Pecari tajacu*), yellow armadillo and agouti had almost identical activity levels between strict and multiple-use PAs.

On the other hand, contrary to our predictions, there was not a clear shift in daily activity patterns towards the night in multiple-use PAs for any of the species assessed – although collared peccaries have slightly reduced diurnal activity (Fig. 4.3). Five of the eight species investigated presented similar daily activity patterns in the two PA types, with coefficients of overlap around 0.8 or higher. Among those species, brocket deer and agouti had diurnal activity peaks that were virtually at the same time in both management regimes. Conversely, collared peccary, *Dasypus* armadillos and yellow armadillo had distinct daily activity patterns in each PA type with a lower coefficient of overlap than other species. However the main difference seems to be in the peak of activity, which shifted a few hours, but never from being diurnal to nocturnal (or vice-versa; Fig. 4.3). In yellow armadillo, activity peaked during daytime in both PA types; just before midday in strict PAs and around 14:00hs in multiple-use PAs. *Dasypus* armadillos were slightly more active during daytime in multiple-use PAs and its main activity peak shifted from around 19:00hs in multiple-use PAs to midnight in strict PAs. On the other hand, collared peccary had slightly higher levels of diurnal activity in strict PAs with more activity in the afternoon and early in the morning than in multiple-use PAs. Collared peccary’s main activity peak was earlier in strict PAs but still nocturnal, whereas the morning peak happened roughly at the same time in both PA types (Fig. 4.3).

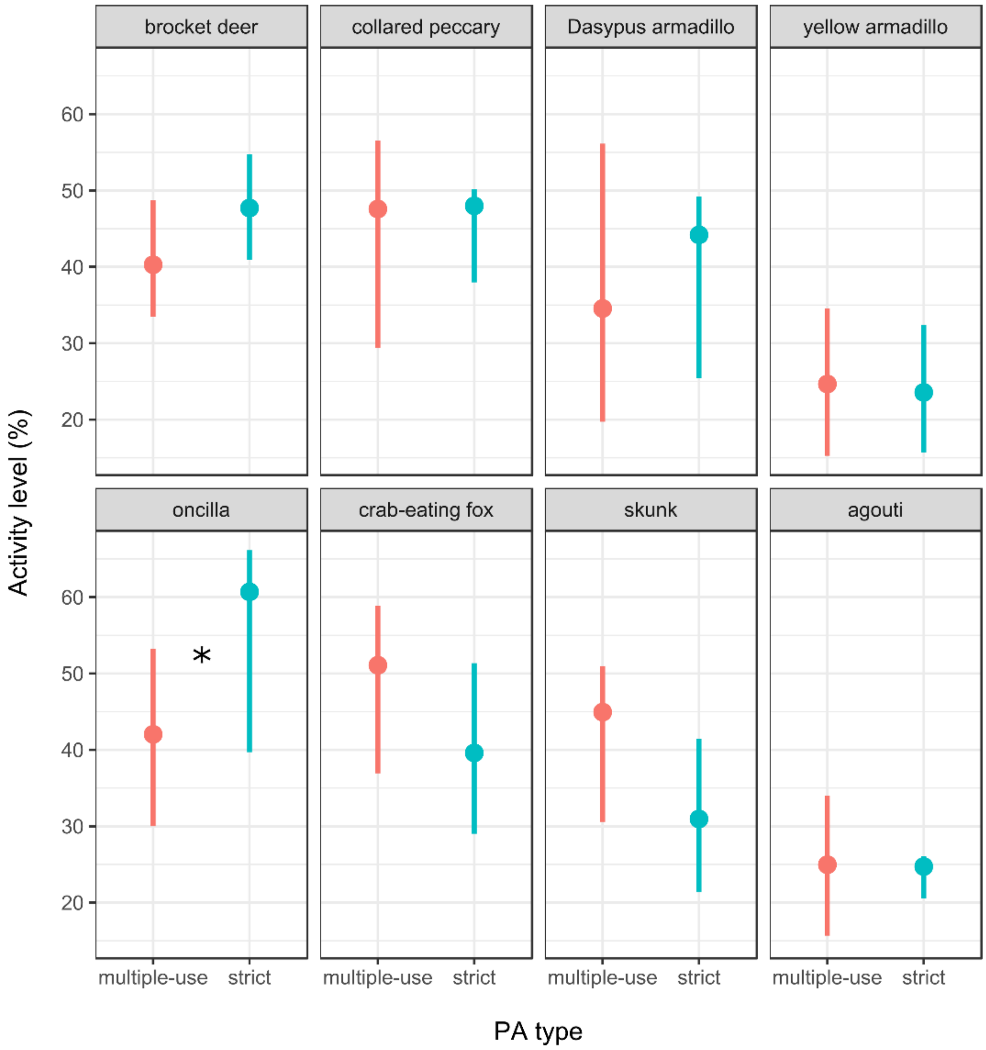


Figure 4.2: Activity level (proportion of time active) of eight mammal species at contrasting protected area (PA) types in the Brazilian Cerrado. Asterisk (*) denotes Wald test p-value < 0.05. See Table S1 for Latin names.

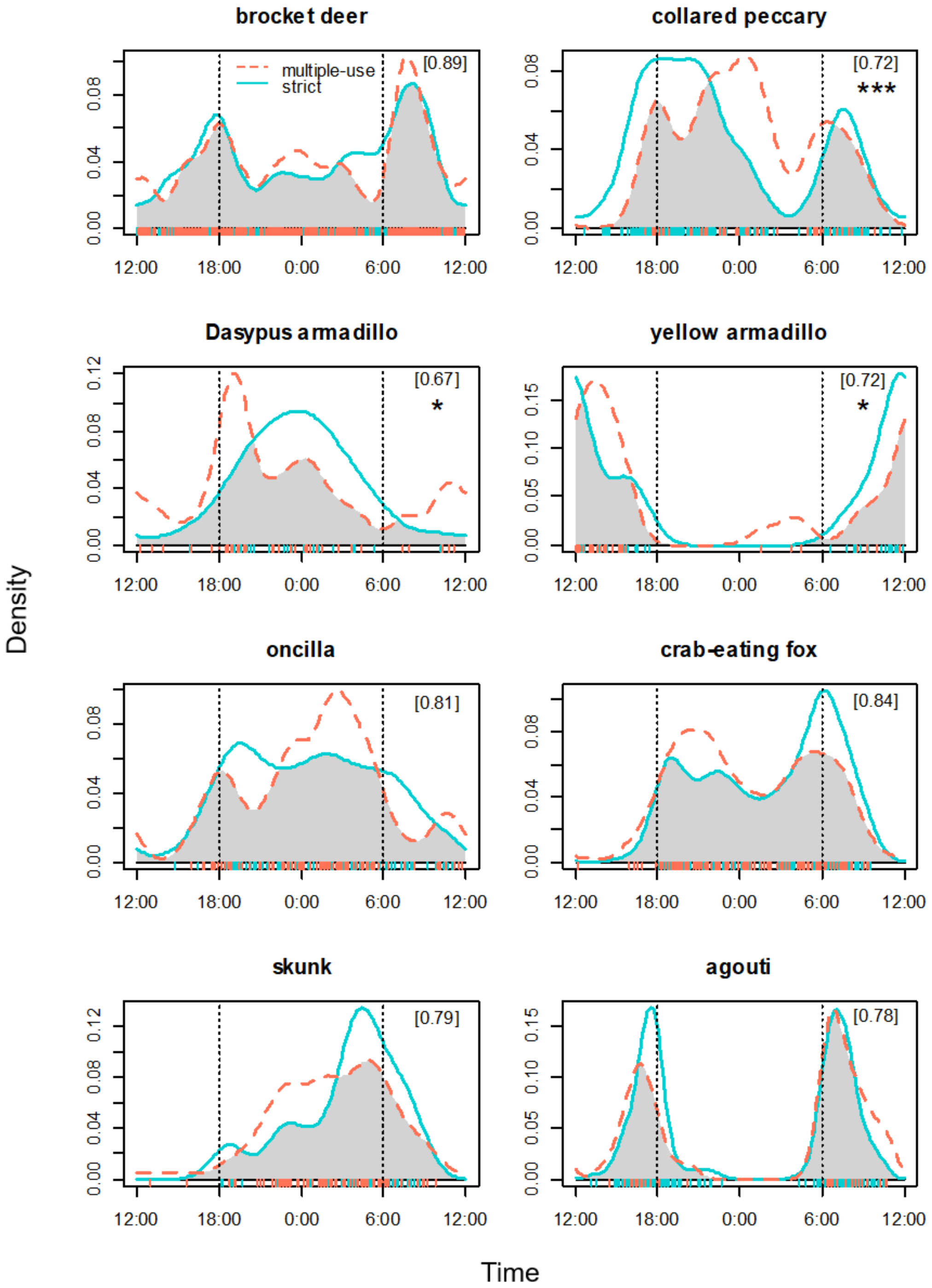


Figure 4.3: Overlap in daily activity patterns of eight mammal species at contrasting protected area types (multiple-use and strict) in the Brazilian Cerrado. Estimates inside square brackets are the coefficient of overlap (0 indicates no overlap and 1 indicates identical activity pattern). Asterisks indicate p-value of Watson's two-sample test of homogeneity: <0.05 (*) and <0.001 (***). Note that plots are centred at midnight (0:00). See Table S1 for Latin names.

4.3.2 Probability of diurnal activity

Again contrary to our predictions, indicators of anthropogenic pressure had very little influence on probability of diurnal activity of 15 mammal species, with the effect of PA type and distance to households often being estimated close to 0 (Fig. 4.4). Tamandua was the only species that responded to one of the anthropogenic variables; it was more likely to be active during daytime further away from households (Fig. 4.4). At SVP, environmental factors seem to have greater influence on daytime activity than anthropogenic pressure: NDVI affected probability of diurnal activity in three species and distance to water sources had an effect also on three species (Fig. 4.4). An increase in NDVI, and therefore in vegetation cover, resulted in higher probability of diurnal activity for agouti (*Dasyprocta azarae*) and yellow armadillo, but in lower probability for *Dasypus* armadillos. Giant anteater (*Myrmecophaga tridactyla*) and *Dasypus* armadillos were more likely to be active during daytime in camera trap sites further away from water sources, whereas the opposite was observed for ocelot. Additionally, there is some indication that greater vegetation cover may increase diurnal activity in collared peccary and that hoary fox is more likely to be active in the daytime further away from water, but the 95% CIs of these parameter estimates overlap 0. The additional analysis focusing on a more restricted diurnal activity (07:00-16:00hs) also revealed very little influence of anthropogenic pressure (Fig. S1), with only one species responding to indicators of pressure and the effect was not in the direction we anticipated (agouti probability of being active in this core diurnal period was higher closer to households).

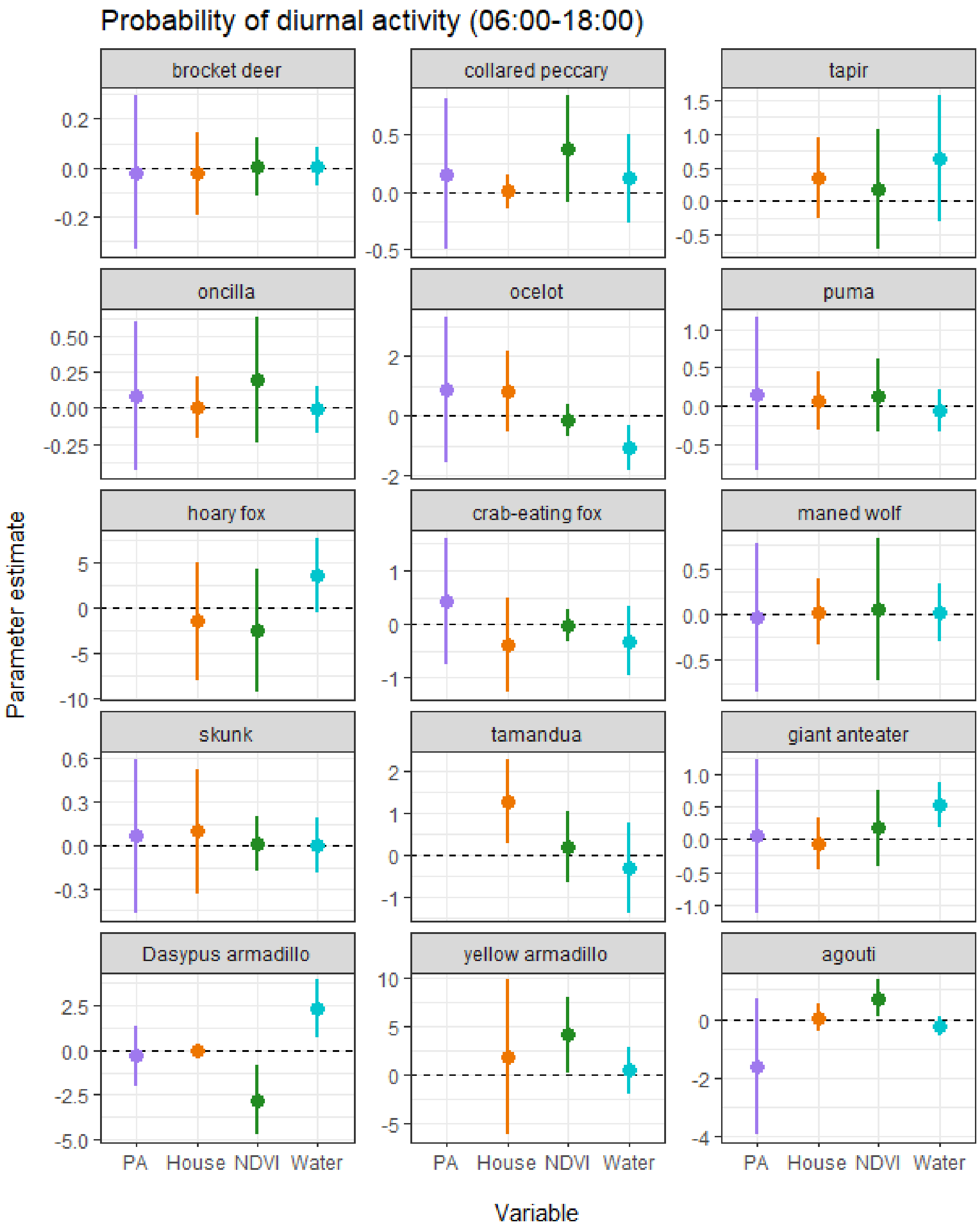


Figure 4.4: Averaged parameter estimates of models assessing the effect of distinct variables on the probability of diurnal activity for 15 mammal species. Parameters are on logit scale and vertical lines represent the 95% confidence interval. Positive parameter values indicate higher probability of diurnal activity in strict protected areas (PA), further away from households (House), in sites with greater vegetation cover (NDVI) and further away from water sources (Water). Results for brocket deer, puma, crab-eating fox, hoary fox and *Dasypus* armadillo are from a binomial GLMM, whereas for all other species are from a binomial GLM. See Material and methods for details on the variables used and Table S1 for species' Latin names.

4.4 Discussion

4.4.1 Effect of anthropogenic pressure on species activity

Our results revealed that the great majority of mammal species investigated did not change activity due to increased anthropogenic pressure. This is very different from findings of a recent global study showing consistent increase in nocturnality in mammals as a response to human disturbance (Gaynor et al. 2018). It is also distinct from field studies in South America showing that some of the species we focused on here (or their congeners) shifted activity in locations with greater human pressure (Di Bitetti et al. 2008; Paviolo et al. 2009; Norris et al. 2010; Cruz et al. 2018; Massara et al. 2018). Reasons for the lack of response observed in our study region may include the low level of anthropogenic impact, spatial response to PA type showed by some species, and low diurnal activity among most of the species investigated.

SVP is still largely covered with natural vegetation (WWF-Brasil 2011), large scale conversion of natural habitats is not widespread, most roads are unpaved and human density is relatively low (Chapter 1). These factors taken together with our survey design of maintaining at least 10 km between a town and camera trap arrays in multiple-use PAs, could suggest that anthropogenic pressure close to our camera trap sites is not high enough to cause a shift in animal activity. As with any other impact, the intensity of human disturbance is likely to be important in determining a change in activity. For instance, at least some of the studies in South America that found an effect of human disturbance on activity were conducted in much more fragmented areas than ours (Norris et al. 2010; Massara et al. 2018). However, even if the intensity of anthropogenic pressure at our study region is not as high as in other areas where species have changed activity patterns, using this same dataset we showed that higher levels of protection have a strong and positive impact on the spatial distribution of the local mammal community (Chapter 3). Additionally, in one of the national parks we surveyed here, collared peccary occupancy is known to decrease sharply closer to households (Ferreira 2018). Thus, there is clear evidence that the current level of anthropogenic pressure at SVP, even if relatively low when compared to more human-dominated landscapes, is enough to have an important effect over the mammal community studied. However this effect is spatial, not temporal.

We believe that this spatial response to PA type may have contributed to the lack of temporal effect of anthropogenic pressure on the species assessed. By avoiding the use of areas under higher anthropogenic pressure (multiple-use PAs) some species potentially minimised the need to shift activity pattern to cope with increased disturbance. The opposite has been reported for several mammal species: a shift in activity to avoid periods of intense human activity, without changing spatial distribution or abundance (Carter et al. 2012; Ramesh & Downs 2013; Reilly et al. 2017; Oberosler et al. 2017). There are also instances of species responding both spatially and temporally to human disturbance (Zapata-Ríos & Branch 2016; Shamoon et al. 2018), including species similar to those we investigated here. For example, abundance of red brocket deer and puma seem to decrease and nocturnal activity to increase in areas with higher levels of poaching and logging (Di Bitetti et al. 2008; Paviolo et al. 2009). Another factor potentially limiting the increase of nocturnality in our study is the overall low level of daytime activity in most species, possibly due to high daytime temperature. Of the 15 species with enough data to investigate the probability of diurnal activity, only brocket deer, yellow armadillo and agouti had most of their activity during daytime (Fig. S2). This fact alone limits the possibility of observing an increase in nocturnality in many species.

Despite the lack of consistent change in activity associated with indicators of anthropogenic pressure, in five cases there was a change in the metrics assessed. In two of these cases species changed their activity in response to higher pressure in the way we predicted: tamandua increased the probability of diurnal activity further away from households and collared peccary was moderately more active during daytime in strict PAs. In the other three cases the change in activity metrics observed did not follow our initial predictions: oncilla was more active in strict PAs (when we predicted no difference), whereas yellow armadillo and

Dasypus armadillos, although showing distinct daily activity patterns in each PA type, did not reduce diurnal activity in multiple-use PAs.

At SVP, collared peccaries strongly favoured strict PAs (Chapter 3) as well as sites further away from households (Ferreira 2018). Thus the species' distinct activity patterns in each PA type (Fig. 4.3) may be an additional strategy to cope with anthropogenic pressure, reaching its activity peak later in the night and minimising diurnal activity in multiple-use PAs to avoid encounters with humans. However, collared peccary's probability of diurnal activity was not influenced by anthropogenic factors (Fig. 4.4) and the species strong spatial response to PA type suggests that a temporal shift in activity may have limited effectiveness in mitigating the negative impacts associated with human presence. On the other hand, tamanduas did not respond spatially to PA type in the study region (Chapter 3) suggesting that the increased nocturnality closer to households is a plausible mechanism enabling the species to use sites under greater human pressure that could otherwise be unsuitable. As tamanduas spend part of their time within the tree canopy (Hayssen 2011), our result does not necessarily mean the species is less active during daytime when pressure is higher, it could also be that tamanduas are avoiding diurnal activity at the ground level when close to households but are active in the trees where they are probably less vulnerable, particularly to domestic dogs. Increasing nocturnal activity close to houses and settlements have also been reported for ocelots in Brazil (Massara et al. 2018) as well as for wild boar (*Sus scrofa*) and sika deer (*Cervus nippon*) in Japan (Ohashi et al. 2013; van Doormaal et al. 2015).

Several factors may be responsible for oncilla's distinct levels of activity in each PA type such as prey abundance, hunting success, intra- and inter-specific competition and even predation risk. The spatial distribution of mammal species in the study region (Chapter 3) may suggest that risk of predation and intra-specific competition with other predators is greater in strict PAs, but we have no information on the other factors to allow for a more conclusive inference. Regardless of the underlying cause, the additional time oncillas are active in strict PAs are likely to result in increased energetic costs that may be detrimental to the species if it is not driving higher reproduction or survival rates. Alternatively, if the reduced activity in multiple-use PAs results in sub-optimal use of resources it may lead to population decline in these areas in the medium to long-term. As oncilla is a globally threatened felid which seems to have most of its population outside PAs (Payan & Oliveira 2016), this difference in activity levels should be investigated further to determine whether it is specific to our study region or a more general pattern observed across the species' geographic range. Finally, both yellow and *Dasypus* armadillos had distinct daily activity patterns in each PA type but the difference observed does not seem to be influenced by protection level, as diurnal activity was not reduced in multiple-use PAs (in fact, it was slightly higher for one species).

4.4.2 Influence of environmental factors on diurnal activity

In our study region, environmental factors seem to have greater influence than human pressure on the probability of mammal species being active during daytime. The amount of vegetation cover and availability of water could reduce thermal stress in animals (Tuff et al. 2016; Elmore et al. 2017), favouring an increase in diurnal activity in a region where daytime temperature reaches around 30°C even in the winter. Milder temperatures in areas with greater vegetation cover (Demarchi & Bunnell 1993; Mourão & Medri 2007; Pfeifer et al. 2019) probably enabled higher daytime activity in yellow armadillo and agouti, particularly for the former species, which had its activity peak during the warmest hours of the day (Fig. 4.3 and Fig. S3). For example, a study tracking yellow armadillos with GPS devices in the Pantanal revealed that the species selected forest habitats when temperature was high (Attias et al. 2018). Similarly, the higher probability of diurnal activity closer to water sources in ocelot may be related to greater vegetation cover provided by narrow forest strips along rivers and creeks, that are not adequately represented by NDVI extracted from a 500-m buffer around the camera trap site (mean NDVI at the 500-m buffer is not strongly correlated to distance to water sources at SVP;

cor = 0.21). In addition, large mammals may directly use water or mud (wallow) as a thermoregulation strategy (Ayeni 1975; Carrillo et al. 2002; Bracke 2011; Khongdee et al. 2011), although it is unknown whether ocelots engage in such behaviour.

Probability of daytime activity in giant anteater and *Dasypus* armadillos was also influenced by environmental factors, however these species responded contrary to what would have been expected to cope with high daytime temperatures (Fig. 4.4). It is unclear why diurnal activity in these species increased further away from water and at sites with lower vegetation cover (for *Dasypus* armadillos only), but it could in part be linked to the physiological characteristics of Xenarthra (McNab 1984). In fact, our data suggests that Xenarthra species seem to be more flexible in their activity pattern. The two armadillos studied shifted activity peak a few hours between PA types (Fig. 4.3) – but not in the direction hypothesized to mitigate human pressure – and probability of diurnal activity in three of the four Xenarthra species assessed was influenced by environmental variables (Fig. 4.4). This flexibility is probably due to the fact that Xenarthra species have limited ability to use their metabolism to regulate body temperature (McNab 1984, 1985), favouring behavioural thermoregulation strategies that include shifts in activity patterns. Indeed, GPS tracking studies of giant anteaters and several armadillos showed they usually change activity patterns as well as habitat use in response to variation in air temperature (Camilo-Alves & Mourão 2006; Maccarini et al. 2015; Attias et al. 2018).

4.5 Conclusion

We found little evidence of anthropogenic pressure influencing activity metrics of 15 mammal species in a mosaic of protected areas in the Brazilian Cerrado. Despite the recent report of widespread increases in nocturnality in mammals due to human disturbance (Gaynor et al. 2018), in our study region only tamanduas and, to a lesser extent, collared peccaries reduced diurnal activity in areas under higher human influence. At SVP, lower levels of protection negatively impacted the distribution of mammals (Chapter 3), but had little effect on the period these species were active. Rather, our results suggest that environmental factors have greater influence on the probability of diurnal activity than indicators of anthropogenic pressure in the study region.

The relationship between ambient temperature, environmental conditions and mammal activity deserves a detailed investigation in the Cerrado, particularly considering the synergistic effects that climate change and ongoing habitat loss may have on fine-scale behavioural responses of these species. Such investigation is particularly important for Xenarthra species as the physiological characteristics of this group make them more responsive to variation in ambient temperature (e.g. Camilo-Alves and Mourão 2006; Maccarini et al. 2015). In extreme cases, the combination of a warmer climate and less vegetation cover in the future may compromise the ability of species to adopt temporal shifts in activity to avoid predators or competitors, leading to a cascade of changes in species interactions (Traill et al. 2010; Attias et al. 2018; Shamoon et al. 2018) with unknown consequences for the Cerrado mammal community.

4.6 Supporting information

Supporting table and figures

Table S1: Number of independent records, occurrence at camera trap sites and at camera trap arrays for 27 mammal species at Sertão Veredas-Peruaçu mosaic.

Common name	Latin name	GSV	CAJ	VP	CP	MS	PD	CL	VB	GB	Strict PAs	Multiple-use PAs	Total	Sites	Arrays
grey brocket deer	*Mazama gouazoubira*	215	139	137	144	81	71	140	128	105	716	444	1160	303	9
agouti	*Dasyprocta azarae*	103	1	107	99	21	30	4	0	0	331	34	365	74	7
collared peccary	*Pecari tajacu*	172	22	0	43	20	0	37	0	15	257	52	309	90	6
crab-eating fox	*Cerdocyon thous*	14	1	3	76	43	57	20	26	17	137	120	257	92	9
lowland tapir	*Tapirus terrestris*	123	77	27	0	0	0	0	0	0	227	0	227	69	3
oncilla	*Leopardus tigrinus*	6	13	50	13	9	21	37	15	22	91	95	186	114	9
giant anteater	*Mymercophaga tridactyla*	86	9	34	11	2	0	4	4	7	142	15	157	80	8
striped hog-nosed skunk	*Conepatus semistriatus*	4	8	15	6	24	22	33	13	10	57	78	135	81	9
hoary fox	*Lycalopex vetulus*	4	0	0	0	0	70	7	10	15	4	102	106	43	5
paca	*Cuniculus paca*	2	0	0	5	2	15	1	0	66	9	82	91	11	6
puma	*Puma concolor*	18	14	25	7	7	1	8	1	0	71	10	81	58	8
yellow armadillo	*Euphractus sexcinctus*	19	0	25	4	1	4	5	10	6	49	25	74	42	8
ocelot	*Leopardus pardalis*	2	1	9	14	38	0	4	3	3	64	10	74	41	8
white-lipped peccary	*Tayassu pecari*	44	0	28	0	0	0	0	0	0	72	0	72	18	2
nine- and seven-banded armadillo	*Dasypus* spp.	18	0	1	3	6	15	2	14	6	28	37	65	33	8
maned wolf	*Chrysocyon brachyurus*	6	13	14	0	0	2	14	2	0	33	18	51	34	6
tamandua	*Tamandua tetradactyla*	9	2	0	12	4	4	3	6	1	27	14	41	31	8
tayra	*Eira barbara*	7	3	1	7	13	0	0	5	0	31	5	36	27	6
Pampas deer	*Ozotoceros bezoarticus*	7	4	0	0	0	20	0	0	0	11	20	31	17	3
southern naked-tailed armadillo	*Cabassous unicinctus*	7	1	0	4	0	5	1	0	5	12	11	23	17	6
jaguarundi	*Puma yagouaroundi*	0	0	1	3	7	1	1	2	0	11	4	15	13	6
Pampas cat	*Leopardus colocolo*	0	0	0	0	0	1	0	1	4	0	6	6	5	3
crab-eating racoon	*Procyon cancrivorus*	0	0	1	0	5	0	0	0	0	6	0	6	4	2
lesser grison	*Galicts cuja*	1	0	1	0	1	0	1	0	0	3	1	4	4	4
capybara	*Hydrochoerus hydrochaeris*	0	0	0	0	2	1	0	0	0	2	1	3	2	2
South American coati	*Nasua nasua*	0	0	0	2	0	0	0	0	0	2	0	2	2	1
bush dog	*Speothos venaticus*	0	0	1	0	0	0	0	0	0	1	0	1	1	1

Strict protected areas (PAs): National Parks – Grande Sertão Veredas (GSV), Cavernas do Peruaçu (CP); State Parks – Veredas do Peruaçu (VP), Mata Seca (MS); Private Reserve (RPPN) – Porto Cajueiro (CAJ). Multiple-use PAs: Environmental Protection Areas (APA) – Rio Pandeiros (3 arrays: PD, CL, VB), Cochá Gibão (GB).

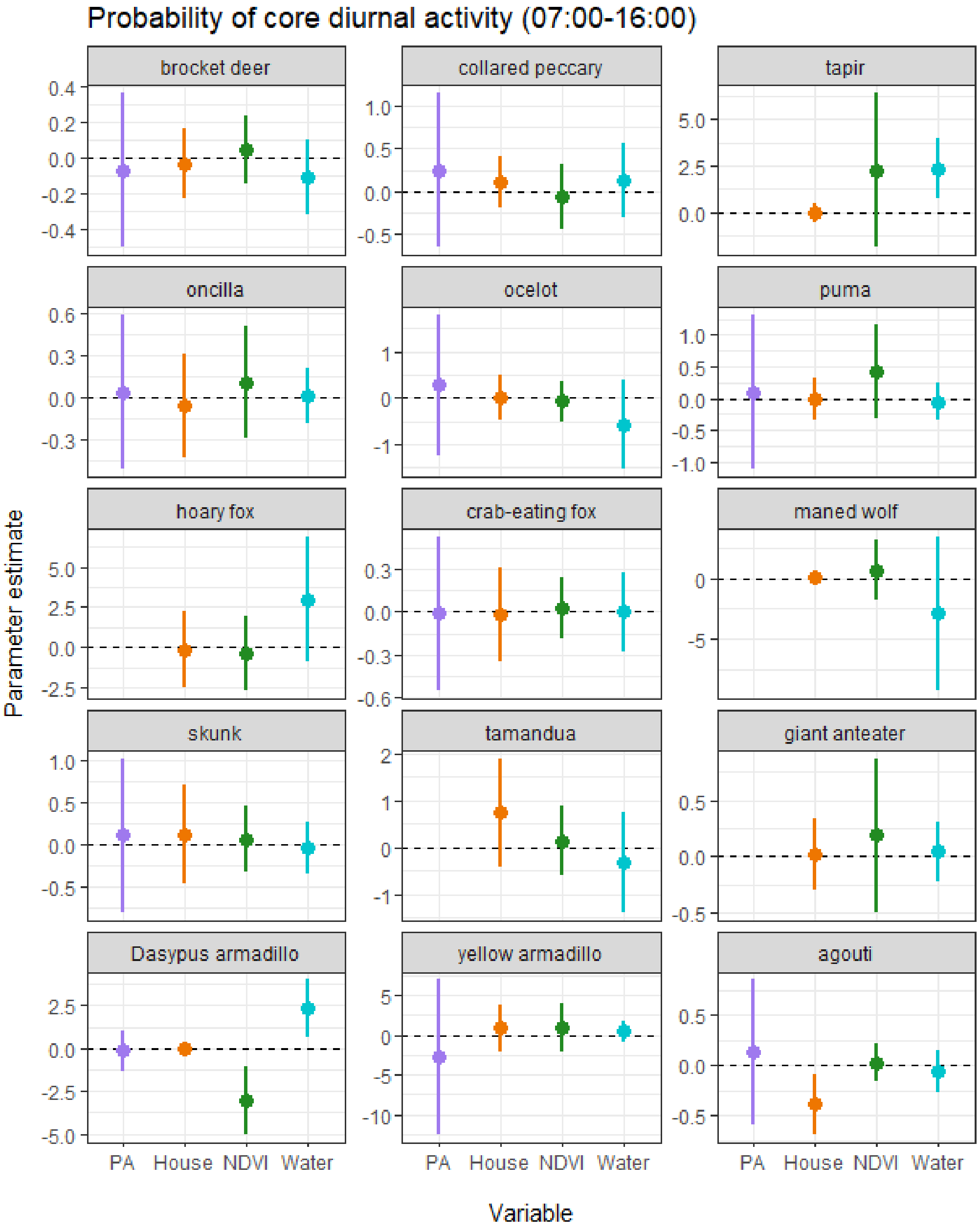


Figure S1: Averaged parameter estimates of models assessing the effect of distinct variables on the probability of activity between 07:00-16:00hs (core diurnal activity) for 15 mammal species. Parameters are on logit scale and vertical lines represent the 95% confidence interval. Positive parameter values indicate higher probability of activity during the core period in strict protected areas (PA), further away from households (House), in sites with greater vegetation cover (NDVI) and further away from water sources (Water). Results for brocket deer, puma, crab-eating fox, hoary fox and *Dasypus* armadillo are from a binomial GLMM, whereas for all other species are from a binomial GLM. See Material and methods for details on the variables used and Table S1 for species' Latin names.

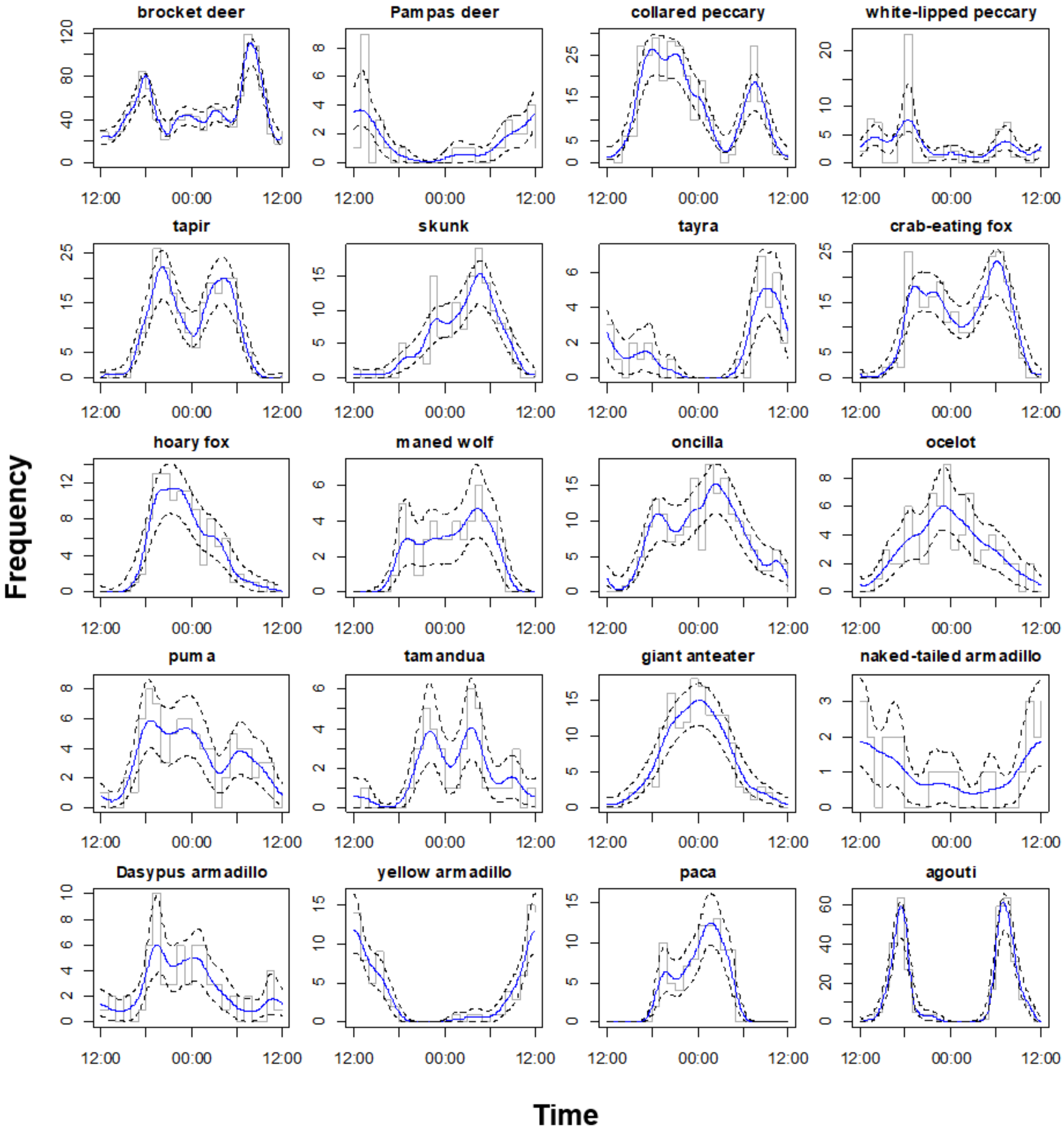


Figure S2: Overall daily activity patterns across all camera trap arrays for mammal species with at least 20 independent records in total. See Table S1 for Latin names.

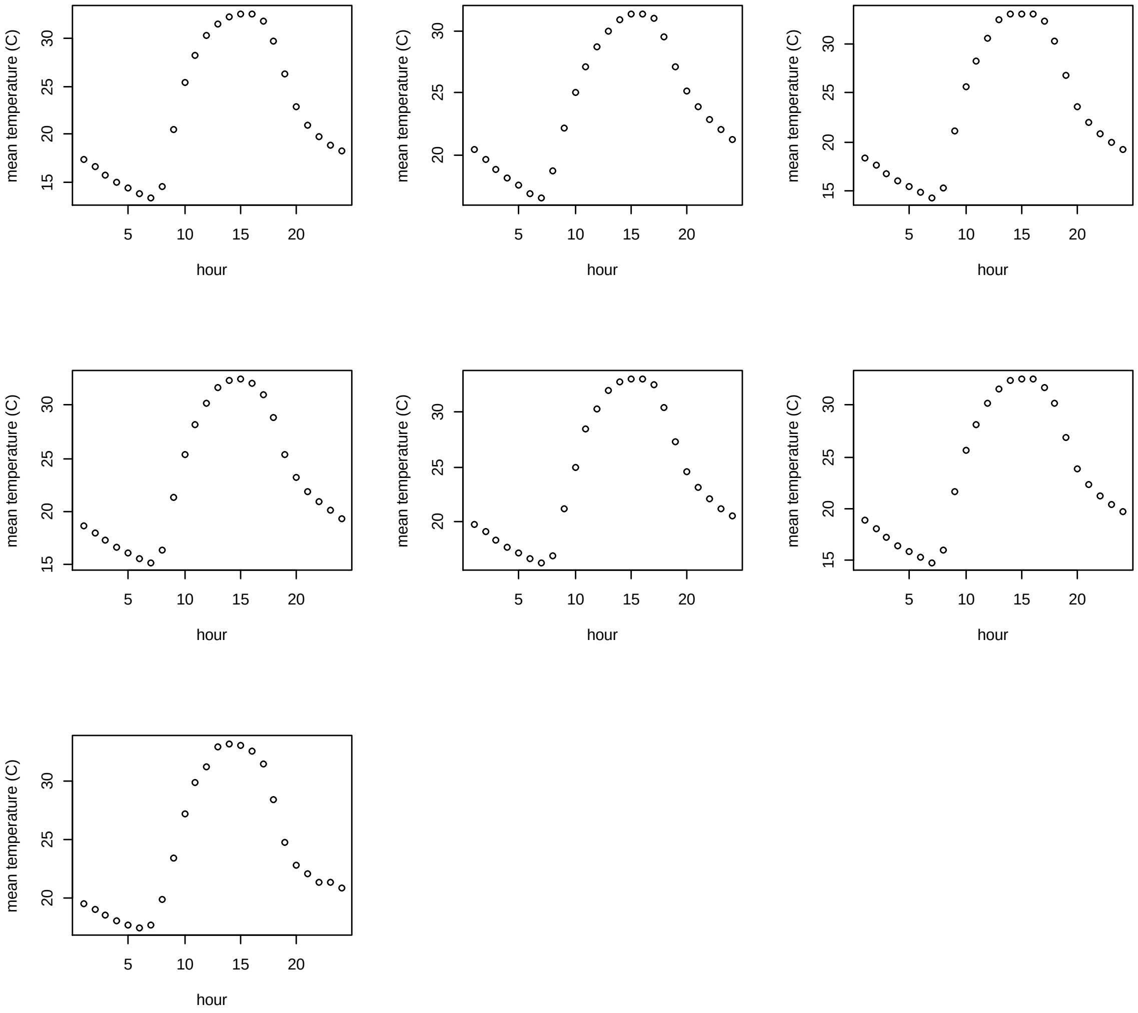


Figure S3: Mean hourly temperature between May and August 2013 obtained from seven sensors deployed at Mata Seca State Park. This is the only camera trap array where daily temperature data is available for the surveyed period. Data from the Tropi-Dry network (http://www.tropi-dry.org/) kindly provided by M. M. Espirito-Santo.

Chapter 5: Applying the Random Encounter Model to investigate animal density and its relation to occupancy in camera trap surveys

Oxbow lake at Grande Sertão Veredas National Park

5.1 Introduction

Accurate estimates of population-level metrics are key to ecological and conservation sciences, as well as to wildlife management. Among those metrics, abundance of individuals is probably the most informative one, which has led ecologists and statisticians to develop a wide range of methods to estimate animal density and abundance (e.g. Seber 1986; Buckland 2001; Royle 2004; Borchers & Efford 2008). However, the type of data needed to estimate abundance is usually more difficult and expensive to obtain than the data necessary to estimate metrics based on occurrence of species (MacKenzie et al. 2002; O'Connell & Bailey 2011). Often the use of occurrence metrics in ecology and conservation is, at least in part, rooted in the assumption of a positive relationship between the area occupied by a species and its abundance (He & Gaston 2003). Indeed a significant and positive occupancy-abundance (OA) relationship has been documented for a multitude of taxa (see review in Gaston et al. 2000) and is regarded as one of the few highly general patterns in ecology (Holt et al. 2002).

The existence of a positive OA relationship has practical implications for camera trap studies, as they can readily produce large amounts of presence-absence data needed to estimate occupancy for a wide range of species (e.g. Ahumada et al. 2011; Rich et al. 2017; Deere et al. 2017). Nonetheless, camera traps can also provide abundance estimates in some circumstances. For example, the influential work by Karanth & Nichols (1998) has clearly shown the potential of combining photographs and the capture-recapture analytical framework to estimate density of rare and elusive animals. This approach, however, is restricted to animals that can be individually recognized (usually by their natural marks, such as spotted or striped felids), thus excluding a large proportion of the species recorded in camera trap surveys. Furthermore, the need for individual identification adds another step to the processing stage of camera trap data, which is already time-consuming when dealing with species identification only. More recently, Rowcliffe et al. (2008) developed a Random Encounter Model (REM) based on ideal gas models to estimate density from camera trap data without the need of individual recognition, potentially enabling scientists to obtain abundance estimates for a wider range of species. REM explicitly accounts for the relationship between factors influencing the number of camera trap detections and the underlying detection process. However, accounting for these factors requires a relatively complex process to obtain the positions of animals relative to the camera and estimation of additional parameters for which tools that allow an integrated implementation of the modelling approach have only recently been developed (e.g. Rowcliffe et al. 2016) or are still under development.

Due to limitations of the approaches to estimate density and the cost-effectiveness of camera trapping in gathering presence-absence data (O'Connell & Bailey 2011), occupancy modelling has become a popular analytical framework in camera trap studies (Burton et al. 2015). Occupancy is broadly defined as the proportion of sites occupied by a species and relies on replicated presence-absence (or more precisely detection/non-detection) surveys to account for detection probability while estimating occupancy probability, the state variable of interest (MacKenzie et al. 2006). The original formulation of occupancy models envisaged a situation in which the occupancy status of discrete and independent sites (e.g. ponds) by a species remained constant for the duration of the sampling period (season) (MacKenzie et al. 2002). Given that camera trap surveys focus on mobile animals ranging over much larger areas than the camera's detection zone, this site closure assumption is unlikely to hold (Burton et al. 2015; Neilson et al. 2018). However, MacKenzie et al. (2006) argued that this assumption could be relaxed as long as movement in and out the sampling site was random (which is not unreasonable given the small size of the camera's detection zone in relation to species use of space) and then occupancy probability should be interpreted as probability of use.

Another concern raised by some authors on the use of occupancy in camera trap surveys is the influence that variation in home range and movement patterns could have on estimates, effectively changing the relationship between abundance and occupancy (Efford & Dawson 2012). Indeed, computer simulations revealed that under the same density, variation in movement would produce distinct occupancy estimates (Efford & Dawson 2012; Neilson et al.

2018). Although illustrative, these simulations often compared scenarios with wide variation in the parameters of interest (home range, speed and density), possibly not reflecting more subtle changes that occur in natural populations. Therefore, it remains important to conduct empirical investigations of the OA relationship in camera trap studies.

These field-based empirical investigations have important implications for the use of camera traps in ecology, conservation and management, but to our knowledge only three studies so far have conducted such assessment using field data, all focusing on a single species and conducted in North America (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017). Here we implement the REM and a multi-species occupancy model to investigate the relationship between occupancy and density estimates in four Neotropical mammals using data from standardized camera trap surveys conducted in the Brazilian Cerrado. We focus our investigation on species from genera that are frequently recorded in camera trap surveys across the Neotropics and that have large variation in body size and diet (both predictors of space use – McNab 1963; Jetz et al. 2004): the giant anteater *Myrmecophaga tridactyla*, a 30-kg vulnerable insectivore; the brocket deer *Mazama gouazoubira*, a 18-kg least concern herbivore; the agouti *Dasyprocta azarae,* a 3-kg data deficient frugivore; and the oncilla *Leopardus tigrinus* a 2.5-kg vulnerable carnivore.

We expect occupancy and density to be positively correlated, as revealed in previous studies (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017). However, we expect a species-specific relationship because occupancy derived from camera trap data is influenced by abundance and use of space (Efford & Dawson 2012; Neilson et al. 2018) and space use requirements vary with size and diet among species (Jetz et al. 2004). Moreover, as it has been suggested that occupancy surveys are more directly related to abundance when sampling occurs at the home range scale (MacKenzie et al. 2006), we expect occupancy to be more strongly correlated with abundance for agouti and brocket deer, species whose home ranges are unlikely to consistently include more than one camera trap site. In addition, we explore the potential consequences of using either occupancy or density estimates to inform conservation and management decisions, by comparing species' responses in these metrics to protected area type and distance to water sources. Finally, because this study is one of the first to implement REM using the full suite of tools developed to obtain the analysis's parameters solely from camera trap images, we provide descriptive results of our estimates and compare them to the published literature.

5.2 Material and methods

5.2.1 Study area

We conducted our study at the Sertão Veredas-Peruaçu mosaic (SVP), a region of approximately 18,000 km^2 enclosing 14 protected areas in a transitional zone between two major Brazilian biomes: Cerrado and Caatinga (see Chapter 1 for a description of SVP). We focused our assessment on two strict PAs and two multiple-use PAs (Fig. 5.1) that support the region's typical Cerrado vegetation, composed mainly of savannas with a range of tree and shrub density (cerrado *sensu stricto*) and palm swamps (*veredas*) along the margins of rivers and creeks. Strict PAs have biodiversity conservation as their primary goal, whereas multiple-use PAs represent the least restrictive category of PA in Brazil allowing some degree of native vegetation conversion to agriculture and human occupation (Brasil 2000; Rylands & Brandon 2005). Human population in the multiple-use PAs surveyed is low and usually scattered in small rural villages connected by unpaved roads; average human density at camera trap arrays in these areas was 2.7 people/km^2. No one was living within the polygon formed by camera traps in the two strict PAs surveyed. Despite the low regulation levels, multiple-use PAs surveyed still hold large areas of native vegetation (WWF-Brasil 2011) and SVP as a whole harbours more than 80% of all mammals >1 kg found in the Brazilian Cerrado (Ferreira & Oliveira 2014).

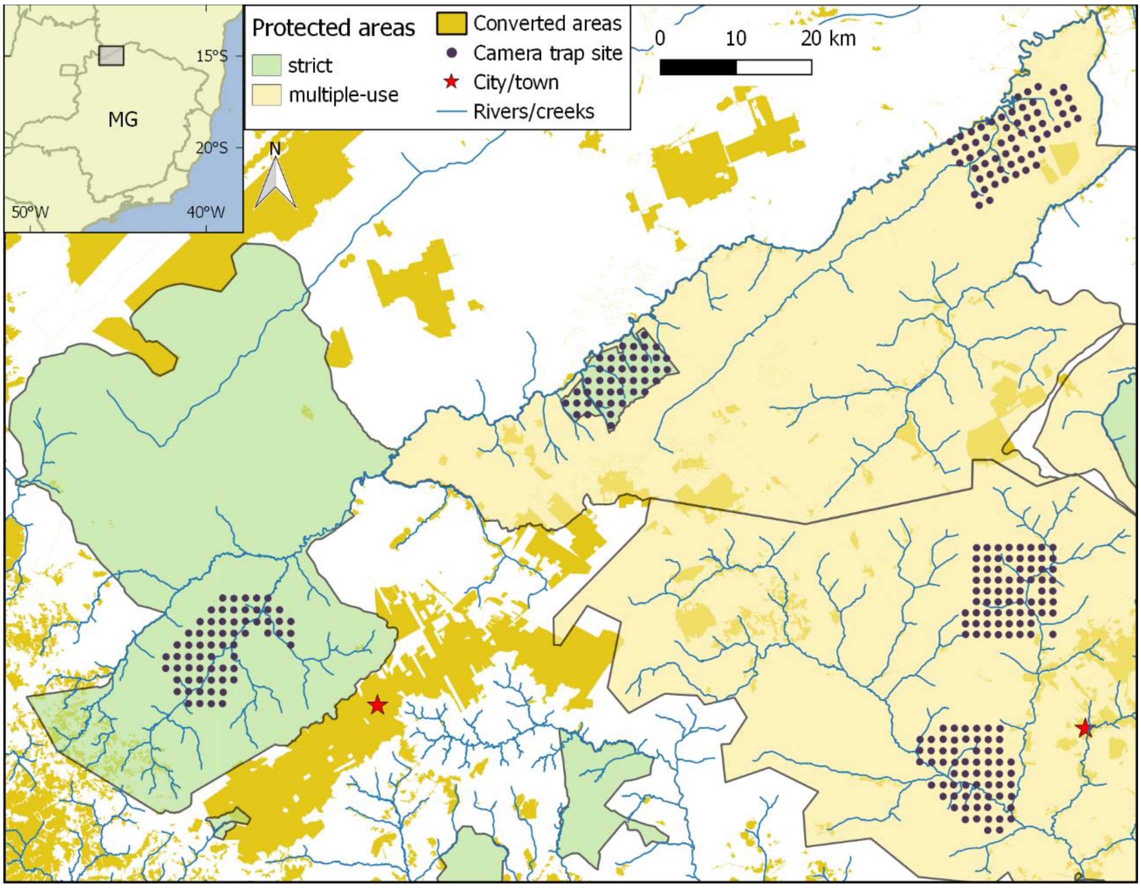


Figure 5.1: Protected areas surveyed and location of camera trap arrays at Sertão Veredas-Peruaçu mosaic. Inset shows study region location within Minas Gerais state (MG), south-eastern Brazil.

5.2.2 Camera trapping

Data collection followed the same survey design and camera trapping protocol described in detail in Chapter 3. We collected data at five independent camera trap arrays, three in multiple-use PAs and two in strict PAs. Each array had between 43 and 70 sampling sites equipped with one camera trap unit (Bushnell TrophyCam or Bushnell Agressor) and systematically distributed at a distance of 1.5 km (Fig. 5.1). We deployed camera traps considering a 50-m buffer around the pre-determined geographic coordinates of sampling sites and always in areas of native vegetation. Due to challenging access conditions, 8% of camera traps were deployed outside the 50-m buffer but only two camera traps were deployed further than 100 m from the original coordinates. Overall, we established 301 sampling sites but after accounting for malfunctioning and theft we retained data from 289 of them, totalling 16,178 survey days and an average survey effort of 55.9 days per camera trap site (range: 7-74). Surveys were conducted between 2015 and 2017, always during the dry season (mid-April to mid-October), and no bait or lure was used to attract animals.

5.2.3 REM density analysis overview

The REM requires estimates of animal speed and camera detection zone size (Rowcliffe et al. 2008), both of which are best estimated from data on the positions of captured animals relative to the camera. Previously, measurements of animal positions have been made manually in the field (Rowcliffe et al. 2011, 2016). To generate position data more efficiently, we instead developed a simple computer vision model that allowed us to predict ground position in front of the camera from image pixel position. The workflow for this computer vision model has three steps. First, a camera calibration model is created, using calibration objects of known size at known distance to define the focal length-sensor size ratio of the camera. This allows us to predict distance from camera of any object of known size. Second, the camera calibration model is used to predict the distances of calibration objects of known size placed at the camera monitoring sites, and these distances are used to parameterise site calibration models that translate from image pixel to ground position. Finally, the site calibration model is used to predict the angular and radial distances of animals from the camera based on their pixel positions within images.

These predicted positions are used as inputs to a data analysis step that provides estimates of camera detection zone dimensions and animal movement speeds. These estimates are then combined with estimates of activity level derived from time of trigger data (Rowcliffe et al. 2014), as well as animal trigger rates, in order to parameterise the model of animal density (REM). This workflow is summarised in Fig. 5.2.

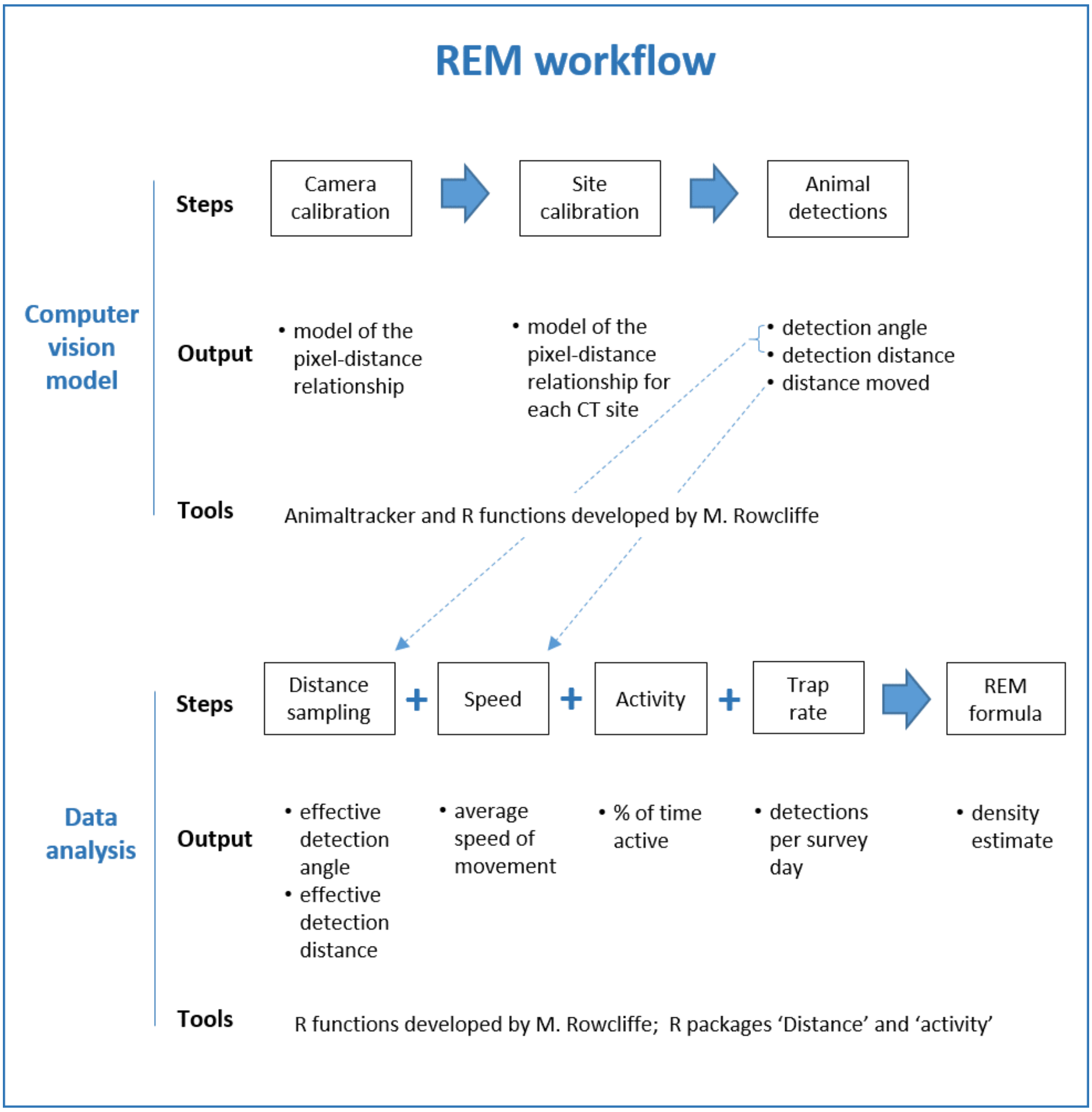


Figure 5.2: Workflow of the Random Encounter Model (REM) with its two main components: computer vision model and data analysis.

5.2.4 Generating vision calibration images

For the camera calibration component of the computer vision model, we took pictures of an array of poles of known length spread across the camera's field of view at known distances from the camera trap. In our setting we had four rows of seven poles at 3, 5, 7 and 9 m from the camera trap (totalling 28 poles; Fig. 5.3A), each with a 90 cm span visibly demarcated with tape. Because the camera traps used differed in age and model, we conducted camera calibrations for six different groups of cameras based on the first digits of the serial number to allow for possible variations in hardware between production runs.

For the site calibration component of the computer vision model, the calibration object was a 1 m pole marked with ten 10 cm black and white bands (Fig. 5.3B-D). At each site, we set the camera trap to take photos of the calibration pole positioned in a wide range of places covering the camera's field of view (Fig. 5.3B-D).

Figure 5.3: Calibration procedure that enables extracting distance and angle from camera trap images of animals. A) Camera calibration with 28 1-m poles equally distributed in four rows located at 3, 5, 7 and 9 m from the camera trap. Length of the segment between red bands (indicated by arrows) is 90 cm. B-D) Examples of site calibration pictures using a 1-m pole marked with 10-cm black and white bands. Approximately 15 pictures at distinct positions covering the camera's field of view were taken at each sampling site.

5.2.5 Image processing

The computer vision process outlined above requires as input digitised x-y pixel positions from both calibration pole and animal images. For camera calibration images, we digitised the demarcation points on each pole indicating the span of known length (arrows in Fig. 5.3A). For site calibration images, we digitised two points on each pole at known heights above ground, based on the black and white bands. The difference between digitised heights was then used to derive the length of pole digitised, and, in cases where the base of the pole was not clearly visible (e.g. Fig. 5.3D), linear extrapolation was used to define the pixel position of the pole base.

Due to the settings used, distance moved by the animal could only be calculated from camera traps recording videos (not the cameras recording pictures). Therefore we only digitised records from these camera traps, which represented approximately 85% of sampling sites. To digitise animal images, we extracted 20 frames from each 10 s camera trap video containing the focal species (corresponding to 2 frames/second). Animals were digitised at a position judged to be on the ground directly below the animal's centre of gravity. To obtain data for estimating detection distance and angle, only the first frame of each animal sequence was used (Fig. 5.4A), where we define a sequence as footage of a single individual animal passing the camera. For total distance moved (feeding into speed estimation), one point was digitised in each frame from sequences consisting of at least two frames, generating a virtual movement path (Fig. 5.4B-D). To ensure measurements of distance moved represented as close as possible situations of natural animal behaviour, we did not digitise frames in which we deemed the animal was interacting with the camera trap. Such instances would be for example when an animal evidently moves towards or away from the equipment after perceiving it, as well as when it stands still sniffing or staring at the camera. In total we digitised 703 trigger events and 596 movement events (Table 5.1). All digitisation was carried out manually using the software 'animaltracker' (https://robinfreeman.github.io/animaltracker/).

Figure 5.4: Example of the digitisation process of a grey brocket deer record using animaltracker (https://robinfreeman.github.io/animaltracker/). A) First frame of a 10-second camera trap video with arrow indicating the pixel location from which detection distance and angle from the camera trap will be extracted. B-D) Example of subsequent frames of the same video used to track animal movement. Total length of the blue line is the distance moved. Note that some frames between B-C and C-D are not shown.

Table 5.1: Sample sizes of the data used to estimate parameters for the Random Encounter Model.

Sample sizes	brocket deer	giant anteater	agouti	oncilla	Total
Trigger data - N	444	85	91	83	703
Trigger data - sites	137	38	14	54	NA
Movement data - N	395	55	89	57	596
Movement data - sites	138	39	14	54	NA
Activity data - N	677	106	138	99	1020
Activity data - sites	178	50	21	66	NA

N = number of events; sites = number of sites providing data.

5.2.6 Computer vision model fitting and evaluation

Following digitisation, camera calibration models were fitted using data on the pixel sizes of known lengths of poles at known distances from camera (Fig. 5.3A). Distances from camera to site calibration poles were then predicted using data on the pixel sizes of known lengths of pole (Fig. 5.3B-D), and pixel-to-ground mapping was calibrated using the positions of pole bases at known distance from camera. Animal pixel positions were then translated to ground positions (angular and radial distance from camera) using site calibration models. For movement sequences, total distance travelled could then be calculated, and divided by elapsed time based on number of frames and frame rate, to give a speed estimate for each sequence.

In order to evaluate the reliability of calibration models, we inspected replica pole images (Fig. S1, right column) and goodness-of-fit plots (Fig. S1, left column) to ensure respectively that digitisation had been carried out sufficiently accurately, and that model fit was sufficient to give reliable predictions. For camera calibration models (Fig. S1, top row), goodness of fit was indicated by plots of actual-to-pixel size ratio against distance from camera. In this case, a strong linear relationship through the origin is expected, and was readily achieved in all cases. For site calibration models (Fig. S1, bottom two rows), goodness of fit was indicated by a plot of distance from camera against y-pixel position in the image, with the expectation of a strong reciprocal relationship. On this basis, we deemed site calibration model fit to be too poor for use in three sites, either because only a few useable calibration pole images were obtained, or because the ground in front of the camera was too rough. We therefore did not obtain animal position data from these sites. All model fitting and evaluation was performed in R (R Development Core Team 2015) using functions available at https://github.com/MarcusRowcliffe/CTtracking.

5.2.7 Density analysis

The REM formula (Rowcliffe et al. 2008) provides an estimate of animal density as a function of trap rate (number of independent contacts divided by survey effort: *y/t*), day range (*v*; product of average speed of movement and proportion of time the animal is active), and area of the camera trap detection zone (defined by radius *r* and angle θ):

$$D = \frac{y}{t} \frac{\pi}{vr(2 + \theta)}$$

Number of independent contacts is simply the number of times each species triggered the camera trap and then left the camera's field of view. Sequential triggers in which the animal does not move out of the field of view are not considered independent and only one of them is counted towards the number of independent contacts. Survey effort is the total length of time (in days) camera traps were functioning at each sampling site. Proportion of time active for each species is estimated using the package 'activity' to fit flexible circular distributions to time-of-detection data (Rowcliffe et al. 2014). As neither the number of independent records nor time of detection need image digitisation, we used data from all camera trap sites to derive these parameters, including sites where camera traps were taking pictures (instead of videos) and where pole calibration was unreliable or had not been conducted (Table 5.1).

We followed the process developed by Rowcliffe et al. (2016) to estimate speed from camera trap images. In this process average speed of movement for each species was estimated by fitting data on distance moved divided by the time taken to move across that distance to models with three distinct Probability Density Functions: log-normal, Weibull, and gamma. The estimated speed from the best-supported model according to AIC value was retained to estimate density. To obtain radius and angle of the camera's detection zone, we implemented an adapted distance sampling approach (Rowcliffe et al. 2011). This approach assumes that detection probability decreases as linear and angular distance from the camera trap increases (Rowcliffe et al. 2011) and uses detection models from distance sampling to estimate the effective detection zone (Buckland et al. 2001). We thus fitted species-specific data on angle and distance extracted from camera trap images (see 'Computer vision model fitting and evaluation') to distinct detection models (half-normal and hazard rate). Additionally, these detection models were fitted using up to five cosine terms to add flexibility to the functions (Buckland 2001). Estimates of effective detection distance and angle from the best-supported model according to AIC values were retained. Before fitting the models we truncated angle to 1 radian (57.3 degrees) and distance to 15 m, meaning that records beyond these thresholds were not used to estimate the effective detection zone. Truncation is regularly adopted in distance sampling analysis because extreme values add very little information to the estimation process but can be difficult to model (Buckland et al. 2001).

After some data transformation to harmonise units (i.e. distance into km and speed into km/day), all these parameters and their SEs (for estimated parameters) were brought together to estimate density. We obtained density estimates for each camera trap array individually as well as an overall estimate by aggregating data over the five camera trap arrays. REM was implemented in R (R Development Core Team 2015) using functions available at https://github.com/MarcusRowcliffe/camtools and the packages 'activity' (Rowcliffe et al. 2014) and 'Distance' (Miller 2017).

5.2.8 Occupancy-abundance relationship

We used linear models to investigate the OA relationship based on camera trap array-level estimates of density and occupancy for our target species. Density was estimated through REM (described above) and occupancy was estimated via the Bayesian implementation of a multispecies occupancy model (Zipkin et al. 2010; Kery & Royle 2016). We adopted exactly the same multi-species occupancy model formulation as in Chapter 3, with the only difference being this time we restricted camera trap data to the five arrays where REM calibration had been conducted. Posterior means and 95% credible intervals (CRI) of array-level occupancy estimates were obtained as a derived parameter in the model for the four target species.

We first implemented a linear model where occupancy was used as an explanatory variable of density. Then to allow for a species-specific relationship between density and occupancy, we implemented a second linear model with an interaction between occupancy and species as explanatory variables. Support for models was assessed using AIC and R^2 values. Because diagnostic plots of this second model (which had a better fit) suggested non-normality in the residuals, we used the same model formulation and implemented generalised least square (GLS) models to account for variance structure in the explanatory variables (Zuur et al 2009) via the package 'nlme' (Pinheiro et al. 2018) in R (R Development Core Team 2015). We implemented three distinct GLS models to allow for variation of residual spread along occupancy values (varExp variance structure) and different residual spread per species (varIdent variance structure), as well as a combination of both (varComb variance structure) (Zuur et al. 2009). However, the results obtained for GLS models were very similar to the linear model (Table S1) and conclusions about the OA relationship based on any of these models would be the same. Therefore, we decided to only present results of the simpler linear model.

Finally, to explore the effect of using either occupancy or abundance to inform conservation and management decisions, we investigated the responses of target species to protected area type (PA type; either strict or multiple-use) and distance to water sources using both metrics (see Chapter 3 for details on how we measured distance between camera trap sites and source of water). We selected these variables because they represent relevant questions in a conservation management context and because among the continuous variables distance to water was the one with more contrast in the values, resulting in a stronger test of the different approaches' ability to detect trends.

Comparing the effect of PA type on occupancy and abundance is straightforward because it is a categorical variable, but as a continuous variable, distance to water was treated differently in the two modelling approaches. In occupancy modelling, we included distance to water as a covariate and obtained a posterior mean and 95% CRI for its regression coefficient. For REM we assigned camera trap sites as being close (<0.5 km) or distant (>2 km) to water sources, discarding sites that fell between these two categories. This was necessary because at this point REM does not allow for inclusion of covariates in the model. We inferred PA type had a strong effect on occupancy if the 95% CRI of the difference between posterior occupancy means for strict and multiple-use PAs did not include 0 ($\psi_{\text{strict}} - \psi_{\text{multiple-use}} \neq 0$; where ψ is occupancy probability). Similarly, distance to water sources was deemed as having a strong effect on occupancy if the 95% CRI of the regression coefficient did not overlap 0. For density, we used a Wald's test to check whether the difference between two estimates was statistically significant.

5.3 Results

Confirming our expectation of a species-specific OA relationship, variation in density was better explained by the linear model with an interaction term between occupancy and species (density ~ occupancy X species; R^2= 0.81, AIC= 97.88) than by the occupancy-only model (density ~ occupancy; R^2= 0.3, AIC= 120.13). Results from the best-supported model revealed a positive relationship between density and occupancy for all species, although non-significant for brocket deer (Fig. 5.5; full model results in Table S1). Variation in the regression coefficient was large among species, with the model predicting a very modest increase in density for oncilla and a sharp increase for agouti as occupancy increases (Fig. 5.5).

The direction of species' response to PA type and distance to water was largely consistent regardless of the metric used. In all cases in which the effect of the variable over occupancy was strong (i.e. 95% CRI of the difference in occupancy probability or the regression coefficient did not include 0), density estimates followed the same pattern: PA type effect on agouti, giant anteater and oncilla, and distance to water on brocket deer and agouti (Fig. 5.6). However, due to relatively large standard errors, the difference in density estimates was statistically significant in only two of these cases. There was a suggestion of distance to water having opposite effects over giant anteater's occupancy and density, but there is large uncertainty around the regression coefficient for occupancy and an almost complete overlap in the confidence intervals of density estimates (Fig. 5.6). The only case in which the metrics did not agree was regarding the effect of PA type over brocket deer, with no effect observed on occupancy (similar estimates in both PA types) and a slightly higher density in strict PAs, although not significantly different from multiple-use PAs (Fig. 5.6).

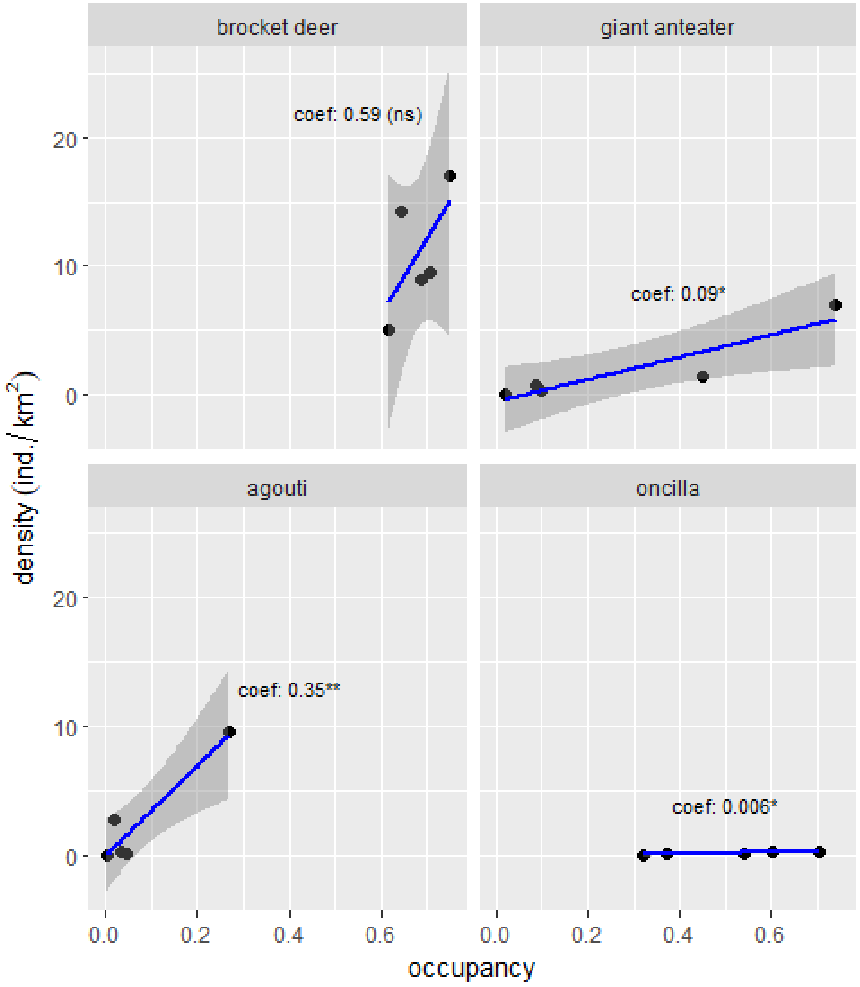


Figure 5.5: Relationship between occupancy and density estimates derived from five camera trap arrays deployed in the Brazilian Cerrado. Blue line represents the linear relationship predicted by the best-supported model (density ~ occupancy X species). Regression coefficients (coef) were estimated transforming occupancy into a percentage (0-100%). Significance level: ns = non-significant; * $p < 0.05$; ** $p < 0.01$.

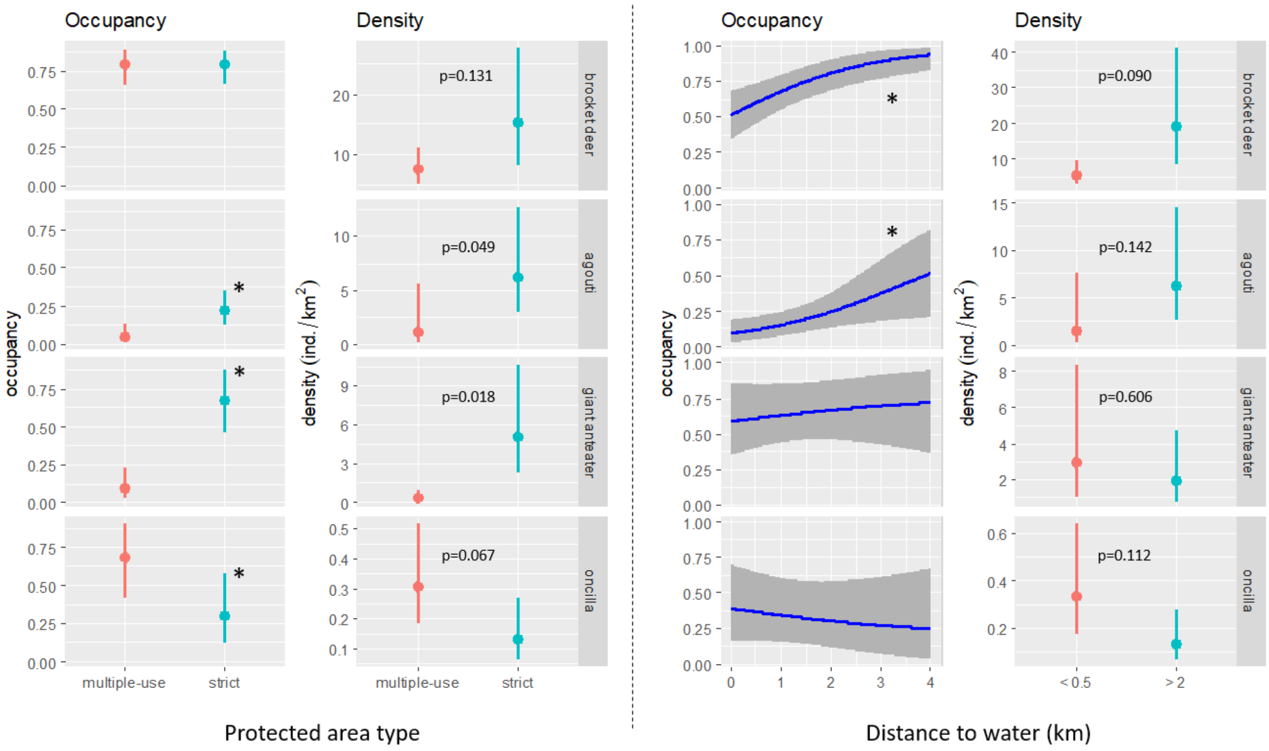


Figure 5.6: Effect of protected area type and distance to water sources on occupancy and density estimates of four mammal species in the Brazilian Cerrado. 95% CRI/CI are shown as coloured lines in point plots and as dark grey area in line plots. Asterisk (*) indicates that the 95% CRI of the difference in occupancy estimates or of the regression coefficient does not include 0.

We observed a large variation in overall estimated density among species, with a fortyfold increase in the number of individuals per km^2 from oncilla to brocket deer, and more intermediate estimates for giant anteater and agouti (Table 5.2). Within species variation in density at the camera trap array level was also substantial: the smallest variation was threefold for brocket deer, whereas for agouti there was a 50-fold increase from lowest to highest density estimate (Table 5.2).

Effective detection distance was very similar among the target species and relatively small (never >3 m), whereas more variation was observed in effective detection angle and particularly estimated speed, which was almost six times faster for oncilla when compared to brocket deer and giant anteater (Table 5.2; Figs S2, S3 and S4). Proportion of time active for agouti was approximately half of that obtained for other species and number of independent contacts with camera traps was at least 4.9 times higher for brocket deer compared to other species (Table 5.2; Fig. S5).

Table 5.2: Functions and parameters used to estimate density of four mammal species using the Random Encounter Model.

	brocket deer	giant anteater	agouti	oncilla
Angle detection function	HR; 3 cos	HR	HR; 3 cos	HR; 2 cos
Effective detection angle (degrees)	22.57 (1.26)	32.09 (1.66)	21.49 (4.58)	26.36 (5.61)
Distance detection function	HR	HR	HR	HN
Effective detection distance (m)	2.82 (0.08)	2.25 (0.15)	2.71 (0.16)	2.63 (0.14)
Speed function	Weibull	Weibull	Weibull	log-normal
Estimated speed (m/s)	0.045 (0.006)	0.041 (0.014)	0.064 (0.013)	0.244 (0.038)
Estimated activity (%)	40.9 (3.1)	41.3 (3.5)	21.7 (2.3)	48.2 (6.5)
Number of contacts	678	107	138	99
Range of array-level densities (ind/km^2)	5.09 - 17.00	0.31 – 6.97*	0.17 – 9.59*	0.06 – 0.38
Overall density (ind/km^2)	10.40 (2.30)	2.01 (0.80)	2.99 (1.13)	0.24 (0.06)

HR: hazard rate; HN: half-normal. Cos: cosine adjustments. * excludes one camera trap array where the species was not recorded. Standard errors of the estimates are inside parenthesis.

5.4 Discussion

5.4.1 Relationship between occupancy and density

We found a positive correlation between occupancy and density estimates derived from camera trap data, agreeing with recent assessments investigating the relationship between these two metrics in North American species (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017). Despite this, we found regression coefficients that varied greatly among species, indicating that OA relationships in camera trap studies are species-specific, probably caused by large inter-specific differences in movement patterns. Indeed, variation in home range and movement can have a large effect on occupancy, meaning that under similar densities animals that move more will have higher occupancy estimates (Efford & Dawson 2012; Neilson et al. 2018). This was clearly observed in our camera trap arrays where agouti and oncilla – the latter with a much larger day range – were found at similar densities (<0.4 ind/km^2) but the felid occupancy was 10-fold higher (0.55 vs 0.05).

It has been proposed that occupancy estimates will match more closely variation in abundance when surveys are conducted roughly at the home range scale of the target species (MacKenzie et al. 2006), and camera trap surveys with one sampling site per potential home range have revealed this is the case for territorial animals occurring at low densities (Clare et al. 2015; Linden et al. 2017). For our survey design, the limited data available on our focal species' home range (Jorge & Peres 2005; Kasper et al. 2016; Bertassoni et al. 2017; Grotta-Neto & Duarte 2019 and references therein) suggest that the area used by individuals of brocket deer and agouti during the survey period is unlikely to consistently encompass more than a single camera trap, whereas for giant anteater and oncilla the area used is likely to cover multiple camera traps.

Therefore, it is interesting to note that brocket deer was the only species for which the relationship between occupancy and density was not significant, despite the species small home range in relation to our camera trap spacing. A possible explanation is the fact that while surveying at the home range scale limits the possibility of the same individual being detected by multiple camera traps, it does not avoid the possibility that more than one individual will use a single camera trap site (Steenweg et al. 2018). This could cause density to increase without an increment in occupancy and is in line with our finding of a relatively large increase in density estimates for brocket deer with a modest increment in occupancy estimates. Additionally, it has been argued that when species occupancy is high (as is the case for brocket deer) an increase in density is more likely than a further increase in occupancy because the availability of suitable areas for 'colonization' is low (Gaston et al. 2000). Alternatively, our low sample size (five camera trap arrays) and the uncertainty around estimates of density may be partially responsible for the lack of significance for brocket deer.

On the other hand, agouti, giant anteater and oncilla displayed a significant relationship between occupancy and density regardless of the presumed large difference in their home range. This is in accordance with recent simulations showing that in point sampling of mobile animals (as in camera trapping) the spatial scale of the survey (i.e. density of sampling sites) does not affect OA relationships (Steenweg et al. 2018).

5.4.2 Effect of covariates on occupancy and density

We demonstrated a consistent effect of covariates on occupancy and density estimates of species with a wide range of ecological requirements and use of space. Even for species with larger home ranges (giant anteater and oncilla) there was agreement between the metrics. This is an encouraging result for the use of camera trap surveys combined with occupancy modelling to investigate response of mammal species to environmental and anthropogenic factors. Indeed, there is some indication that this consistent response may be relatively common in camera trap studies, as it has been observed for different species and under distinct survey designs in recent investigations. For instance, a comparison of white-tailed deer (*Odocoileus virginianus*) response to pairs of areas with contrasting levels of hunting found that density and occupancy derived from camera trap data agreed in almost 90% of the pair-wise comparisons (Parsons et al. 2017). Disagreement between the metrics happened in paired sites where besides contrasting hunting pressure there was also a stark difference in habitat or surrounding matrix (e.g. urban parks surrounded by housing compared to more natural areas). Similarly, data from large-scale camera trap surveys used to estimate occupancy and density of fisher (*Pekania* *pennant*) and bobcat (*Lynx rufus*) revealed that landscape covariates had the same effects on both metrics for the two species (Clare et al. 2015; Linden et al. 2017).

Our study provides evidence of the feasibility of using occupancy modelling to inform conservation management. Conclusions about the effect of PA type or distance to water sources on the species investigated were largely the same regardless of the metric used. In five of the eight cases assessed occupancy indicated the variable had an important effect on the species and in all of them density estimates were in agreement. In the other three occasions neither occupancy nor density indicated a strong effect of the variable. However, we acknowledge that occupancy is a coarser metric than density, and there will be situations in which high densities of the focal species will lead to a saturation in estimates of occupancy limiting the ability to detect additional change in abundance. This has been observed for white-tailed deer occurring at high densities in North America (Parsons et al. 2017) and might be the case for brocket deer in our comparison between multiple-use and strict PAs. This limitation, however, is inherent to occupancy modelling *per se* (MacKenzie et al. 2006), and it is not exclusive to camera trap studies.

The influence of animal movement on occupancy estimates has caused some concerns about occupancy modelling of camera trap data (Burton et al. 2015). This is because large increases in animal movement could increase occupancy estimates even if the number of animals remains constant (Efford & Dawson 2012; Neilson et al. 2018), impacting how well occupancy reflects abundance. However, more limited variation in movement is likely to have a much weaker influence on occupancy estimates. We believe this is one of the factors behind the consistent response of occupancy and density to covariates in our study, as we did not expect extreme intra-specific variation in use of space across SVP, particularly during our short camera trap surveys (camera trap arrays surveyed for <75 days). Other factors that probably contributed to the consistency between both metrics were standardisation of survey design and relatively low density of most focal species. In any case, the effect of interactions between density, animal movement and survey design on occupancy estimates is only starting to be addressed (e.g.

Neilson et al. 2018; Steenweg et al. 2018) and further research is needed to fully understand these connections and their implications for camera trapping.

5.4.3 Estimated density

Using solely data from camera trap images and without the need of individual identification we estimated density of four species representing four distinct mammalian orders. This highlights the potential of REM to provide abundance data that is lacking for most of the distribution of Neotropical mammals >1 kg. For instance, a search in two databases returned a single peer-reviewed study estimating density in the Cerrado for any of our target species and even when we did not restrict for biome we found published density estimates for only a few localities (Table S2). The only study we found in the Cerrado used line transect and distance sampling to estimate densities varying from 0.034 to 0.085 giant anteater/km^2 in Emas National Park (Silveira et al. 1999). These estimates are much lower than the densities we obtained for the species at any of our camera trap arrays. This study, however, was conducted less than a year after a catastrophic wildfire killed many giant anteaters in the area (Silveira et al 1999), which may explain the low densities. Diniz & Brito (2015) citing a grey literature work provided a density estimate of 0.4 giant anteater/km^2 in this same national park, probably at least a few years after the catastrophic fire event. Giant anteater's density in other Brazilian biomes have been found to be between 0.1 and 0.8 ind/km^2 (Peres et al. 2003; Desbiez et al. 2010; Desbiez & Medri 2010; Kreutz et al. 2012) and are more similar to the estimates we obtained in multiple-use PAs (0.31 and 0.77 ind/km^2). However, only one study surveying commercial timber plantations in northern Brazil found giant anteater density >1 ind/km^2 (Kreutz et al. 2012), which is more comparable to our estimates in strict PAs.

The extensive within species variation in density estimates observed in our study area was also reported elsewhere and seems to be a natural pattern of species responding to local conditions and resources available (Jorge & Peres 2005; Desbiez et al. 2010; Kreutz et al. 2012).

The density estimates we obtained via REM for brocket deer, agouti and oncilla are within the range of known densities for natural populations of these species (including congeners in the case of agouti) in other parts of Brazil and South America (Chiarello 2000; Hurtado-Gonzales & Bodmer 2004; Jorge & Peres 2005; Noss et al. 2006; Desbiez et al. 2010; Oliveira-Santos et al. 2012; Ferreguetti et al. 2015), although for brocket deer and oncilla our estimates tend to be on the upper end of the published estimates and the opposite is observed for agouti. Finally, our relatively high density estimates for oncilla and giant anteater suggest the existence of large populations of these globally threatened species in SVP, confirming the study region’s status as a priority area for biodiversity conservation in Brazil (WWF-Brasil & MMA 2015).

5.4.4 REM parameters

We focus our comparison of camera detection zones and average speeds on a dataset from Barro Colorado Island (BCI) in Panama (Rowcliffe et al. 2011, 2016), as this the only other instance in which these parameters have been estimated from camera trap data for Neotropical mammals. Agreeing with results from BCI (Rowcliffe et al. 2011), the hazard rate detection function had better support to estimate effective detection angles and distances for most species in our study. Our estimated detection angle for brocket deer and agouti were very similar to the values obtained for their congeners in BCI, although in our data (admittedly with a smaller sample size) there is no indication of the positive relationship between body size and angle observed by Rowcliffe et al. (2011). In the Cerrado, agouti had similar detection angle as the much larger brocket deer, and it was even wider for oncilla, our smallest target species. A similar pattern was observed when comparing detection distances: estimated values were relatively similar for congeners, but in the Cerrado variation in effective detection distance among species was minimal and again we did not notice the positive relationship between body size and distance observed in BCI (Rowcliffe et al. 2011).

Average speeds for agouti and brocket deer were respectively 2 and 3.4 times higher in BCI (Rowcliffe et al. 2016) than our estimates for congeners in the Cerrado. On the other hand, our estimated day range (average speed in km/day multiplied by proportion of time active) of 1.46 km for giant anteater matches closely the average daily distance moved of 1.32 km by a giant anteater individual monitored via GPS device in Brazil (Bertassoni et al. 2017), though the interval of 69 minutes between fixes may have underestimated the total distance moved in the GPS-tracking study. Again inconsistent with our study, Rowcliffe et al. (2016) found that the log-normal distribution had better fit to estimate speed for most species, including brocket deer and agouti. However, for our data difference between average speeds estimated using either Weibull or log-normal distributions was not substantial (although the latter consistently returned higher estimated speed; Table S3). Thus, the large difference observed in estimated speeds for congeners between the Cerrado and BCI cannot be attributed to the type of distribution. Nevertheless, we acknowledge that the distribution used to estimate speed have an impact on densities obtained via REM. For instance, in our study density estimates were 15-30% lower and slightly more precise when using the log-normal rather than Weibull distribution to estimate speed (Table S3). Further research is needed to clarify under which conditions each one of these distributions works better, as well as to explore the suitability of alternative distributions (Rowcliffe et al. 2016). One way of achieving this is by comparing estimated speed from camera trap data using distinct distributions with high-resolution and high-precision movement data from GPS devices fitted on animals.

Although REM requires estimation of additional parameters that are not needed in the capture-recapture framework, tools and functions developed since its original inception (e.g. Rowcliffe et al. 2011, 2014, 2016) has made it possible to obtain such data fully from camera trap images and in a more standardized way. For instance, we showed that when comparable data were available, the distance sampling approach estimated similar effective detection values for studies conducted in different ecosystems (Brazilian Cerrado vs tropical forests of BCI) and using distinct camera trap models (Bushnell vs Reconyx). Further empirical comparisons are needed to allow for definite conclusions, but so far distance sampling theory seems to provide a reliable way of correcting for variation in detection probability among species in surveys adopting random or systematic camera trap placement. Additionally, the field process to collect data necessary for REM has become less labour-intensive than in its first iteration (Rowcliffe et al. 2008), and the digitisation process may become less demanding in the near future with the development of semi-automated or automated tools to track moving animals in videos.

5.5 Limitations

Our observations of the relationship between occupancy and density are based on few data points (five camera trap arrays) not allowing definite conclusions. However, they should be viewed as a step towards the better understanding of OA relationship in camera trap studies and can be used to help guide further empirical research on this topic. We highlight, though, that our surveys cover 301 camera trap sites over an aggregated area of more than 500 km^2 and it would be extremely costly (financially and logistically) to have a much larger number of data points in our analysis. Perhaps this can be achieved in large camera trapping schemes supported by a network of citizen scientists (e.g. Parsons et al. 2017), but it is unrealistic to imagine such schemes implemented in the near future in developing regions with low human density and poor road infrastructure, as our study area.

As with any other statistical analysis, particularly in ecological field studies, small effect sizes are more difficult to unveil (Guillera-Arroita & Lahoz-Monfort 2012; Barata et al. 2017) and this may be compounded in occupancy modelling of mobile animals by variation in movement. Thus, it could be the case that we only observed a consistent response of both occupancy and density to covariates because the effects investigated were relatively large. It is plausible that more modest effects of other covariates on abundance would not be detected by our occupancy estimates, however, in such conditions a very precise estimate of abundance would be required to reveal an existing effect.

Our density estimates are within the known range for the target species, but we have no previous information on the abundance of these species in the study area to fully validate our REM results. When compared with other methods to estimate density in wild populations, REM has provided both similar (Zero et al. 2013; Anile et al. 2014) and diverging estimates (Rovero & Marshall 2009; Caravaggi et al. 2016). However, extremely reliable estimates of density are very frequently unavailable in field settings, leaving open the debate as to which method was most accurate. In a study where true population size was known with high confidence, REM provided comparable density estimates after restricting camera trap data to periods when movement in relation to camera was more likely to be random (Cusack et al. 2015).

REM is a relatively new method with still few published examples obtained from more natural conditions (e.g. Zero et al. 2013; Anile et al. 2014; Cusack et al. 2015), although a small-scale semi-captive field study demonstrated proof of concept (Rowcliffe et al. 2008). Clearly the REM approach would benefit from further studies in areas where population size of the target species is relatively well-known. This would not only allow cross-validation (especially using the latest camera-based parameter estimates), but also to investigate the influence of distinct functions to estimate the camera's detection zone and species' average speed on the accuracy of density estimates. Alternatively, adopting REM together with a suite of other density estimation methods would at least allow to assess consistency between methods and understand how comparable they are.

REM relies on unbiased parameters of camera detection zone, animal movement and activity to correctly estimate density (Rowcliffe et al. 2008). Researchers implementing REM should think carefully about potential sources of bias to avoid or circumvent them. For instance, in our study we noticed that species interacted with camera traps on some occasions, which could lead to biased estimates of average speed, and consequently of day range. We tried to prevent this bias by excluding occasions where animals were interacting with the camera, however, failing to identify all occasions may lead to some level of bias.

5.6 Conclusions

Applying both occupancy modelling and REM to the same camera trap dataset we revealed that the occupancy-density relationship tends to be positive, but with large variation among species. Moreover, we showed that occupancy estimates can adequately track the effect of covariates on animal density, with practical implications for the use of camera traps in research and monitoring. For example, our results suggest that occupancy modelling of presence-absence data derived from camera traps can reveal the effect of landscape features on species density and may even indicate areas potentially supporting high abundance of animals. Given some of the limitation of camera trap-derived occupancy (Burton et al. 2015) and the influence of animal movement on estimates (Efford & Dawson 2012) we do not expect consistency between occupancy and density to exist under all circumstances, but our results combined with recent assessments (Clare et al. 2015; Linden et al. 2017) indicate that under certain conditions occupancy estimates will reflect estimates of abundance.

Density estimation via camera traps continues to be mostly restricted to marked species with individuals that can be uniquely identified (Burton et al. 2015). REM has the potential to drastically change this pattern providing density estimates for a large number of species without the need of individual recognition. Adopting REM and using a single camera trapping design that has been implemented widely (e.g. Ahumada et al. 2011; Beaudrot et al. 2016), we obtained rare density data for Cerrado mammals, including globally threatened species. In fact, REM may be extremely useful in regions where more traditional techniques to estimate abundance of unmarked animals are unsuitable (Gray 2018) and can even be a cost-effective method for long-term monitoring of population abundance (Zero et al. 2013). Furthermore, as the sampling design required for REM is also appropriate for occupancy modelling, the two analytical methods can be jointly implemented in long-term monitoring initiatives, with the more labour-intensive REM methods being applied to a subset of the data to validate or correct trends and patterns revealed by occupancy estimates.

5.7 Supporting information

Table S1: Full results of models assessing the relationship between density and occupancy estimates at the camera trap array level for four mammal species.

Model	Estimate	SE	p-value
1) LM (density ~ occupancy x species)			
(Intercept)	0.081	1.054	0.939
occupancy x agouti	0.349	0.091	0.001
oncilla	-0.162	3.472	0.963
brocket deer	-29.265	13.090	0.040
giant anteater	-0.545	1.607	0.739
occupancy x oncilla	-0.342	0.110	0.007
occupancy x brocket deer	0.241	0.212	0.272
occupancy x giant anteater	-0.262	0.096	0.015
2) GLS (density ~ occupancy x species); var = occupancy			
(Intercept)	0.124	0.569	0.830
occupancy x agouti	0.342	0.062	0.000
oncilla	-0.211	3.137	0.947
brocket deer	-28.528	17.061	0.114
giant anteater	-0.304	0.932	0.749
occupancy x oncilla	-0.335	0.089	0.002
occupancy x brocket deer	0.236	0.260	0.377
occupancy x giant anteater	-0.269	0.070	0.002
3) GLS (density ~ occupancy x species); var = species			
(Intercept)	0.081	0.732	0.913
occupancy x agouti	0.349	0.063	0.000
oncilla	-0.162	0.739	0.829
brocket deer	-29.265	23.330	0.228
giant anteater	-0.545	1.005	0.595
occupancy x oncilla	-0.342	0.063	0.000
occupancy x brocket deer	0.241	0.348	0.499
occupancy x giant anteater	-0.262	0.066	0.001
4) GLS (density ~ occupancy x species); var = species and occupancy			
(Intercept)	0.151	0.758	0.845
occupancy x agouti	0.337	0.094	0.003
oncilla	-0.245	0.767	0.754
brocket deer	-28.329	24.183	0.259
giant anteater	-0.261	0.822	0.754
occupancy x oncilla	-0.330	0.094	0.003
occupancy x brocket deer	0.238	0.371	0.531
occupancy x giant anteater	-0.269	0.096	0.013

LM: linear model; GLS: generalised least squares model; var: model accounts for variance structure on explanatory variables. GLS models were implemented because there was some degree of non-normality in the residuals of the LM. However, accounting for non-normality (GLS models) did not change the slopes of the occupancy-density relationship or their significance levels, and we decided to present results from the simpler LM.

Table S2: Density estimates from the peer-reviewed literature for the target species (and congeners for agouti) in South America. Searches conducted on Web of Science and Google Scholar.

Species common name	Species latin name	Density (ind/km^2)	Method	Location	Source
agouti	*Dasyprocta agouti*	53.8	line transect and distance sampling	Brazilian Amazon	Peres et al 2004
agouti	*Dasyprocta leporina*	4.82	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello 2000
agouti	*Dasyprocta leporina*	24.54	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello 2000
agouti	*Dasyprocta leporina*	17.27	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello 2000
agouti	*Dasyprocta leporina*	0.95	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello 2000
agouti	*Dasyprocta leporina*	11.9	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello 2000
agouti	*Dasyprocta leporina*	21	line transect and distance sampling	Brazilian Atlantic Rainforest	Ferreguetti et al 2018
agouti	*Dasyprocta leporina*	61	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	20	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	37	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	17	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	23	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	9	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta leporina*	31	line transect and distance sampling	Brazilian Amazon	Jorge & Peres 2005
agouti	*Dasyprocta prymnolopha*	321.9*	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello & Arruda 2017
agouti	*Dasyprocta prymnolopha*	373.3*	line transect and distance sampling	Brazilian Atlantic Rainforest	Chiarello & Arruda 2017
agouti	*Dasyprocta* spp.	197.53*	line transect and distance sampling	Brazilian Atlantic Rainforest	Bovendrop & Galetti 2007
agouti	*Dasyprocta azarae*	1.2	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
agouti	*Dasyprocta azarae*	10	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
agouti	*Dasyprocta azarae*	6.22	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
giant anteater	*Myrmecophaga tridactyla*	0.8	line transect and distance sampling	Brazilian Amazon	Peres et al 2005
giant anteater	*Myrmecophaga tridactyla*	0.1	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
giant anteater	*Myrmecophaga tridactyla*	0.2	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
giant anteater	*Myrmecophaga tridactyla*	0.14	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
giant anteater	*Myrmecophaga tridactyla*	0.15	line transect with fixed width	Brazilian Pantanal	Desbiez & Medri 2010
giant anteater	*Myrmecophaga tridactyla*	0.034	line transect and distance sampling	Brazilian Cerrado	Silveira et al 1999
giant anteater	*Myrmecophaga tridactyla*	0.079	line transect and distance sampling	Brazilian Cerrado	Silveira et al 1999

Table S2 (continued)

giant anteater	*Myrmecophaga tridactyla*	0.085	line transect and distance sampling	Brazilian Cerrado	Silveira et al 1999
giant anteater	*Myrmecophaga tridactyla*	2.9	line transect with fixed width	Brazilian Amazon (savanna)	Kreutz et al 2012
giant anteater	*Myrmecophaga tridactyla*	0.1	line transect with fixed width	Brazilian Amazon (savanna)	Kreutz et al 2012
grey brocket deer	*Mazama gouazoubira*	1.8	line transect and distance sampling	Brazilian Amazon	Peres et al 2003
grey brocket deer	*Mazama gouazoubira*	2.35	line transect and distance sampling	Bolivian Chaco	Noss et al 2006
grey brocket deer	*Mazama gouazoubira*	1.72	line transect and distance sampling	Bolivian Chaco	Noss et al 2006
grey brocket deer	*Mazama gouazoubira*	12	drive and total count	Bolivian Chaco	Noss et al 2006
grey brocket deer	*Mazama gouazoubira*	14	drive and total count	Bolivian Chaco	Noss et al 2006
grey brocket deer	*Mazama gouazoubira*	<0.5	line transect and distance sampling	Peruvian Amazon	Hurtado-Gonzales & Bodmer 2004
grey brocket deer	*Mazama gouazoubira*	<0.5	line transect and distance sampling	Peruvian Amazon	Hurtado-Gonzales & Bodmer 2004
grey brocket deer	*Mazama gouazoubira*	<0.5	line transect and distance sampling	Peruvian Amazon	Hurtado-Gonzales & Bodmer 2004
grey brocket deer	*Mazama gouazoubira*	4.41	pellet count	Argentinan Chaco	Periago & Leynaud 2009
grey brocket deer	*Mazama gouazoubira*	5.12	pellet count	Argentinan Chaco	Periago & Leynaud 2009
grey brocket deer	*Mazama gouazoubira*	0.39	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
grey brocket deer	*Mazama gouazoubira*	3.16	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
grey brocket deer	*Mazama gouazoubira*	3.82	line transect and distance sampling	Brazilian Pantanal	Desbiez et al 2010
grey brocket deer	*Mazama gouazoubira*	21	line transect and distance sampling	Brazilian Atlantic Rainforest	Ferreguetti 2015
grey brocket deer	*Mazama gouazoubira*	6.77	pellet count	Chiquitano dry forest, Bolivia	Rivero et al 2004
grey brocket deer	*Mazama gouazoubira*	4.4	line transect and distance sampling	Chiquitano dry forest, Bolivia	Rivero et al 2004
grey brocket deer	*Mazama gouazoubira*	30.57	pellet count	Chiquitano dry forest, Bolivia	Rivero et al 2004
grey brocket deer	*Mazama gouazoubira*	7.7	line transect and distance sampling	Chiquitano dry forest, Bolivia	Rivero et al 2004
grey brocket deer	*Mazama gouazoubira*	6.9	line transect with fixed width	Argentinan Chaco	Romero & Chatellenaz 2013
grey brocket deer	*Mazama gouazoubira*	11.2	line transect with fixed width	Argentinan Chaco	Romero & Chatellenaz 2013
grey brocket deer	*Mazama gouazoubira*	3.6	line transect with fixed width	Argentinan Chaco	Romero & Chatellenaz 2013
grey brocket deer	*Mazama gouazoubira*	5.5	line transect with fixed width	Argentinan Chaco	Romero & Chatellenaz 2013
oncilla	*Leopardus tigrinus*	0.07	capture-recapture with camera traps	Brazilian Atlantic Rainforest	Oliveira-Santos et al 2012
oncilla	*Leopardus tigrinus*	0.13	capture-recapture with camera traps	Brazilian Atlantic Rainforest	Oliveira-Santos et al 2012
oncilla	*Leopardus tigrinus*	0.08	telemetry, individuals within MCP	Brazilian Atlantic Rainforest	Kasper et al 2016

* reinforced/introduced populations in isolated forest fragments

References for Table S2

Desbiez ALJ, Bodmer RE, Tomas WM. 2010. Mammalian Densities in a Neotropical Wetland Subject to Extreme Climatic Events. Biotropica **42**:372–378.

Ferreguetti AC, Tomas WM, Bergallo HG. 2018. Density, habitat use, and daily activity patterns of the Red-rumped Agouti (*Dasyprocta leporina*) in the Atlantic Forest, Brazil. Studies on Neotropical Fauna and Environment **53**:143–151.

Ferreguetti ÁC, Tomás WM, Bergallo HG. 2015. Density, occupancy, and activity pattern of two sympatric deer (Mazama americana and M. gouazoubira) in the Atlantic Forest, Brazil. Journal of Mammalogy **96**:1245–1254. The Oxford University Press.

Hurtado-Gonzales JL, Bodmer RE. 2004. Assessing the sustainability of brocket deer hunting in the Tamshiyacu-Tahuayo Communal Reserve, northeastern Peru. Biological Conservation **116**:1–7.

Kasper CB, Schneider A, Oliveira TG. 2016. Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil. Brazilian Journal of Biology **76**:228–232.

Kreutz K, Fischer F, Linsenmair KE. 2012. Timber plantations as favourite habitat for giant anteaters. Mammalia **76**:137–142.

Noss AJ, Salidas RLC, Crespo JA. 2006. Drive counts for grey brocket deer Mazama gouazoubira in the Bolivian Chaco. Mammalia **70**:64–69.

Oliveira-Santos LGR, Graipel ME, Tortato MA, Zucco CA, Cáceres NC, Goulart FVB. 2012. Abundance changes and activity flexibility of the oncilla, Leopardus tigrinus (Carnivora: Felidae), appear to reflect avoidance of conflict. Zoologia (Curitiba) **29**:115–120.

Peres CA, Barlow J, Haugaasen T. 2003. Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx **37**:97–109.

Periago ME, Leynaud GC. 2009. Density estimates of Mazama gouazoubira (Cervidae) using the pellet count technique in the arid Chaco (Argentina). Ecología Austral **19**:73–77.

Rivero K, Rumiz DI, Taber AB. 2004. Estimating brocket deer (Mazama gouazoubira and M. americana) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz, Bolivia. European Journal of Wildlife Research **50**:161–167.

Romero V, Chatellenaz M. 2013. Densidad de Mazama gouazoubira (Artiodactyla, Cervidae) en un Parque Nacional del nordeste de Argentina. Acta Zoológica Mexicana **29**:388–399.

Silveira L, Henrique F, Rodrigues G, de Almeida Jácomo AT, Filho JAFD. 1999. Impact of wildfires on the megafauna of Emas National Park, central Brazil. Oryx 33:108–114.

Table S3: Overall estimated density via the Random encounter Model using two distinct probability density functions (PDF) to obtain species' average speed[1].

Species	PDF	Avg. speed (m/s)	Density (ind/km^2)	SE	CV	LCI	UCI	L:W
brocket deer	Weibull	0.045	10.40	2.36	0.23	6.71	16.13	
brocket deer	log-normal	0.053	8.86	1.79	0.20	5.99	13.09	0.85
giant anteater	Weibull	0.041	2.01	0.83	0.41	0.92	4.39	
giant anteater	log-normal	0.058	1.43	0.44	0.31	0.80	2.58	0.71
agouti	Weibull	0.064	2.99	1.19	0.40	1.41	6.34	
agouti	log-normal	0.078	2.46	0.89	0.36	1.23	4.90	0.82
oncilla	Weibull	0.173	0.34	0.12	0.34	0.18	0.66	
oncilla	log-normal	0.244	0.24	0.06	0.26	0.15	0.41	0.71

SE: standard error; CV: coefficient of variation; LCI: 95% lower confidence interval; UCI: 95% upper confidence interval; L:W: log-normal estimated density divided by Weibull density.

[1] Speed is used to calculate the species day range, which is part of the REM formula, therefore influencing values obtained for estimated density.

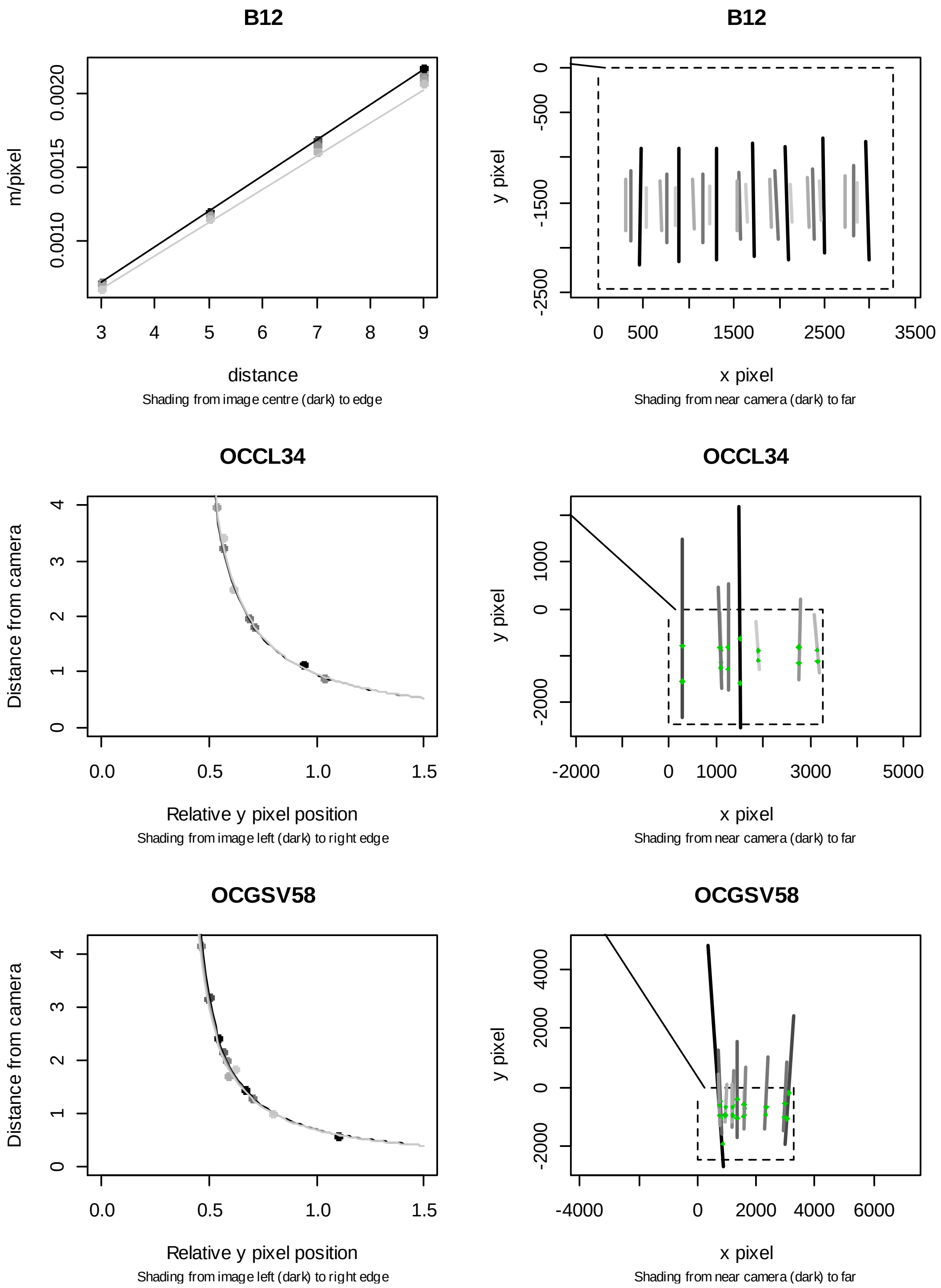


Figure S1: Top row, left: Example of camera model showing the relationship between distance from camera (in meters) and meters per pixel for 'B12' camera trap units. Other five camera models were built to allow for difference between camera trap units. Middle and bottom rows, left: example of site models showing the relationship between pixel position and distance from camera trap at 'OCCL34' and 'OCGSV58' sampling sites. A distinct site model was built for each sampling site to obtain measurements of distance, angle and movement from animal records. All panels on the right column show position of poles digitised in relation to camera's field of view (dashed box) during camera calibration (top right panel; note how the poles represented in this panel match the actual position of poles in Fig. 5.3A) and site calibration procedures (middle and bottom right panels).

Camera models (top row, left) are used to predict the distance between calibration poles and camera traps at the sampling site (see Fig. 5.3B-D), and these predicted distances are used to parameterise the site model (middle and bottom left panels). Site models are then used to predict the angular and radial distances of animals from the camera trap based on digitised images (pixel position) of animal records.

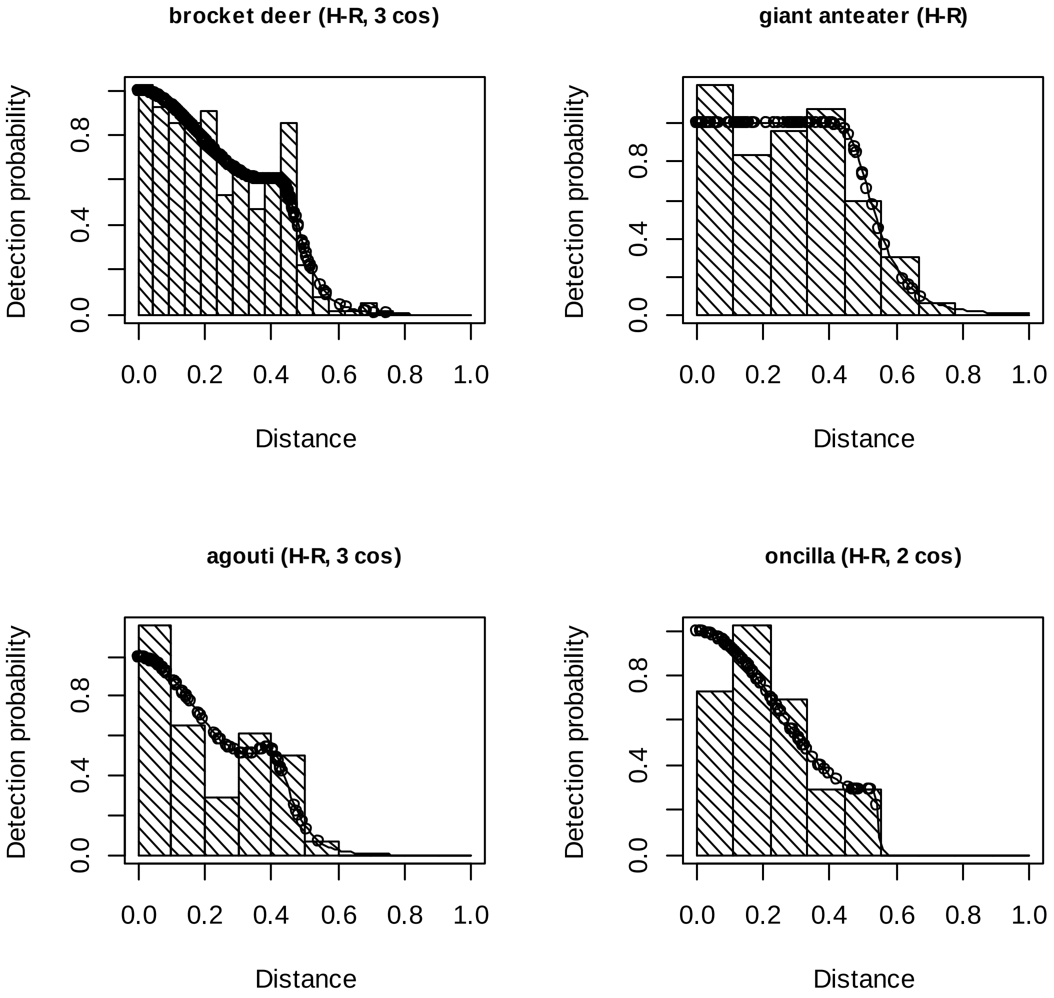


Figure S2: Detection function used to estimate effective detection angle via distance sampling based on camera trap detections of four mammal species. ‘Distance’ in the x-axis represents angular distance from the camera and is given in radians. Angular distance was truncated at the value of 1.0. Two detection functions (H-R: hazard ratio; H-N: half normal) were used to estimate effective detection distance for each species; estimate from the function with the lowest AIC was retained to estimate density. cos: number of cosine adjustment used to add flexibility to the detection function.

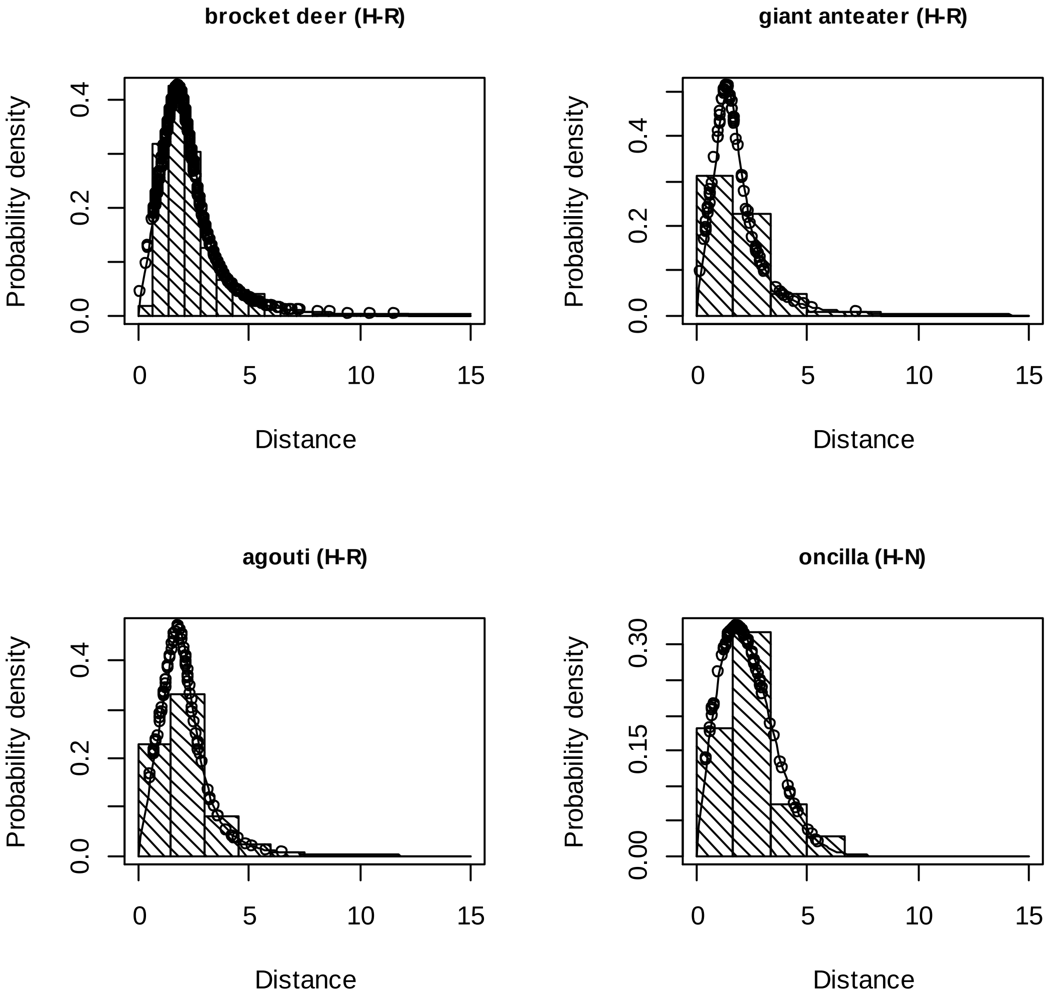


Figure S3: Detection function used to estimate effective detection distance via distance sampling based on camera trap detections of four mammal species. 'Distance' in the x-axis represents linear distance from the camera and is given in meters. Distance was truncated at the value of 15. Two detection functions (H-R: hazard ratio; H-N: half normal) were used to estimate effective detection distance for each species; estimate from the function with the lowest AIC was retained to estimate density.

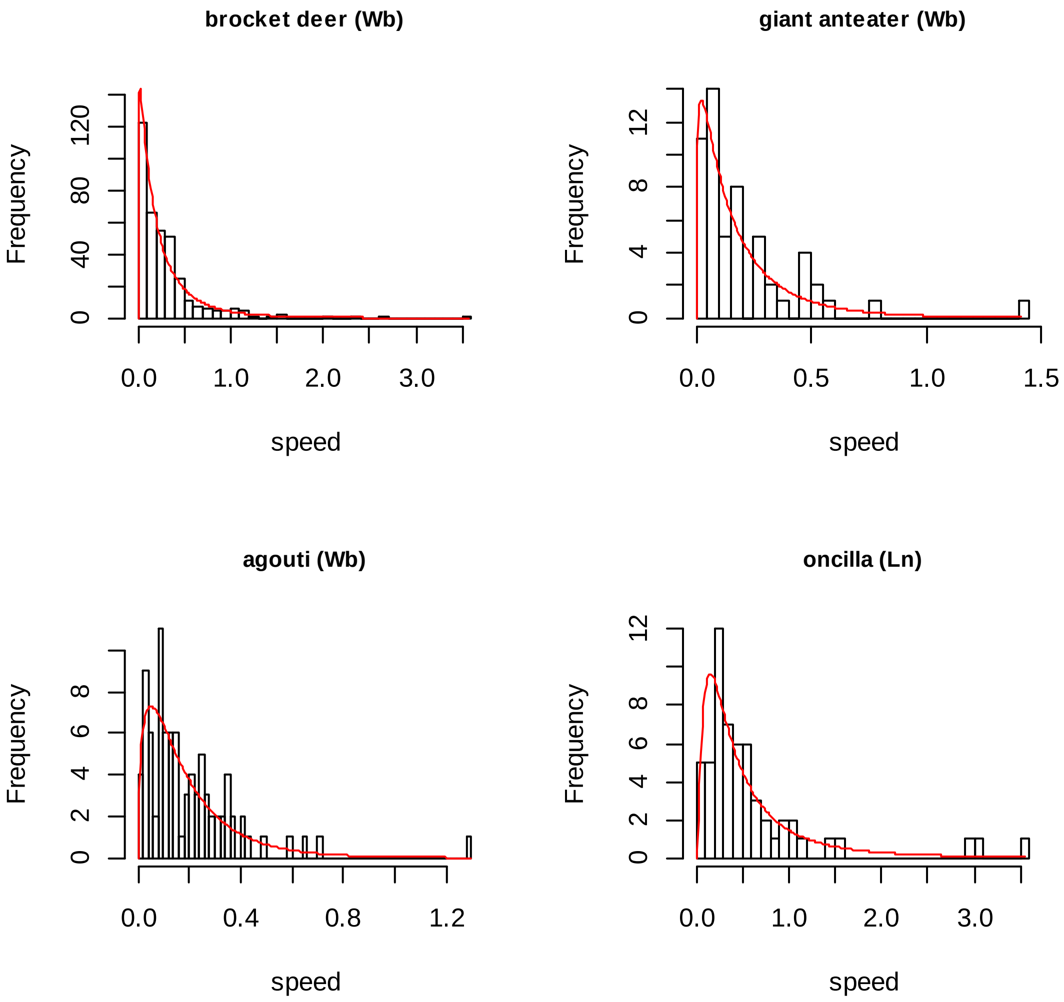


Figure S4: Estimated average speed (m/s) of four mammal species based on measurements from camera trap videos. Frequency represents the number of sequences (camera trap videos of animals moving) a given speed was recorded. Probability Density Functions used to estimate speed are either Weibull (Wb) or log-normal (Ln) and were selected based on the model with the lowest AIC value.

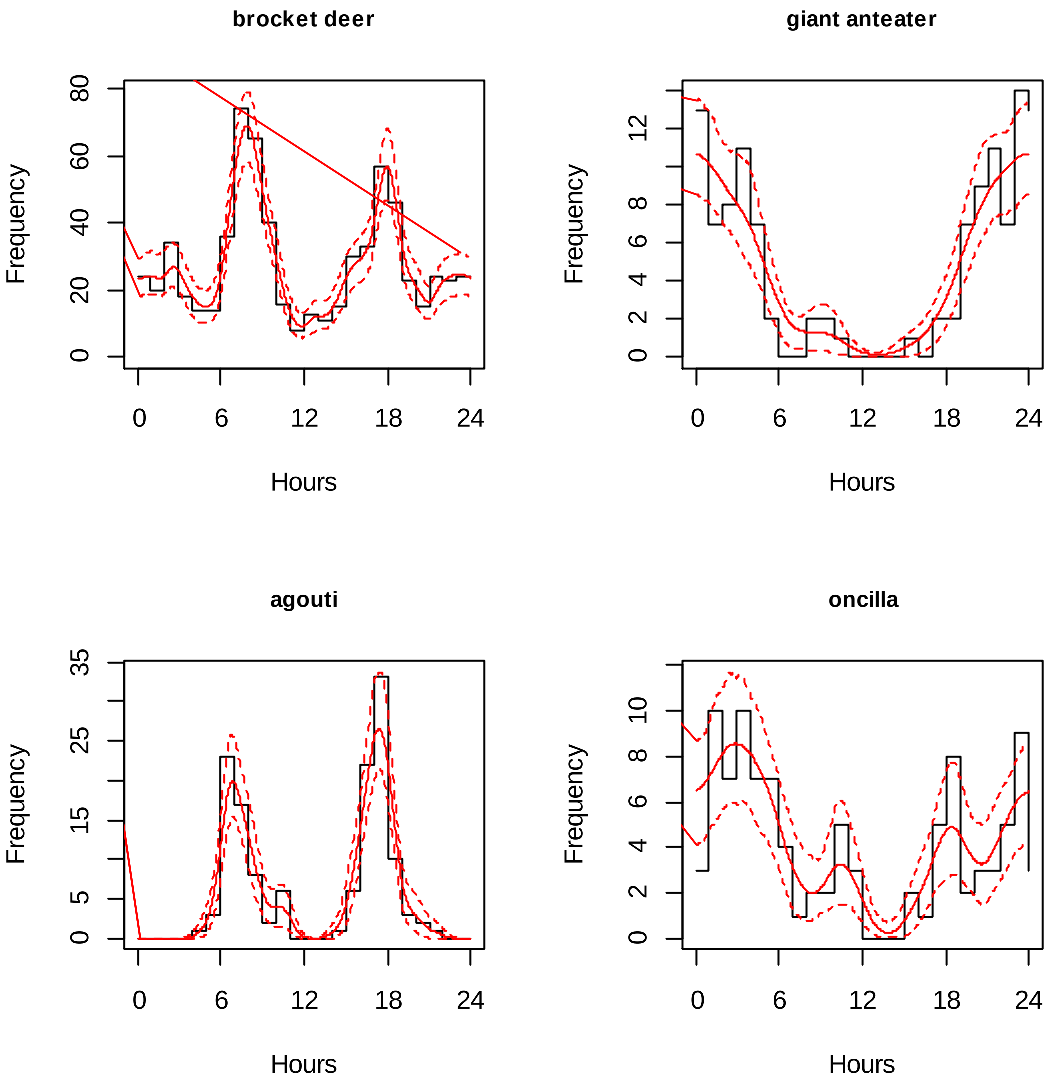


Figure S5: Estimated activity pattern used to estimate the proportion of time active based on camera trap detections of four mammal species. Frequency represents the number of camera trap records at a given time.

Chapter 6: Overall discussion

A typical tree of the Brazilian Cerrado at Rio Pandeiros Environmental Protection Area

6.1 Key findings

In this thesis I presented novel findings regarding the effectiveness of protected areas (PAs) at safeguarding local biodiversity, the influence of anthropogenic pressure on the Cerrado large mammal community, and the use of camera traps in wildlife research. These findings are based on intensive sampling effort totalling more than 25,000 survey days at 517 camera trap sites conducted in an important but understudied region of the Brazilian Cerrado – the mosaic of protected areas Sertão Veredas-Peruaçu (SVP). In this chapter I synthesize the main results of the thesis and discuss their conservation and management implications.

6.1.1 Importance of strict protected areas

In Chapter 3, I conducted the first assessment of PA effectiveness at safeguarding local biodiversity in the Cerrado and revealed that strict PAs are essential for the conservation of many larger (>15 kg) and threatened mammal species. Occupancy probability of functionally important species such as tapirs, white-lipped and collared peccaries, pumas, maned wolves and giant anteaters was at least five times higher in strict PAs than in the less restrictive multiple-use PAs. Similarly, species richness at each camera trap site was always higher in strict PAs, particularly for subsets of the community formed by larger or globally threatened species. Given the low human density and substantial vegetation cover in the study region, these findings are likely to hold in many other parts of the Brazilian Cerrado that are under greater anthropogenic pressure and have less natural vegetation.

This is a significant contribution to the understanding of PA effectiveness in the Neotropics, as large-scale counter-factual assessments of local biodiversity are virtually non-existent in this zoogeographic region (Chapter 1). It also agrees with broader scale patterns of positive effect of habitat protection on local biodiversity (Coetzee et al. 2014; Gray et al. 2016) and adds to the still small body of literature revealing the effectiveness of Cerrado PAs (Carranza et al. 2014a; Françoso et al. 2015). At the regional scale my results confirm the importance of

SVP’s strict PAs and together with further assessments presented in Appendix 1 can be used to inform the decision-making process around a complex case of overlapping designations between a national park and an indigenous land at SVP. In this overlapping case, still to undergo the full legal designation process, the Xacriabá Indigenous Land would be expanded towards one-third (ca. 180 km^2) of Cavernas do Peruaçu National Park, potentially reducing the park’s effectiveness at avoiding habitat conversion and protecting biodiversity (Appendix 1).

6.1.2 Effect of anthropogenic pressure on Cerrado mammals

Considering the contrast in human use between the two types of PAs compared in this thesis and that the sampling design and analytical approach controlled for confounding factors, the poorer large mammal community observed in multiple-use PAs (Chapter 3) is evidence of a negative impact of anthropogenic pressure. Further evidence of anthropogenic impact on the spatial distribution of sensitive mammal species is given by the negative influence of distance to households on collared peccary occupancy within one of SVP’s national park (Appendix 1). Negative anthropogenic impacts on biodiversity even in areas with substantial natural cover is in line with recent assessments conducted in the tropics revealing that habitat degradation (Barlow et al. 2016), chronic disturbance (Ribeiro et al. 2015, 2016) and poaching (Benítez-López et al. 2019) can all cause biodiversity loss without significant changes in vegetation. This highlights the need to mitigate other sources of anthropogenic pressure and not only land conversion, as well as the necessity of conducting on the ground biodiversity monitoring that complements remote sensing assessments (Roque et al. 2018).

Interestingly, despite the strong spatial influence anthropogenic pressure had on the large mammal community, in Chapter 4, I did not find a similar effect on the period these species were active. Very few species shifted to being more nocturnal in multiple-use PAs or in areas close to households, contradicting findings from a recent global analysis showing widespread reduction of diurnal activity in response to human disturbance (Gaynor et al. 2018). This indicates that a temporal shift to deal with higher anthropogenic pressure (Carter et al. 2012) is not an effective strategy at the study region. Overall, my results show that at SVP, mammal species are more likely to respond spatially (Chapter 3, Appendix 1) than temporally (Chapter 4) to human use and occupation of an area.

A more conspicuous consequence of anthropogenic pressure in the Brazilian Cerrado is deforestation (Klink & Machado 2005). Despite currently having higher rates of land conversion than the Amazon (INPE 2018), some Cerrado formations are particularly resilient and can regenerate in case of land abandonment, offsetting part of the loss in natural cover (Jepson 2005; Espírito-Santo et al. 2016). However, this secondary vegetation is distinct from the original one (Pezzini et al. 2014; Gomes & Maillard 2015) and the extent to which it can support similar animal communities as old growth vegetation is virtually unknown. Therefore it is encouraging that in Chapter 2 I found that succession stage of the savanna vegetation (i.e. old growth vs secondary) did not have a negative impact on mammal occupancy. At one of SVP's parks, secondary savanna that regenerated from clear cut supports a diverse community of large mammals, including globally threatened species. These results are in accordance with earlier findings demonstrating the conservation value of secondary tropical forests (Naidoo 2004; Barlow et al. 2007; Chazdon et al. 2009), but to my knowledge this was the first assessment of the effect of vegetation succession stage on Cerrado fauna.

Such results give reason for cautious optimism about the conservation potential of an estimated 53,000 km^2 that need to be restored in parts of the Cerrado to comply with national environmental law (Soares-Filho et al. 2014). Nonetheless, features of the study area such as level of protection, presence of source animal populations and advanced stage of regeneration (between 16 and 28 years) are likely to have produced high-quality secondary habitats (Chazdon et al. 2009; Dent & Wright 2009) that will not always be present in other regions of the Cerrado, particularly in highly fragmented areas with low vegetation cover. Furthermore, the impact of secondary savannas on other taxonomic groups is unknown, and it cannot be assumed that less mobile taxa or highly specialised nectarivorous and frugivorous animals would fare well in secondary habitats.

6.1.3 Contributions to the use of camera traps in wildlife research

In Chapter 5, I assessed the relationship between occupancy and density estimates derived from camera trap surveys for four species representing distinct orders of mammals. Thus far, recent single-species studies using camera traps had revealed a positive occupancy-abundance relationship (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017), but it was uncertain whether this positive relationship would still be found in a simultaneous survey of multiple species with distinct space use requirements. This uncertainty was mostly due to the influence of variation in movement on occupancy estimates (Efford & Dawson 2012; Neilson et al. 2018) and to the fact that in a multi-species survey the number of camera trap units per home range is not fixed across species (because home range size varies among species), implying that the proposed ideal distribution of one sampling site (i.e. one camera trap) per home range cannot be achieved for all species assessed (MacKenzie et al. 2006).

Despite the presumed variation in movement and home range size among the four species assessed, my results showed that the positive intra-specific occupancy-abundance relationship tends to hold for multiple species under a single survey design – although the strength of the relationship appears to be species-specific. Of practical importance and agreeing with the previous single-species studies conducted (Clare et al. 2015; Linden et al. 2017; Parsons et al. 2017), I provided empirical evidence that occupancy estimates from a single camera trapping design can adequately reveal the effect of covariates on the abundance of multiple species. This suggests that, for short surveys in areas where intra-specific variation in movement is not expected to be large, camera trap-derived occupancy will often reflect changes in species' abundance across the landscape, and is a useful metric in the study and monitoring of mammal populations.

The camera trapping protocol I used in this thesis was originally developed for surveying vertebrate communities in tropical forests and with the occupancy analytical framework in mind (Rovero & Ahumada 2017). Nonetheless, in Chapter 2, I revealed that it also produces precise occupancy estimates for globally threatened mammal species in the Cerrado and can be seamlessly integrated with the Random Encounter Model (REM) framework (Rowcliffe et al. 2008) to obtain both occupancy and density estimates, which I presented in Chapter 5. This integration between REM and a camera trapping protocol widely used across the tropics (Rovero & Ahumada 2017) opens the possibility of using an additional metric in pantropical assessments (e.g. Ahumada et al. 2011; Beaudrot et al. 2019) and of validating occupancy trends used in long-term monitoring (e.g. Beaudrot et al. 2016). Finally, this was the first implementation of REM in the Neotropics (Chapter 5) and it illustrates the great potential of the technique to provide abundance data that is lacking for many mammal species in this region and globally.

6.2. Implications for conservation and management at multiple scales

6.2.1 National protected area policy

Results presented here and from earlier studies asserting the effectiveness of Cerrado PAs at avoiding conversion of natural vegetation (Carranza et al. 2014a; Françoso et al. 2015) clearly show the importance of formal habitat protection at a time when the future existence of many Brazilian PAs is not secure (de Marques & Peres 2014; Silveira et al. 2018). Additionally, these results give much-needed evidence in favour of previous recommendations to increase the scant PA cover in the Cerrado (MMA 2014a; Strassburg et al. 2017). However, because the counterfactual sites used to investigate PA effectiveness in this thesis were located in Environmental Protection Areas (APA in the Portuguese acronym), our results also suggest that APAs have limited capacity to protect more sensitive mammal species.

Therefore, despite the positive message about the effectiveness of parks and more restrictive reserves at protecting local biodiversity, my findings also paint a bleak picture about conservation of large-sized sensitive mammals in extensive parts of the Cerrado that are not under strict management and have higher human pressure than SVP. These findings have important implications for PA policy in Brazil, as 60% of the PA coverage in the Cerrado is conferred by APAs and strict PAs only cover 3% of the biome. In fact, the situation is similar in most of the country: excluding the Amazon, all other terrestrial biomes have less than 5% of the original area under strict PAs and the additional protection conferred by multiple-use PAs is almost exclusively represented by APAs (Table 6.1).

Table 6.1: Percentage of protected area (PA) coverage in terrestrial Brazilian biomes.

	Amazon	Atlantic Forest	Caatinga	Cerrado	Pantanal	Pampa	Brazil
Overall PA cover	28.6	10.5	9.0	8.6	4.6	3.2	18.6
Strict PA*	10.2	2.7	1.9	3.1	4.6	0.7	6.4
Multiple-use PA	18.4	7.8	7.1	5.5	-	2.5	12.2
only APA	4.9	7.6	7.0	5.4	-	2.5	5.4

Data from the national database of protected areas (MMA 2018); it does not include Indigenous Land. Strict PA: IUCN categories I-IV; Multiple-use: IUCN categories V and VI. APA is the least restrictive category of multiple use PAs in Brazil.

*Includes private reserves (RPPNs). Although this category of PA is legally classified as multiple-use PA, its sole objective is biodiversity conservation and the only activities allowed are research and tourism (Brasil 2000), being in practice as restrictive as other strict PAs.

While multiple-use PAs can deliver conservation outcomes (Nolte & Agrawal 2013; Nolte et al. 2013), APAs are the least restrictive PA in Brazil, imposing very few restrictions on the level of land conversion allowed (Rylands & Brandon 2005) and do not avoid deforestation in the Cerrado (Françoso et al. 2015). This extensive coverage by APAs in the Cerrado and in other parts of the country may produce a false sense of protection that can be damaging for long-term conservation objectives (Barnes et al. 2018; Coad et al. 2019). Since the mid-1980s, the growth in multiple-use PAs in Brazil has been greater than in strict PAs, with creation of more restrictive categories of PAs virtually stagnating in the last decade (Vieira et al. 2019). The results presented here indicate that this pattern needs to be readdressed urgently and the creation of strict PAs should be prioritised in the Cerrado and in other biomes with small strict PA cover if large mammals of conservation concern are to be safeguarded in the future.

6.2.2 Management of protected areas

Although my results show that SVP's strict PAs are effective at safeguarding species of conservation concern, it is known that some of these areas have significant management shortfalls and are not adequately funded or staffed (WWF-Brasil & IEF-MG 2016), therefore not being completely free of anthropogenic pressure. As anthropogenic pressure has negative effects on mammal species at SVP (Chapter 3 and Appendix 1), it is reasonable to assume that the strict PAs assessed could perform even better under improved management conditions. Indeed, the existent anthropogenic pressure within strict PAs – albeit much lower than in APAs – may be partially responsible for the absence in our surveys of jaguars, giant armadillos and marsh deer, three of the largest and most sensitive mammals occurring at SVP (Ferreira & Oliveira 2014). Although, according to local reports, these species were likely to be rare in the region even before the establishment of PAs, reducing pressure inside strict PAs to lower levels may be necessary to allow their populations to recover.

Given the serious consequences of anthropogenic pressure in natural areas (Barlow et al. 2016; Benítez-López et al. 2019) and that many Brazilian PAs have significant management shortfalls (ICMBio & WWF-Brasil 2011), the most pressing management issue for strict PAs (not only at SVP) is to keep anthropogenic pressure as low as possible and to reduce it where possible. To this end managers must have the resources (human, technical and financial) to adopt actions that curb illegal activities, such as establishing an adequate patrolling routine and remote surveillance of key access routes. Additionally, the complex issue of land tenure in strict PAs must be addressed, with financial compensation payed to landowners who eventually reach an agreement with the governmental body managing the PA. It has been shown that Cerrado PAs where land tenure issues have been solved are less likely to lose natural vegetation (Françoso et al. 2015) and probably less likely to lose biodiversity due to direct anthropogenic pressure.

On the other hand, the scope to reduce anthropogenic pressure in APAs is limited due to the low level of restrictions imposed on human activity in these areas. Nonetheless, there are some opportunities to improve their management and potentially increase their performance. All APAs must have a management plan that determines a zoning system for the area, which may include more restricted zones for biodiversity conservation (Brasil 2000). Even if established over only a small portion of the whole APA, a properly adopted and enforced conservation zone could play a role in the regional conservation landscape, supporting source populations of some species and functioning as steppingstones to strict PAs or to areas of higher habitat quality. At SVP conservation zones within APAs could benefit the subset of the mammal community that seems to thrive in those areas (Chapter 3), which although being composed mostly by smaller and non-threatened species, also includes three small carnivores of conservation concern. Ideally, these more restrictive zones should prioritise areas of natural vegetation within large rural properties that have the conditions to accommodate conservation measures, sparing smaller landowners that might be operating under challenging economic conditions (Stefanes et al. 2018).

6.2.3 Post-2020 protected area targets

In 2020 the Convention on Biological Diversity will adopt a new global biodiversity framework replacing the strategic plan that established the Aichi Biodiversity targets (https://www.cbd.int/conferences/post2020). Some proposals for the PA component of this new framework suggest that post-2020 targets and indicators should be explicitly linked to desired conservation outcomes, focusing on quality rather than on quantity of PAs (Barnes et al.

2018). It is true that expansion of the PA estate will still be needed given the underrepresentation of some habitats and species (Butchart et al. 2015; Venter et al. 2018), but a systematic monitoring scheme relying on metrics that can inform whether PAs are being effective in maintaining or restoring local biodiversity will be crucial in a future framework (Visconti et al. 2019).

Adoption of such schemes in Brazil would be particularly important due to the large representation of APAs in the national system (Table 6.1). Here I showed that conservation performance differ between PA types, highlighting the need to go beyond metrics of coverage. Better integration of current biodiversity and deforestation monitoring initiatives in the country (Roque et al. 2018) within a counterfactual framework (Mascia et al. 2017) could provide outcome-based indicators to assess PAs, complementing indicators of cover. This thesis provides a local scale example of PA assessment using indicators directly linked to conservation outcomes, which could be scaled up to the biome or national level. Only by adopting metrics that reflect conservation end-goals will it be possible to know whether PAs are reaching their objectives and to direct the necessary actions to improve effectiveness of those that are not.

References

Abreu RCR de, de Assis GB, Frison S, Aguirre A, Durigan G. 2011. Can native vegetation recover after slash pine cultivation in the Brazilian Savanna? Forest Ecology and Management **262**:1452–1459.

Agostinelli C, Lund U. 2017. R package “circular”: Circular Statistics (version 0.4-93).

Ahumada JA et al. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical transactions of the Royal Society of London. Series B, Biological sciences **366**:2703–2711.

Ahumada JA, Hurtado J, Lizcano D. 2013. Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: a tool for conservation. PloS one **8**:e73707.

Ament JM, Cumming GS. 2016. Scale dependency in effectiveness, isolation, and social-ecological spillover of protected areas. Conservation Biology **30**:846–855. John Wiley & Sons, Ltd (10.1111).

Andam KS, Ferraro PJ, Pfaff A, Sanchez-Azofeifa GA, Robalino JA. 2008. Measuring the effectiveness of protected area networks in reducing deforestation. Proceedings of the National Academy of Sciences of the United States of America **105**:16089–94. National Academy of Sciences.

Andresen L, Everatt KT, Somers MJ. 2014. Use of site occupancy models for targeted monitoring of the cheetah. Journal of Zoology **292**:212–220.

Anile S, Ragni B, Randi E, Mattucci F, Rovero F. 2014. Wildcat population density on the Etna volcano, Italy: A comparison of density estimation methods. Journal of Zoology **293**:252–261.

Ariefiandy A, Purwandana D, Seno A, Ciofi C, Jessop TS. 2013. Can camera traps monitor Komodo Dragons a large ectothermic predator? PLoS ONE **8**:1–8.

Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G. 2018. Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms. Animal Behaviour **140**:129–140. Academic Press.

Ayeni JSO. 1975. Utilization of waterholes in Tsavo National Park (East). African Journal of Ecology **13**:305–323.

Backéus I. 1992. Distribution and vegetation dynamics of humid savannas in Africa and Asia.

Journal of Vegetation Science **3**:345–356.

Bailey LL, Hines JE, Nichols JD, MacKenzie DI. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. Ecological Applications **17**:281–290.

Baker J, Venditti C. 2019. Rapid Change in Mammalian Eye Shape Is Explained by Activity Pattern. Current Biology **29**:1082-1088.e3. Cell Press.

Barata IM, Griffiths RA, Ferreira GB. 2018. Activity Pattern and Behavior of an Endemic Bromeliad Frog Observed through Camera Trapping. Herpetological Review **49**:432–438.

Barata IM, Griffiths RA, Ridout MS. 2017. The power of monitoring: optimizing survey designs to detect occupancy changes in a rare amphibian population. Scientific Reports **7**:16491. Nature Publishing Group.

Barger NN, D'Antonio CM, Ghneim T, Brink K, Cuevas E. 2002. Nutrient limitation to primary productivity in a secondary savanna in Venezuela. Biotropica **34**:493–501.

Barlow J et al. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America **104**:18555–60.

Barlow J et al. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature **535**:144–147. Nature Publishing Group.

Barnes M. 2015. Protect biodiversity, not just area. Nature **526**:195–195.

Barnes MD et al. 2016. Wildlife population trends in protected areas predicted by national socio-economic metrics and body size. Nature Communications **7**:12747. Nature Research.

Barnes MD, Glew L, Wyborn C, Craigie ID. 2018. Prevent perverse outcomes from global protected area policy. Nature Ecology & Evolution **2**:759–762. Nature Publishing Group.

Barton K. 2018. MuMIn: Multi-Model Inference.

Batalha MA. 2011. O cerrado não é um bioma. Biota Neotropica **11**:21–24. Programa BIOTA/FAPESP.

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software **67**:1–48.

Beaudrot L et al. 2016. Standardized Assessment of Biodiversity Trends in Tropical Forest Protected Areas: The End Is Not in Sight. PLoS Biology **14**:e1002357. Public Library of Science.

Beaudrot L et al. 2019a. Local temperature and ecological similarity drive distributional dynamics of tropical mammals worldwide. Global Ecology and Biogeography:geb.12908. John Wiley & Sons, Ltd (10.1111).

Beaudrot L, Ahumada J, O'Brien TG, Jansen PA. 2019b. Detecting tropical wildlife declines through camera-trap monitoring: An evaluation of the Tropical Ecology Assessment and Monitoring protocol. Oryx **53**:126–129. Cambridge University Press.

Beck H, Thebpanya P, Filiaggi M. 2010. Do Neotropical peccary species (Tayassuidae) function as ecosystem engineers for anurans? Journal of Tropical Ecology **26**:407–414. Cambridge University Press.

Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF, Peres CA, Ovaskainen O, Jordano P. 2015. Defaunation affects carbon storage in tropical forests. Science Advances **1**:e1501105–e1501105. American Association for the Advancement of Science.

Benítez-López A, Santini L, Schipper AM, Busana M, Huijbregts MAJ. 2019. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. PLOS Biology **17**:e3000247. Public Library of Science.

Bernard E, Penna LAO, Araújo E. 2014. Downgrading, downsizing, degazettement, and reclassification of protected areas in Brazil. Conservation Biology **28**:939–50.

Bertassoni A, Mourão G, Ribeiro RC, Cesário CS, Oliveira JP de, Bianchi R de C. 2017. Movement patterns and space use of the first giant anteater (*Myrmecophaga tridactyla*) monitored in São Paulo State, Brazil. Studies on Neotropical Fauna and Environment **52**:68–74. Taylor & Francis.

Beschta RL, Ripple WJ. 2016. Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. Biological Conservation **198**:93–103. Elsevier.

Bobrowiec PED, Gribel R. 2010. Effects of different secondary vegetation types on bat community composition in Central Amazonia, Brazil. Animal Conservation **13**:204–216.

Borchers DL, Efford MG. 2008. Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies. Biometrics **64**:377–385. John Wiley & Sons, Ltd (10.1111).

Boron V, Deere NJ, Xofis P, Link A, Quiñones-Guerrero A, Payan E, Tzanopoulos J. 2019. Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. Biological Conservation **232**:108–116. Elsevier.

Bracke MBM. 2011. Review of wallowing in pigs: Description of the behaviour and its motivational basis. Applied Animal Behaviour Science **132**:1–13. Elsevier.

Brasil. 2000. SNUC – Sistema Nacional de Unidades de Conservação da Natureza: Lei nº 9.985, de 18 de julho de 2000.

Buckland S, Anderson D, Burnham K, Laake J, Borchers D, Thomas L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press.

Bueno AA, Motta-Junior JC. 2006. Small Mammal Selection and Functional Response in the Diet of the Maned Wolf, Chrysocyon Brachyurus (Mammalia: Canidae), in Southeast Brazil. Mastozoología Neotropical **13**:11–19.

Bueno ML, Dexter KG, Pennington RT, Pontara V, Neves DM, Ratter JA, de Oliveira-Filho AT. 2018. The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. Journal of Ecology **106**:2109–2120. John Wiley & Sons, Ltd (10.1111).

Burnham KP, Anderson D. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, USA.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675–685.

Butchart SHM et al. 2015. Shortfalls and Solutions for Meeting National and Global Conservation Area Targets. Conservation Letters **8**:329–337. John Wiley & Sons, Ltd (10.1111).

Cain JW, Jansen BD, Wilson RR, Krausman PR. 2008. Potential thermoregulatory advantages of shade use by desert bighorn sheep. Journal of Arid Environments **72**:1518–1525. Academic Press.

Camilo-Alves CDSEP, Mourão GDM. 2006. Responses of a specialized insectivorous mammal (Myrmecophaga tridactyla) to variation in ambient temperature. Biotropica **38**:52–56. John Wiley & Sons, Ltd (10.1111).

Caravaggi A, Zaccaroni M, Riga F, Schai-Braun SC, Dick JTA, Montgomery WI, Reid N. 2016. An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. Remote Sensing in Ecology and Conservation **2**:45–58. Wiley-Blackwell.

Carbone C, Gittleman JL. 2002. A common rule for the scaling of carnivore density. Science **295**:2273–2276.

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis

A. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239–41.

Carranza T, Balmford A, Kapos V, Manica A. 2014a. Protected area effectiveness in reducing conversion in a rapidly vanishing ecosystem: the Brazilian Cerrado. Conservation Letters **7**:216–223.

Carranza T, Manica A, Kapos V, Balmford A. 2014b. Mismatches between conservation outcomes and management evaluation in protected areas: A case study in the Brazilian Cerrado. Biological Conservation **173**:10–16.

Carrillo E, Saenz JC, Fuller TK. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. Biological Conservation **108**:317–324.

Carrillo E, Wong G, Cuarón AD, Rica C. 2000. Monitoring Mammal Populations in Costa Rican Protected Areas under Different Hunting Restrictions **14**:1580–1591.

Carter N, Jasny M, Gurung B, Liu J. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. Global Ecology and Conservation **3**:149–162. Elsevier.

Carter NH, Shrestha BK, Karki JB, Pradhan NMB, Liu J. 2012. Coexistence between wildlife and humans at fine spatial scales. Proceedings of the National Academy of Sciences of the United States of America **109**:15360–5. National Academy of Sciences.

Cassano CR, Barlow J, Pardini R. 2012. Large Mammals in an Agroforestry Mosaic in the Brazilian Atlantic Forest. Biotropica **44**:818–825.

CBD. 2013. Quick guides to the Aichi Biodiversity Targets.

Ceballos G, Ehrlich PR. 2002. Mammal Population Losses and the Extinction Crisis. Science **296**:904–907.

Chapman CA, Chapman LJ, Wangham R, Hunt K, Gebo D, Gardner L. 1992. Estimators of Fruit Abundance of Tropical Trees. Biotropica **24**:527.

Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE. 2009. The potential for species conservation in tropical secondary forests. Conservation Biology **23**:1406–1417.

Chiarello AG. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biological Conservation **89**:71–82.

Chiarello AG. 2000. Density and Population Size of Mammals in Remnants of Brazilian Atlantic Forest. Conservation Biology **14**:1649–1657.

Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, Boyce MS. 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. PLoS ONE **7**:e50611. Public Library of Science.

Clare JDJ, Anderson EM, MacFarland DM. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. The Journal of Wildlife Management **79**:469–480. John Wiley & Sons, Ltd.

Clinchy M, Zanette LY, Roberts D, Suraci JP, Buesching CD, Newman C, Macdonald DW. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behavioral Ecology **27**:1826–1832. Narnia.

Coad L et al. 2015. Measuring impact of protected area management interventions: Current and future use of the global database of protected area management effectiveness. Philosophical Transactions of the Royal Society B: Biological Sciences **370**.

Coad L, Watson JE, Geldmann J, Burgess ND, Leverington F, Hockings M, Knights K, Di Marco M. 2019. Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. Frontiers in Ecology and the Environment:fee.2042. John Wiley & Sons, Ltd.

Coetzee BWT, Gaston KJ, Chown SL. 2014. Local scale comparisons of biodiversity as a test for global protected area ecological performance: a meta-analysis. PloS one **9**:e105824.

Cooke RSC, Eigenbrod F, Bates AE. 2019. Projected losses of global mammal and bird ecological strategies. Nature Communications **10**:2279. Nature Publishing Group.

Corlett RT. 2007. The Impact of Hunting on the Mammalian Fauna of Tropical Asian Forests. Biotropica **39**:292–303. Blackwell Publishing Inc.

Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Hutton JM. 2010. Large mammal population declines in Africa's protected areas. Biological Conservation **143**:2221–2228. Elsevier Ltd.

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution **23**:194–201.

Cruz P, Iezzi ME, De Angelo C, Varela D, Di Bitetti MS, Paviolo A. 2018. Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. PLOS ONE **13**:e0200806. Public Library of Science.

Cusack JJ, Swanson A, Coulson T, Packer C, Carbone C, Dickman AJ, Kosmala M, Lintott C, Rowcliffe JM. 2015. Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. Journal of Wildlife Management **79**:1014–1021. Wiley-Blackwell.

Dalponte JC, Tavares-Filho JA. 2004. Diet of the Yellow Armadillo, Euphractus sexcinctus, in South-Central Brazil. Edentata **6**:37.

Damuth J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biological Journal of the Linnean Society **31**:193–246.

Davies AB, Gaylard A, Asner GP. 2018. Megafaunal effects on vegetation structure throughout a densely wooded African landscape. Ecological Applications **28**:398–408. John Wiley & Sons, Ltd.

de Marques AAB, Peres CA. 2014. Pervasive legal threats to protected areas in Brazil. Oryx **49**:25–29.

Deere NJ, Guillera-Arroita G, Baking EL, Bernard H, Pfeifer M, Reynolds G, Wearn OR, Davies ZG, Struebig MJ. 2018. High Carbon Stock forests provide co-benefits for tropical biodiversity. Journal of Applied Ecology **55**:997–1008.

Demarchi MW, Bunnell FL. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). Canadian Journal of Forest Research **23**:2419–2426. NRC Research Press Ottawa, Canada .

Dent DH, Wright SJ. 2009. The future of tropical species in secondary forests: A quantitative review. Biological Conservation **142**:2833–2843. Elsevier Ltd.

Desbiez AL, Bodmer RE, Aparecida S. 2009. Wildlife habitat selection and sustainable resources management in a Neotropical wetland. International Journal of Biodiversity and Conservation **1**:11–20.

Desbiez ALJ, Bodmer RE, Tomas WM. 2010. Mammalian densities in a Neotropical wetland subject to extreme climatic events. Biotropica **42**:372–378. Blackwell Publishing Inc.

Desbiez ALJ, Kluyber D. 2013. The Role of Giant Armadillos (Priodontes maximus) as Physical Ecosystem Engineers. Biotropica **45**:537–540.

Desbiez ALJ, Medri ÍM. 2010. Density and Habitat use by Giant Anteaters (Myrmecophaga tridactyla) and Southern Tamanduas (Tamandua tetradactyla) in the Pantanal Wetland, Brazil. Edentata **11**:4–10. IUCN/SSC Anteater, Sloth and Armadillo Specialist Group.

Di Bitetti MS, Paviolo A, Ferrari CA, De Angelo C, Di Blanco Y. 2008. Differential responses to hunting in two sympatric species of brocket deer (Mazama americana and M. nana). Biotropica **40**:636–645.

Di Marco M, Santini L. 2015. Human pressures predict species' geographic range size better than biological traits. Global Change Biology **21**:2169–2178. John Wiley & Sons, Ltd (10.1111).

Diniz MF, Brito D. 2015. Protected areas effectiveness in maintaining viable giant anteater (Myrmecophaga tridactyla) populations in an agricultural frontier. Natureza & Conservação **13**:145–151. Elsevier.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014. Defaunation in the Anthropocene. Science **345**:401–406.

Dorazio RM, Royle JA, Söderström B, Glimskär A. 2006. Estimating species richness and accumulation by modeling species occurence and detectability. Ecology **87**:842–854.

Drouilly M, Clark A, O'Riain MJ. 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally. Biological Conservation **224**:16–25. Elsevier.

Dudley N. 2008. Guidelines for applying protected area management categories. IUCN, Gland, Switzerland.

Durigan G, Ratter JA. 2006. Successional changes in cerrado and cerrado/forest ecotonal vegetation in western São Paulo state, Brazil, 1962–2000. Edinburgh Journal of Botany **63**:119. Cambridge University Press.

Efford MG, Dawson DK. 2012. Occupancy in continuous habitat. Ecosphere **3**:1–15.

Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, Windels SK. 2017. Implications of the thermal environment for terrestrial wildlife management. Wildlife Society Bulletin **41**:183–193. John Wiley & Sons, Ltd.

Erb PL, McShea WJ, Guralnick RP. 2012. Anthropogenic influences on macro-level mammal occupancy in the appalachian trail corridor. PLoS ONE **7**.

Espírito-Santo MM, Leite ME, Silva JO, Barbosa RS, Rocha AM, Anaya FC, Dupin MG V. 2016. Understanding patterns of land-cover change in the Brazilian Cerrado from 2000 to 2015. Philosophical Transactions of the Royal Society of London B: Biological Sciences **371**.

Fernandes GW et al. 2016. Cerrado: em busca de soluções sustentáveis. Vertente, Rio de Janeiro.

Ferraro PJ, Pattanayak SK. 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology **4**:e105.

Ferreguetti AC, Davis CL, Tomas WM, Bergallo HG. 2018. Using activity and occupancy to evaluate niche partitioning: the case of two peccary species in the Atlantic Rainforest, Brazil. Hystrix, the Italian Journal of Mammalogy **29**:168–174. Associazione Teriologica Italiana.

Ferreguetti ÁC, Tomás WM, Bergallo HG. 2015. Density, occupancy, and activity pattern of two sympatric deer (Mazama americana and M. gouazoubira) in the Atlantic Forest, Brazil. Journal of Mammalogy **96**:1245–1254. The Oxford University Press.

Ferreira GB. 2018. When the blanket is too short: Potential negative impacts of expanding indigenous land over a national park in a high priority area for conservation. Land Use Policy **76**:359–364.

Ferreira GB, Ahumada JA, Oliveira MJR, de Pinho FF, Barata IM, Carbone C, Collen B. 2017a. Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado. Biotropica **49**:734–744.

Ferreira GB, Barros C de S, Costa AB da, Dias TS, Oliveira MJRR. 2017b. First ever record of a black-coloured maned wolf. Canid Biology & Conservation **20**:42–45.

Ferreira GB, Oliveira MJR. 2014. Discovering mammals – a guide to the species of northern Minas Gerais/Descobrindo os mamíferos – um guia para as espécies do norte de Minas Gerais, 1st edition. Biografa, Januária, Brazil.

Ferreira GB, Oliveira MJR, De Paula RC, Rodrigues FHG, Carmo EDC. 2015. Regionally extinct species rediscovered: the bush dog Speothos venaticus in Minas Gerais, south-eastern Brazil. Oryx **49**:60–63.

Ferreira GB, Oliveira MJR, Junior EAM, Silva JA, Rodrigues FHG. 2011. Mamíferos de médio e grande porte do Parque Estadual Veredas do Peruaçu: riqueza, composição e estratégias de conservação. MG Biota **4**:6–19.

Ferreira LG, Yoshioka H, Huete A, Sano E. 2003. Seasonal landscape and spectral vegetation index dynamics in the Brazilian Cerrado: An analysis within the Large-Scale Biosphere–Atmosphere Experiment in Amazônia (LBA). Remote Sensing of Environment **87**:534–550.

Ferreira LG, Yoshioka H, Huete A, Sano EE. 2004. Optical characterization of the Brazilian Savanna physiognomies for improved land cover monitoring of the cerrado biome: preliminary assessments from an airborne campaign over an LBA core site. Journal of Arid Environments **56**:425–447.

Fiske IJ, Chandler RB. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**:1–23.

Flynn DFB, Uriarte M, Crk T, Pascarella JB, Zimmerman JK, Aide TM, Caraballo Ortiz MA. 2010. Hurricane Disturbance Alters Secondary Forest Recovery in Puerto Rico. Biotropica

42:149–157.

Françoso RD, Brandão R, Nogueira CC, Salmona YB, Machado RB, Colli GR. 2015. Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. Natureza & Conservação **13**:35–40.

Frey S, Fisher JT, Burton AC, Volpe JP. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sensing in Ecology and Conservation **3**:123–132.

Fundação Biodiversitas. 2005. Biodiversidade em Minas Gerais: um Atlas para sua Conservação. Belo Horizonte.

Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH. 2000. Abundance-occupancy relationships. Journal of Applied Ecology **37**:39–59.

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232–1235. American Association for the Advancement of Science.

Geldmann J et al. 2015. Changes in protected area management effectiveness over time: A global analysis. Biological Conservation **191**:692–699.

Geldmann J et al. 2018. A global analysis of management capacity and ecological outcomes in terrestrial protected areas. Conservation Letters **11**:e12434. Wiley/Blackwell (10.1111).

Geldmann J, Barnes M, Coad L, Craigie ID, Hockings M, Burgess ND. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation **161**:230–238.

Gelman A, Hill J. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK, UK.

Gertler PJ, Martinez S, Premand P, Rawlings LB, Vermeersch CMJ. 2016. Impact Evaluation in Practice, Second Edition. The World Bank.

Gibson L et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature **478**:378–81. Nature Publishing Group.

Gomes MF. 2006. Avaliação de dados Radarsat-1 e CBERS-2 para estimativa da estrutura do cerrado: uma abordagem utilizando dados alométricos e históricos. Universidade Federal de Minas Gerais.

Gomes MF, Maillard P. 2015. Using spectral and textural features from RapidEye images to estimate age and structural parameters of Cerrado vegetation. International Journal of

Remote Sensing **36**:3058–3076. Taylor & Francis.

Grace J, Jose JS, Meir P, Miranda HS, Montes RA. 2006. Productivity and carbon fluxes of tropical savannas. Journal of Biogeography **33**:387–400. Blackwell Science Ltd.

Gray CL, Hill SLL, Newbold T, Hudson LN, Börger L, Contu S, Hoskins AJ, Ferrier S, Purvis A, Scharlemann JPW. 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nature Communications **7**:12306. Nature Research.

Gray TNE. 2012. Studying Large Mammals With Imperfect Detection: Status and Habitat Preferences of Wild Cattle and Large Carnivores in Eastern Cambodia. Biotropica **44**:531–536.

Gray TNE. 2018. Monitoring tropical forest ungulates using camera-trap data. Journal of Zoology **305**:173–179. John Wiley & Sons, Ltd (10.1111).

Greene DF, Johnson EA. 1994. Estimating the Mean Annual Seed Production of Trees. Ecology **75**:642–647. Ecological Society of America.

Grotta-Neto F, Duarte JMB. 2019. Movements of Neotropical forest deer: What do we know? Pages 95–109 Movement Ecology of Neotropical Forest Mammals. Springer International Publishing.

Guillera-Arroita G, Lahoz-Monfort JJ. 2012. Designing studies to detect differences in species occupancy: Power analysis under imperfect detection. Methods in Ecology and Evolution **3**:860–869.

Harmsen BJ, Foster RJ, Silver S, Ostro L, Doncaster CP. 2010. Differential Use of Trails by Forest Mammals and the Implications for Camera-Trap Studies: A Case Study from Belize. Biotropica **42**:126–133.

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ **6**:e4794. PeerJ Inc.

Hayssen V. 2011. Tamandua tetradactyla (Pilosa: Myrmecophagidae). Mammalian Species **43**:64–74. Narnia.

He F, Gaston KJ. 2003. Occupancy, Spatial Variance, and the Abundance of Species. The American Naturalist **162**:366–375. The University of Chicago Press .

Hernández-Ordóñez O, Urbina-Cardona N, Martínez-Ramos M. 2015. Recovery of Amphibian and Reptile Assemblages During Old-Field Succession of Tropical Rain Forests. Biotropica **47**:377–388.

Hines JE. 2006. GENPRES - Software to Generates patch occupancy data and analyze using programs MARK or PRESENCE. USGS-PWRC.

Hockings M. 2003. Systems for Assessing the Effectiveness of Management in Protected Areas. BioScience **53**:823–832. Narnia.

Hoffmann WA. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model predictions. Ecology **80**:1354–1369.

Holt AR, Gaston KJ, He F. 2002. Occupancy-abundance relationships and spatial distribution: A review. Basic and Applied Ecology **3**:1–13. Urban & Fischer.

Hurtado-Gonzales JL, Bodmer RE. 2004. Assessing the sustainability of brocket deer hunting in the Tamshiyacu-Tahuayo Communal Reserve, northeastern Peru. Biological Conservation **116**:1–7. Elsevier.

Hurtt GC et al. 2011. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. Climatic Change **109**:117–161.

IBGE. 2004. Mapa de Biomas do Brasil: Primeira aproximação. Brasília, Brazil.

IBGE. 2017. Downloads IBGE. Available from https://downloads.ibge.gov.br/ (accessed July 5, 2017).

IBGE. 2019. IBGE - Brasil em síntese. Available from https://cidades.ibge.gov.br/brasil/panorama (accessed May 12, 2019).

ICMBio, WWF-Brasil. 2011. Avaliação comparada das aplicações do método Rappam nas unidades de conservação federais, nos ciclos 2005-06 e 2010. Brasília, Brazil.

INPE. 2018. TerraBrasilis. Available from http://terrabrasilis.dpi.inpe.br/.

IPBES. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (advance unedited version).

IUCN. 2017. The IUCN Red List of Threatened Species. Version 2017-2. Available from http://www.iucnredlist.org (accessed September 14, 2017).

Jacomo AT de A, Silveira L, Diniz-Filho JAF. 2004. Niche separation between the maned wolf (Chrysocyon brachyurus), the crab-eating fox (Dusicyon thous) and the hoary fox (Dusicyon vetulus) in central Brazil. Journal of Zoology **262**:99–106.

Jammalamadaka SR, SenGupta A. 2001. Nonparametric testing procedures. Pages 151–174 Topics in circular statistics. World Scientific Publishing.

Jenkins CN, Pimm SL, Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proceedings of the National Academy of Sciences of the United States of America **110**:E2602-10. National Academy of Sciences.

Jepson W. 2005. A disappearing biome? Reconsidering land-cover change in the Brazilian savanna. The Geographical Journal **171**:99–111.

Jetz W, Carbone C, Fulford J, Brown JH. 2004. The scaling of animal space use. Science **306**:266–268.

Jones KR, Venter O, Fuller RA, Allan JR, Maxwell SL, Negret PJ, Watson JEM. 2018. One-third of global protected land is under intense human pressure. Science (New York, N.Y.) **360**:788–791. American Association for the Advancement of Science.

Joppa LN, Pfaff A. 2009. High and Far: Biases in the Location of Protected Areas. PLoS ONE **4**:e8273. Public Library of Science.

Joppa LN, Pfaff A. 2011. Global protected area impacts. Proceedings of the Royal Society B: Biological Sciences **278**:1633–1638.

Jorge MSP, Peres CA. 2005. Population Density and Home Range Size of Red-Rumped Agoutis (Dasyprocta leporina) Within and Outside a Natural Brazil Nut Stand in Southeastern Amazonia. Biotropica **37**:317–321. John Wiley & Sons, Ltd (10.1111).

Karanth KU. 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological Conservation **71**:333–338. Elsevier.

Karanth KU, Nichols JD. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology **79**:2852–2862. Ecological Society of America.

Kasper CB, Schneider A, Oliveira TG. 2016. Home range and density of three sympatric felids in the Southern Atlantic Forest, Brazil. Brazilian Journal of Biology **76**:228–232. Instituto Internacional de Ecologia.

Kellner K. 2017. Package jagsUI - A Wrapper Around “rjags” to Streamline “JAGS” Analyses.

Kery M, Royle J. 2016. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS - Volume 1 Prelude and Static Models. Academic Press.

Keuroghlian A, Eaton DP, Desbiez ALJ. 2009. The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian pantanal. International Journal of Biodiversity and Conservation **1**:87–97.

Khongdee T, Sripoon S, Vajrabukka C. 2011. The effects of high temperature and wallow on physiological responses of swamp buffaloes (Bubalus bubalis) during winter season in Thailand. Journal of Thermal Biology **36**:417–421. Pergamon.

Kinnaird MF, O’brien TG. 2012. Effects of Private-Land Use, Livestock Management, and Human Tolerance on Diversity, Distribution, and Abundance of Large African Mammals. Conservation Biology **26**:1026–1039.

Klink C a., Machado RB. 2005. Conservation of the Brazilian Cerrado. Conservation Biology **19**:707–713.

Kolowski JM, Alonso a. 2010. Density and activity patterns of ocelots (Leopardus pardalis) in northern Peru and the impact of oil exploration activities. Biological Conservation **143**:917–925. Elsevier Ltd.

Kreutz K, Fischer F, Linsenmair KE. 2012. Timber plantations as favourite habitat for giant anteaters. Mammalia **76**:137–142.

Kucera T, Barrett R. 2011. A history of camera trapping. Pages 9–26 in A. F. O’Connell, J. D. Nichols, and K. U. Karanth, editors. Camera Traps in Animal Ecology: Methods and Analyses. Springer, Japan.

Kuhlmann M, Ribeiro JF. 2016. Evolution of seed dispersal in the Cerrado biome: ecological and phylogenetic considerations. Acta Botanica Brasilica **30**:271–282. Sociedade Botânica do Brasil.

Lapola DM et al. 2013. Pervasive transition of the Brazilian land-use system. Nature Climate Change **4**:27–35. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.

Leverington F, Costa KL, Pavese H, Lisle A, Hockings M. 2010. A Global Analysis of Protected Area Management Effectiveness. Environmental Management **46**:685–698. Springer-Verlag.

Levick S, Rogers K. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. Biological Conservation **141**:489–498. Elsevier.

Linden DW, Fuller AK, Royle JA, Hare MP. 2017. Examining the occupancy-density relationship for a low-density carnivore. Journal of Applied Ecology **54**:2043–2052. John Wiley & Sons, Ltd (10.1111).

Linkie M, Dinata Y, Nugroho A, Haidir IA. 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation **137**:20–27.

Loucks C, Ricketts TH, Naidoo R, Lamoreux J, Hoekstra J. 2008. Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural suitability. Journal of Biogeography **35**:1337–1348. John Wiley & Sons, Ltd (10.1111).

Maccarini TB, Attias N, Medri ÍM, Marinho-Filho J, Mourão G. 2015. Temperature influences the activity patterns of armadillo species in a large neotropical wetland. Mammal Research **60**:403–409. Springer Berlin Heidelberg.

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics **9**:300–318.

MacKenzie DI, Bailey LL, Nichols JD. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology **73**:546–555.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle AA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248–2255.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE. 2006. Occupancy estimating and modeling – inferring patterns and dynamics of species occurrence. Elsevier Academic Press, London, UK.

Mackenzie DI, Royle JA. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105–1114.

Maillard P, Costa-Pereira PS. 2010. Estimating the age of cerrado regeneration using Landsat TM data. Canadian Journal of Remote Sensing **36**:S243–S256. NRC Research Press Ottawa, Canada.

Marinho-Filho J, Rodrigues FH, Juarez KM. 2002. The Cerrado mammals: diversity, ecology and natural history. Pages 266–284 in P. S.Oliveira and R. J. Marquis, editors. The Cerrados of Brazil. Columbia University Press, New York, USA.

Mascia MB et al. 2017. A novel framework for analyzing conservation impacts: evaluation, theory, and marine protected areas. Annals of the New York Academy of Sciences **1399**:93–115. Wiley/Blackwell (10.1111).

Mascia MB, Pailler S. 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. Conservation Letters **4**:9–20.

Massara RL, Paschoal AM de O, Bailey LL, Doherty PF, Barreto M de F, Chiarello AG. 2018. Effect of humans and pumas on the temporal activity of ocelots in protected areas of Atlantic Forest. Mammalian Biology **92**:86–93. Urban & Fischer.

Mazerolle MJ. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).

McNab BK. 1963. Bioenergetics and the Determination of Home Range Size. The American Naturalist **97**:133–140. Science Press .

McNab BK. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. Journal of Zoology **203**:485–510. John Wiley & Sons, Ltd (10.1111).

McNab BK. 1985. Energetics, population biology, and distribution of Xenarthrans, living and extinct. Pages 219–232 in G. G. Montgomery, editor. The Evolution and Ecology of Armadillos, Sloths and Vermilinguas. Smithsonian Institution Press.

McShea WJ, Stewart C, Peterson L, Erb P, Stuebing R, Giman B. 2009. The importance of secondary forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. Biological Conservation **142**:3108–3119.

Meredith M, Ridout M. 2014. Overview of the overlap package. R project:1–9.

Mesquita RCG, Ickes K, Ganade G, Williamson GB. 2001. Alternative successional pathways in the Amazon Basin. Journal of Ecology **89**:528–537.

Michalski F, Peres CA. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological Conservation **124**:383–396.

Miller DL. 2017. Distance: Distance Sampling Detection Function and Abundance Estimation. version 0.9.7.

Mittermeier RA, Da Fonseca GAB, Rylands AB, Brandon K. 2005. A Brief History of Biodiversity Conservation in Brazil. Conservation Biology **19**:601–607. John Wiley & Sons, Ltd (10.1111).

MMA/IBAMA/Funatura. 2003. Plano de Manejo do Parque Nacional Grande Sertão Veredas. Brasília, Brazil.

MMA/IBAMA/Geoclock. 2005. Plano de Manejo do Parque Nacional Cavernas do Peruaçu. Brasília, Brazil.

MMA/PROBIO. 2007. Áreas prioritárias para conservação, uso sustentável e repartição de benefícios da biodiversidade brasileira. Brasília, Brazil.

MMA. 2014a. Plano de Ação para Prevenção e Controle do Desmatamento e das Queimadas no Cerrado. Brasília, Brazil.

MMA. 2014b. Portaria No 444, 17 de Dezembro de 2014 - Lista nacional oficial de espécies da fauna ameaçadas extinção. Diário Oficial da União, Brasília, Brazil.

MMA. 2018. Cadastro Nacional de Unidades de Conservação. Available from www.mma.gov.br/cadastro_uc (accessed September 11, 2017).

Moreno RS, Kays RW, Samudio R. 2006. Competitive release in diets of ocelot (Leopardus pardalis) and puma (Puma concolor) after jaguar (Panthera onca) decline. Journal of Mammalogy **87**:808–816.

Morris T, Letnic M. 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. Proceedings of the Royal Society B: Biological Sciences **284**:20170111. The Royal Society.

Morrison JC, Sechrest W, Dinerstein E, Wilcove DS, Lamoreux JF. 2007. Persistence of Large Mammal Faunas as Indicators of Global Human Impacts PERSISTENCE OF LARGE MAMMAL FAUNAS AS INDICATORS OF GLOBAL HUMAN IMPACTS **88**:1363–1380.

Mourão G, Medri ÍM. 2007. Activity of a specialized insectivorous mammal (Myrmecophaga tridactyla) in the Pantanal of Brazil. Journal of Zoology **271**:187–192. John Wiley & Sons, Ltd (10.1111).

Myers N, Mittermeier R a, Mittermeier CG, da Fonseca G a, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853–8.

Nagy-Reis MB, Estevo CA, Setz EZF, Ribeiro MC, Chiarello AG, Nichols JD. 2017. Relative importance of anthropogenic landscape characteristics for Neotropical frugivores at multiple scales. Animal Conservation **20**:520–531. Wiley/Blackwell (10.1111).

Naidoo R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. Animal Conservation **7**:93–105.

Naughton-Treves L, Holland MB, Brandon K. 2005. the Role of Protected Areas in Conserving Biodiversity and Sustaining Local Livelihoods. Annual Review of Environment and Resources **30**:219–252.

Negrões N, Revilla E, Fonseca C, Soares AMVM, Jácomo AT a, Silveira L. 2011. Private forest reserves can aid in preserving the community of medium and large-sized vertebrates in the Amazon arc of deforestation. Biodiversity and Conservation **20**:505–518.

Neilson EW, Avgar T, Burton AC, Broadley K, Boutin S. 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. Ecosphere **9**:e02092.

Newbold T et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature

520:45–50. Nature Publishing Group.

Nogueira C, Rodrigues MT. 2007. The genus Stenocercus (Squamata: Tropiduridae) in extra-Amazonian Brazil, with the description of two new species. South American Journal of Herpetology **1**:149–165. Brazilian Society of Herpetology.

Nolte C, Agrawal A. 2013. Linking management effectiveness indicators to observed effects of protected areas on fire occurrence in the Amazon rainforest. Conservation biology : the journal of the Society for Conservation Biology **27**:155–65.

Nolte C, Agrawal A, Silvius KM, Soares-Filho BS. 2013. Governance regime and location influence avoided deforestation success of protected areas in the Brazilian Amazon. Proceedings of the National Academy of Sciences of the United States of America **110**:4956–61. National Academy of Sciences.

Norris D, Michalski F, Peres CA. 2010. Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments. Journal of Mammalogy **91**:551–560. American Society of Mammalogists.

Noss AJ, Salidas RLC, Crespo JA. 2006. Drive counts for grey brocket deer Mazama gouazoupira in the Bolivian Chaco. Mammalia **70**:64–69.

O’Brien TG, Baillie JEM, Krueger L, Cuke M. 2010. The Wildlife Picture Index: monitoring top trophic levels. Animal Conservation **13**:335–343.

O’Brien TG, Kinnaird MF. 2008. A picture is worth a thousand words: the application of camera trapping to the study of birds. Bird Conservation International **18**:S144–S162. Cambridge University Press.

O’Connell AF, Bailey LL. 2011. Inference for occupancy and occupancy dynamics. Pages 191–206 in A. F. O’ Connel, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology - methods and analyses. Springer Japan.

O’Connell AF, Talancy NW, Bailey LL, John R, Cook R, Gilbert AT. 2006. Estimating site occupancy and detection probability parameters for meso- And large mammals in a coastal ecosystem. Journal of Wildlife Management **70**:1625–1633.

Oberosler V, Groff C, Iemma A, Pedrini P, Rovero F. 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. Mammalian Biology **87**:50–61. Urban & Fischer.

Ohashi H et al. 2013. Differences in the activity pattern of the wild boar Sus scrofa related to human disturbance. European Journal of Wildlife Research **59**:167–177. Springer-Verlag.

Oliveira-Santos LGR, Graipel ME, Tortato MA, Zucco CA, Cáceres NC, Goulart FVB. 2012. Abundance changes and activity flexibility of the oncilla, Leopardus tigrinus (Carnivora: Felidae), appear to reflect avoidance of conflict. Zoologia (Curitiba) **29**:115–120. Sociedade Brasileira de Zoologia.

Oliveira-Santos LGR, Zucco CA, Agostinelli C. 2013. Using conditional circular kernel density functions to test hypotheses on animal circadian activity. Animal Behaviour **85**:269–280. Academic Press.

Oliveira U et al. 2017. Biodiversity conservation gaps in the Brazilian protected areas. Scientific Reports **7**:9141. Nature Publishing Group.

Owen-Smith N. 1998. How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (Tragelaphus strepsiceros). Journal of Zoology **246**:183–192. John Wiley & Sons, Ltd (10.1111).

Owen-Smith N. 2019. Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. Biological Conservation **232**:51–58. Elsevier.

Pacheco AA, Neves ACO, Fernandes GW. 2018. Uneven conservation efforts compromise Brazil to meet the Target 11 of Convention on Biological Diversity. Perspectives in Ecology and Conservation **16**:43–48. Elsevier.

Padilla M, Dowler RC. 1994. Tapirus terrestris. Mammalian Species **481**:1–8.

Paglia A et al. 2012. Lista Anotada dos Mamíferos do Brasil/Annotated Checklist of Brazilian Mammals. Occasional Papers in Conservation Biology **6**:1–76.

Parsons AW, Forrester T, McShea WJ, Baker-Whatton MC, Millspaugh JJ, Kays R. 2017. Do occupancy or detection rates from camera traps reflect deer density? Journal of Mammalogy **98**:1547–1557. Oxford University Press.

Paviolo A, Di Blanco YE, De Angelo CD, Di Bitetti MS. 2009. Protection Affects the Abundance and Activity Patterns of Pumas in the Atlantic Forest. Journal of Mammalogy **90**:926–934. American Society of Mammalogists.

Payan E, Oliveira T de. 2016. Leopardus tigrinus. The IUCN Red List of Threatened Species **e.T5401263**.

Penido G, Astete S, Jácomo ATA, Sollmann R, Tôrres N, Silveira L, Marinho Filho J. 2017. Mesocarnivore activity patterns in the semiarid Caatinga: limited by the harsh environment or affected by interspecific interactions? Journal of Mammalogy **98**:1732–1740. Narnia.

Peres CA. 2001. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology **15**:1490–1505.

Peres CA, Barlow J, Haugaasen T. 2003. Vertebrate responses to surface wildfires in a central Amazonian forest. Oryx **37**:97–109. Cambridge University Press.

Pettorelli N, to Bühne HS, Shapiro AC, Glover-Kapfer P. 2018. Satellite remote sensing for conservation. WWF Conservation Technology Series 1(4).

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution **20**:503–510.

Pezzini FF, Ranieri BD, Brandão DO, Fernandes GW, Quesada M, Espírito-Santo MM, Jacobi CM. 2014. Changes in tree phenology along natural regeneration in a seasonally dry tropical forest. Plant Biosystems **148**:965–974. Taylor & Francis.

Pfeifer M, Boyle MJW, Dunning S, Olivier PI. 2019. Forest floor temperature and greenness link significantly to canopy attributes in South Africa's fragmented coastal forests. PeerJ **7**:e6190. PeerJ Inc.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models.

Pinho FF, Ferreira GB, Paglia AP. 2017. Influence of vegetation physiognomy, elevation and fire frequency on medium and large mammals in two protected areas of the Espinhaço range. Zoologia **34**:e11921.

Plummer M. 2013. JAGS Version 3.4.0 user manual.

Pontes MNC. 2010. Detalhamento de áreas de savana arborizada no Bioma Cerrado a partir da análise de séries temporais Modis EVI para o período de 2004 a 2008. Universidade Federal de Goiás.

QGIS Development Team. 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing.

Rada N. 2013. Assessing Brazil's Cerrado agricultural miracle. Food Policy **38**:146–155. Pergamon.

Ramesh T, Downs CT. 2013. Impact of farmland use on population density and activity patterns of serval in South Africa. Journal of Mammalogy **94**:1460–1470. Narnia.

Ratter J, Ribeiro JF, Bridgewater S. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Annals of Botany **80**:223–230.

Redford KH. 1992. The Empty Forest. BioScience **42**:412–422. Oxford University PressAmerican Institute of Biological Sciences.

Reider KE, Carson WP, Donnelly M a. 2013. Effects of collared peccary (Pecari tajacu) exclusion on leaf litter amphibians and reptiles in a Neotropical wet forest, Costa Rica. Biological Conservation **163**:90–98.

Reilly ML, Tobler MW, Sonderegger DL, Beier P. 2017. Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. Biological Conservation **207**:117–126. Elsevier.

Ribeiro EMS, Arroyo-Rodriguez V, Santos BA, Tabarelli M, Leal IR. 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. Journal of Applied Ecology **52**:611–620. Wiley/Blackwell (10.1111).

Ribeiro EMS, Santos BA, Arroyo-Rodríguez V, Tabarelli M, Souza G, Leal IR. 2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology **97**:1583–1592. Wiley-Blackwell.

Ribeiro JR, Walter BMT. 2008. As principais fitofisionomias do bioma Cerrado. Pages 151–212 in S. M. Sano, S. P. de Almeida, and J. F. Ribeiro, editors. Cerrado: ecologia e flora, 1st edition. Embrapa Cerrados, Planaltina, Brazil.

Rich LN et al. 2017a. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. Global Ecology and Biogeography **26**:918–929.

Rich LN, Miller DAW, Robinson HS, McNutt JW, Kelly MJ. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. Journal of Applied Ecology **53**:1225–1235.

Rich LN, Miller DAW, Robinson HS, McNutt JW, Kelly MJ. 2017b. Carnivore distributions in Botswana are shaped by resource availability and intraguild species. Journal of Zoology **303**:90–98. John Wiley & Sons, Ltd (10.1111).

Ridout MS, Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics **14**:322–337.

Ripple WJ et al. 2015. Collapse of the world's largest herbivores. Science Advances **1**:e1400103. American Association for the Advancement of Science.

Ripple WJ et al. 2016a. Saving the World's Terrestrial Megafauna. BioScience **66**:807–812.

Oxford University Press.

Ripple WJ et al. 2016b. Bushmeat hunting and extinction risk to the world’s mammals. Royal Society Open Science **3**:160498. The Royal Society.

Rodrigues ASL et al. 2004. Effectiveness of the global protected area network in representing species diversity. Nature **428**:640–643. Nature Publishing Group.

Roldán AI, Simonetti J a. 2001. Plant-Mammal Interactions in Tropical Bolivian Forests with Different Hunting Pressures. Conservation Biology **15**:617–623.

Roque F de O et al. 2018. A network of monitoring networks for evaluating biodiversity conservation effectiveness in Brazilian protected areas. Perspectives in Ecology and Conservation **16**:177–185. Elsevier.

Rovero F, Ahumada J. 2017. The Tropical Ecology, Assessment and Monitoring (TEAM) Network: An early warning system for tropical rain forests. Science of the Total Environment **574**:914–923.

Rovero F, Marshall AR. 2009. Camera trapping photographic rate as an index of density in forest ungulates. Journal of Applied Ecology **46**:1011–1017. Blackwell Publishing Ltd.

Rovero F, Martin E, Rosa M, Ahumada JA, Spitale D. 2014. Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. PLoS ONE **9**:e103300.

Rowcliffe JM, Carbone C. 2008. Surveys using camera traps: are we looking to a brighter future? Animal Conservation **11**:185–186.

Rowcliffe JM, Carbone C, Jansen P a., Kays R, Kranstauber B. 2011. Quantifying the sensitivity of camera traps: An adapted distance sampling approach. Methods in Ecology and Evolution **2**:464–476.

Rowcliffe JM, Field J, Turvey ST, Carbone C. 2008. Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology **45**:1228–1236.

Rowcliffe JM, Jansen PA, Kays R, Kranstauber B, Carbone C. 2016. Wildlife speed cameras: measuring animal travel speed and day range using camera traps. Remote Sensing in Ecology and Conservation **2**:84–94. John Wiley & Sons, Ltd.

Rowcliffe JM, Kays R, Kranstauber B, Carbone C, Jansen PA. 2014. Quantifying levels of animal activity using camera trap data. Methods in Ecology and Evolution **5**:1170–1179.

Royle JA. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. Biometrics **60**:108–115. John Wiley & Sons, Ltd (10.1111).

Royle JA, Nichols JD. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology **84**:777–790.

Rylands AB, Brandon K. 2005. Brazilian protected areas. Conservation Biology **19**:612–618. Blackwell Science Inc.

Sampaio AB, Holl KD, Scariot A. 2007. Regeneration of Seasonal Deciduous Forest Tree Species in Long-Used Pastures in Central Brazil. Biotropica **39**:655–659.

Sano EE, Rodrigues AA, Martins ES, Bettiol GM, Bustamante MMC, Bezerra AS, Couto AF, Vasconcelos V, Schüler J, Bolfe EL. 2019. Cerrado ecoregions: A spatial framework to assess and prioritize Brazilian savanna environmental diversity for conservation. Journal of Environmental Management **232**:818–828. Academic Press.

Schuette P, Wagner AP, Wagner ME, Creel S. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation **158**:301–312.

Schulze K, Knights K, Coad L, Geldmann J, Leverington F, Eassom A, Marr M, Butchart SHM, Hockings M, Burgess ND. 2018. An assessment of threats to terrestrial protected areas. Conservation Letters:e12435.

Seber GAF. 1986. A Review of Estimating Animal Abundance. Biometrics **42**:267.

SEMAD. 2017. Zoneamento Ecológico-Econômico de Minas Gerais. Available from http://geosisemanet.meioambiente.mg.gov.br/zee/ (accessed August 19, 2017).

Shamoon H, Maor R, Saltz D, Dayan T. 2018. Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects. Biological Conservation **226**:32–41. Elsevier.

Shannon G, Lewis JS, Gerber BD. 2014. Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data. PeerJ **2**:e532.

Silva JF, Farinas MR, Felfili JM, Klink C a. 2006. Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. Journal of Biogeography **33**:536–548. Blackwell Science Ltd.

Silveira FAO, Ferreira MC, Perillo LN, Carmo FF, Neves FS. 2018. Brazil's protected areas under threat. Science **361**:459. American Association for the Advancement of Science.

Silveira L, Henrique F, Rodrigues G, de Almeida Jácomo AT, Filho JAFD. 1999. Impact of wildfires on the megafauna of Emas National Park, central Brazil. Oryx **33**:108–114.

Soares-Filho B, Rajão R, Macedo M, Carneiro A, Costa W, Coe M, Rodrigues H, Alencar A. 2014.

Cracking Brazil’s Forest Code. Science **344**:363–364.

Solar RR de C et al. 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters **18**:1108–1118.

Sollmann R, Furtado MM, Hofer H, Jácomo ATA, Tôrres NM, Silveira L. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammalian Biology **77**:41–46.

Steenweg R et al. 2017. Scaling-up camera traps: monitoring the planet’s biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**:26–34. John Wiley & Sons, Ltd.

Steenweg R, Hebblewhite M, Whittington J, Lukacs P, McKelvey K. 2018. Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. Ecology **99**:172–183. John Wiley & Sons, Ltd.

Stefanes M, Roque F de O, Lourival R, Melo I, Renaud PC, Quintero JMO. 2018. Property size drives differences in forest code compliance in the Brazilian Cerrado. Land Use Policy **75**:43–49. Pergamon.

Strassburg BBN et al. 2017. Moment of truth for the Cerrado hotspot. Nature Ecology & Evolution **1**:0099.

TEAM Network. 2011. Terrestrial vertebrate (camera trap) monitoring protocol, v.3.1. Arlington, USA.

Teixeira M, Amaro RC, Recoder RS, De Sena MA, Rodrigues MT. 2012. A relict new species of Oreobates (Anura, Strabomantidae) from the Seasonally Dry Tropical Forests of Minas Gerais, Brazil, and its implication to the biogeography of the genus and that of South American Dry Forests. Zootaxa **3158**:37–52.

Terborgh J et al. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923–1926.

Terborgh J, Feeley K, Silman M, Nunez P, Balukjian B. 2006. Vegetation dynamics of predator-free land-bridge islands. Journal of Ecology **94**:253–263.

Tobler MW, Hartley AZ, Carrillo-Percastegui SE, Powell GVN. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. Journal of Applied Ecology **52**:413–421.

Traill LW, Lim MLM, Sodhi NS, Bradshaw CJA. 2010. Mechanisms driving change: altered species interactions and ecosystem function through global warming. Journal of Animal

Ecology **79**:937–947. John Wiley & Sons, Ltd (10.1111).

Tuff KT, Tuff T, Davies KF. 2016. A framework for integrating thermal biology into fragmentation research. Ecology Letters **19**:361–374. John Wiley & Sons, Ltd (10.1111).

UNEP-WCMC, IUCN. 2016. Protected Planet Report 2016. Cambridge, UK and Gland, Switzerland.

UNEP-WCMC, IUCN. 2019. Protected Planet: The World Database on Protected Areas. Available from www.protectedplanet.net (accessed May 11, 2019).

UNEP-WCMC, IUCN, NGS. 2018. Protected Planet Report 2018. UNEP-WCMC, IUCN and NGS, Cambridge UK; Gland, Switzerland; and Washington, D.C., USA.

USGS. 2018. EarthExplorer. Available from https://earthexplorer.usgs.gov/ (accessed March 3, 2018).

van Doormaal N, Ohashi H, Koike S, Kaji K. 2015. Influence of human activities on the activity patterns of Japanese sika deer (Cervus nippon) and wild boar (Sus scrofa) in Central Japan. European Journal of Wildlife Research **61**:517–527. Springer Berlin Heidelberg.

Veldman JW et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment **13**:154–162.

Velho N, Sreekar R, Laurance W. 2016. Terrestrial Species in Protected Areas and Community-Managed Lands in Arunachal Pradesh, Northeast India. Land **5**:35. Multidisciplinary Digital Publishing Institute.

Venter O et al. 2014. Targeting global protected area expansion for imperiled biodiversity. PLoS biology **12**:e1001891.

Venter O et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature Communications **7**:12558. Nature Publishing Group.

Venter O, Magrach A, Outram N, Klein CJ, Possingham HP, Di Marco M, Watson JEM. 2018. Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. Conservation Biology **32**:127–134. John Wiley & Sons, Ltd (10.1111).

Vieira RRS, Pressey RL, Loyola R. 2019. The residual nature of protected areas in Brazil. Biological Conservation **233**:152–161. Elsevier.

Vieira RRS, Ribeiro BR, Resende FM, Brum FT, Machado N, Sales LP, Macedo L, Soares-Filho B, Loyola R. 2017. Compliance to Brazil's Forest Code will not protect biodiversity and ecosystem services. Diversity and Distributions.

Visconti P, Butchart SHM, Brooks TM, Langhammer PF, Marnewick D, Vergara S, Yanosky A, Watson JEM. 2019. Protected area targets post-2020. Science (New York, N.Y.):eaav6886. American Association for the Advancement of Science.

Watson JEM, Dudley N, Segan DB, Hockings M. 2014. The performance and potential of protected areas. Nature **515**:67–73. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.

Wearn OR, Rowcliffe JM, Carbone C, Bernard H, Ewers RM. 2013. Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. PloS one **8**:e77598.

Wearn OR, Rowcliffe JM, Carbone C, Pfeifer M, Bernard H, Ewers RM. 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. Biological Conservation **212**:162–171. Elsevier.

Whitfeld TJS, Lasky JR, Damas K, Sosanika G, Molem K, Montgomery RA. 2014. Species Richness, Forest Structure, and Functional Diversity During Succession in the New Guinea Lowlands. Biotropica **46**:538–548.

Woodroffe R, Ginsberg JR. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science **280**.

WWF-Brasil. 2011. Uso e ocupação do solo no Mosaico Sertão Veredas-Peruaçu: ano base 2010.

WWF-Brasil, IEF-MG. 2016. Implementação da Avaliação Rápida e Priorização da Gestão de Unidades de Conservação (RAPPAM) em Unidades de Conservação estaduais de Minas Gerais. Brasília, Brazil.

WWF-Brasil, MMA. 2015. Áreas prioritárias para conservação da biodiversidade no Cerrado e Pantanal. Brasília, Brazil.

WWF. 2018. Living Planet Report - 2018: Aiming Higher. Page (Grooten M, Almond REA, editors). WWF, Gland, Switzerland.

Xavier da Silva M, Paviolo A, Tambosi LR, Pardini R. 2018. Effectiveness of Protected Areas for biodiversity conservation: Mammal occupancy patterns in the Iguaçu National Park, Brazil. Journal for Nature Conservation **41**:51–62. Urban & Fischer.

Zapata-Ríos G, Branch LC. 2016. Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. Biological Conservation **193**:9–16. Elsevier.

Zardo RN, Henriques RPB. 2011. Growth and fruit production of the tree Caryocar brasiliense in the Cerrado of central Brazil. Agroforestry Systems **82**:15–23. Springer Netherlands.

Zeller KA, Nijhawan S, Salom-Pérez R, Potosme SH, Hines JE. 2011. Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. Biological Conservation **144**:892–901.

Zero VH, Sundaresan SR, O'Brien TG, Kinnaird MF. 2013. Monitoring an Endangered savannah ungulate, Grevy's zebra Equus grevyi: choosing a method for estimating population densities. Oryx **47**:410–419. Cambridge University Press.

Zimbres B, Furtado MM, Jácomo ATA, Silveira L, Sollmann R, Tôrres NM, Machado RB, Marinho-Filho J. 2013. The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. Landscape Ecology **28**:259–269.

Zipkin EF, Andrew Royle J, Dawson DK, Bates S. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation **143**:479–484.

Zipkin EF, DeWan A, Andrew Royle J. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. Journal of Applied Ecology **46**:815–822. Wiley/Blackwell (10.1111).

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Springer New York, New York, NY.

Appendix 1: Potential negative impacts of expanding indigenous land over a national park in a high priority area for conservation

I produced this assessment in an attempt to contribute to the discussions about a proposed expansion of the Xacriabá Indigenous Land over Cavernas do Peruaçu National Park, both located at the Sertão Veredas-Peruaçu mosaic. A Portuguese version was first sent to the national park's advisory board and the English version was published as:

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When the blanket is too short: potential negative impacts of expanding indigenous land over a national park in a high priority area for conservation

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Abstract

Land claims by indigenous peoples can cause changes in established protected areas. The consequences of such changes for biodiversity conservation will be context-dependent and influenced by characteristics of the indigenous population as well as the protected area affected. In the Cerrado-Caatinga ecotone of Brazil, there is an ongoing legal process to expand the Xacriabá Indigenous Land. The Xacriabás are claiming an additional 433 km^2, which overlaps with one third of Cavernas do Peruaçu National Park. I used local scale data and occupancy modelling to show that expanding this indigenous land at the expense of the already reduced area under strict protection in the Cerrado and Caatinga is likely to decrease the national park's conservation effectiveness. My analysis suggests that intensification of human presence in the overlapping area between the two land designations will result in loss of native vegetation, increase in the number of fires and might have a negative impact on populations of more sensitive species.

Keywords: protected areas; anthropogenic pressure; co-management; PADDD; deforestation; fire.

1. Introduction

Protected areas (PAs) are a cornerstone of conservation policy and have been established worldwide in order to mitigate the current environmental crisis (Watson et al., 2014). PAs can avoid conversion of natural vegetation (Carranza et al., 2014; Geldmann et al., 2013), support higher levels of biodiversity than unprotected lands (Coetzee et al., 2014; Gray et al., 2016), deliver crucial ecosystem services (Soares-Filho et al., 2010) and contribute to local economies in some regions (Balmford et al., 2009). However, a recent global increase in PA downgrading, downsizing and degazettement events (PADDD - see Mascia and Pailler, 2011 for definition) may pose a threat to the long-term conservation benefits these areas are expected to deliver. As demand to access and use natural resources are increasing worldwide (Rands et al., 2010), PADDD will become a crucial topic of land use and conservation policy in the near future.

In Brazil, PADDD events in the last 15 years were mainly driven by pressures from the agribusiness and energy sector (Bernard et al., 2014), but land claims by indigenous peoples can also result in PADDD. In the latter case the outcome is not necessarily negative from a conservation perspective, as areas managed by traditional populations may be effective in preventing deforestation (Carranza et al., 2014; Nepstad et al., 2006). Therefore, the consequences for biodiversity will be context-dependent and largely influenced by characteristics of the indigenous population claiming the land (population size, population density, intensity of natural resources use, type of land use implemented, etc), as well as features of the PA affected (category, implementation level, management effectiveness, etc).

Recent data show that 20% of all land claims by local communities in Brazilian federal strict PAs are made by indigenous groups, representing 27 cases in total – 18 of them in national parks (Madeira et al., 2015). A case in point is the proposed expansion of the Xacriabá Indigenous Land (XIL) over roughly one third of Cavernas do Peruaçu National Park (CPNP) (FUNAI, 2014), a strict PA (IUCN category II) located in the Cerrado-Caatinga ecotone of Brazil (Fig. 1A). The 568 km^2 CPNP was created in 1999 to protect the unique speleological system of the Peruaçu river valley, as well as the variety of species found in extensive areas of dry forests and savannas. CPNP is a high priority area for biodiversity conservation in Brazil (WWF-Brasil and MMA, 2015), supporting high diversity of endemic species restricted to caves (do Monte et al., 2015; Trajano et al., 2016), several threatened animal and plant species (Geoclock, 2005), and more than 70% of all large mammals found in the Cerrado (Ferreira and Oliveira, 2014). Alongside this impressive biodiversity, the park harbours numerous caves – at least 19 of them are in the area claimed by the Xacriabás – and archaeological sites of international relevance, which is leading to a proposal for recognition of the region as a UNESCO World Heritage site. Currently, the legally designated XIL encompasses 530 km^2 adjacent to CPNP and was established through two decrees, in 1987 and 2003 (ISA, 2018a), following years of struggle for their right to the land (de Almeida, 2006). Approximately 9,000 Xacriabás live in this area (ISA, 2018a) engaged mainly in small scale agriculture and cattle ranching (Clementino and Monte-Mór, 2006; ISA, 2018b; Paraiso, 1987), which are implemented using similar techniques adopted by the local non-indigenous society (Paraiso, 1987).

A study approved by FUNAI (Brazilian government agency for indigenous affairs) argues that the current area does not represent the entirety of the land donated to the Xacriabás in the 18th century and claims an additional 433 km^2 to be designated as indigenous land (FUNAI, 2014), of which around 180 km^2 overlaps with CPNP (Fig. 1A) – mostly in a zone designated to safeguard species and natural habitats of outstanding scientific value according to the national park's management plan (Geoclock, 2005). The remainder of the new claim is privately owned land, part of it designated as a multiple-use protected area (IUCN category V) where human occupation and use of natural resources are permitted. The additional Xacriabá claim has not yet undergone the full legal designation process (FUNAI, 2018) and ICMBio (Brazilian government agency for biodiversity and protected areas) has formally challenged the understanding that the area overlapping with CPNP should be considered part of the indigenous land (ICMBio, 2017a). Recognizing the relevance of such issue a working group has been recently formed by members of CPNP's advisory council to debate this topic (ICMBio, 2017b). This is an ongoing judicial process that may last for a few years with several possible outcomes, ranging from the maintenance of the national park as it is to the *de facto* downsizing of CPNP, with a challenging co-management agreement between ICMBio and the Xacriabás siting anywhere in the middle depending on the restrictions to human activities in the area.

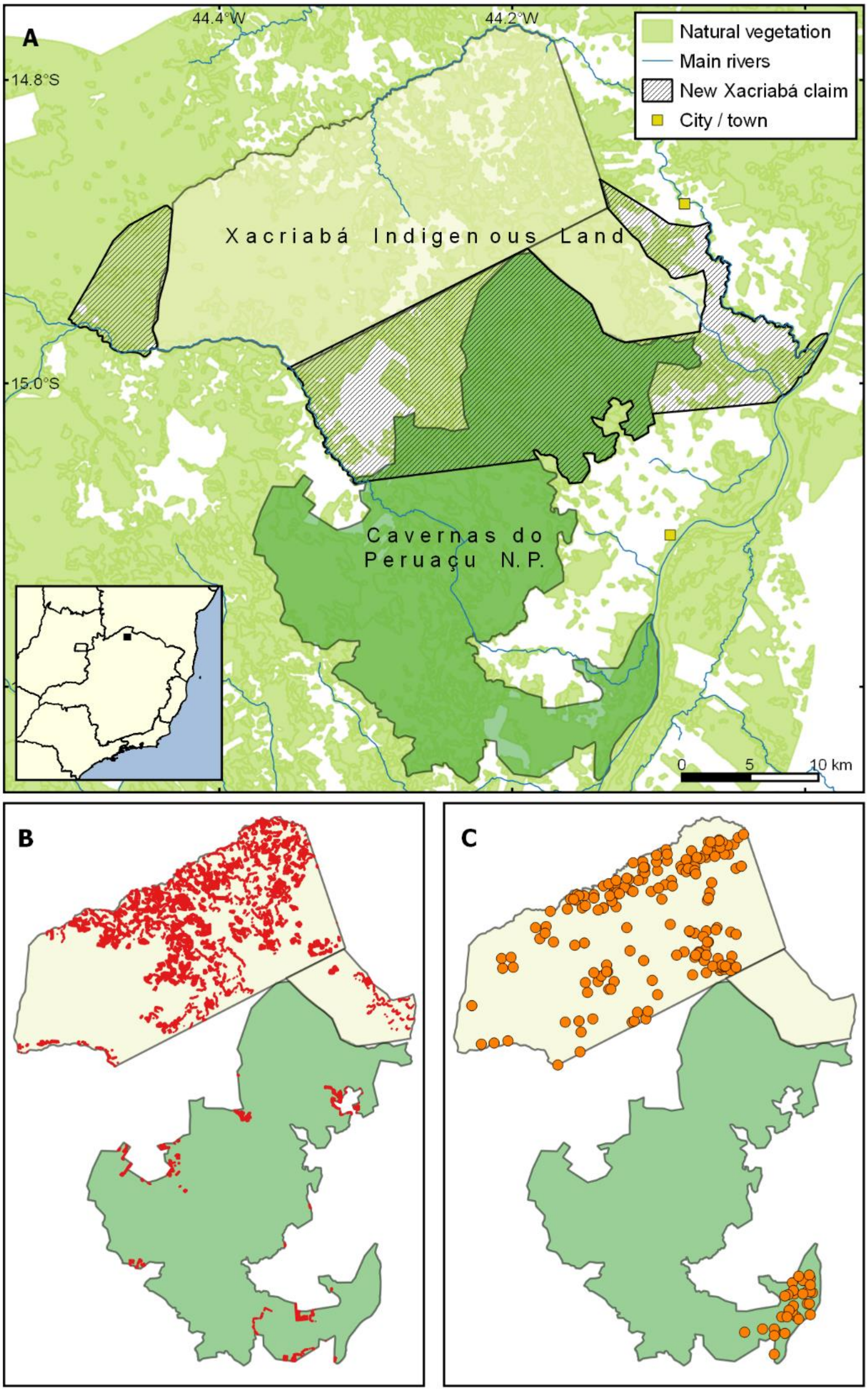

Figure 1: A) Location of Cavernas do Peruaçu National Park, Xacriabá Indigenous Land and the new Xacriabá claim; B) Deforestation between 2010-2012; C) Fire occurrence between 2010-2016.

To help inform this decision-making process from a conservation perspective, I conducted an assessment of potential environmental changes likely to happen at the overlapping area in case anthropogenic pressure increases (driven by direct use or occupation). While this is only one of multiple possible outcomes, such evaluation is needed due to the serious consequences for regional conservation of an eventual *de facto* downsizing of the national park. I must highlight this assessment focus solely on the biodiversity component of a complex issue and does not intend to contest the anthropologic validity of the Xacriabá claim. Furthermore, it is restricted to the overlapping area between the new claim and CPNP, and does not apply to claimed areas outside the national park.

2. Potential negative consequences for Cavernas do Peruaçu National Park

To assess potential changes in vegetation cover at the overlapping area I compared data on deforestation and fire occurrence at CPNP and XIL. I used data on the conversion of natural vegetation between 2010 and 2012 (WWF-Brasil, 2014) and on the occurrence of fires (heat anomalies detected by satellites) between 2010 and 2016 (MCTI/INPE, 2017). To avoid counting the same fire event more than once, I only used data from the reference satellite (AQUA M-T) used by governmental agencies to monitor fires over long temporal series. Although the reference satellite only detects a fraction of all fire events, due to methodological standardizations it provides the most adequate data to investigate spatial and temporal trends in fire occurrence (MCTI/INPE, 2017). Fire data was available for the whole of CPNP and for 86% of XIL (no data available for the Xacriabá-Rancharia area), whereas deforestation data was available for the whole region.

Conversion of natural vegetation and total number of fires are much higher at XIL than at CPNP (Fig. 1B, C). The amount of vegetation lost at XIL was 11 times greater than at CPNP during the period investigated (approximately 5,450 ha vs 480 ha). Similarly, the reference satellite detected five times more fires in the indigenous area than in the national park (171 vs

32) and the annual average of fire occurrence between 2010-2016 was significantly lower at CPNP (24.43 vs 4.57; t-test: t= 3.22, df= 9.16, p= 0.01). Besides the large differences in deforestation and fire occurrence, their spatial distribution also show how anthropogenic pressure is more pervasive at XIL than at CPNP (Fig. 1B, C). Although I did not control for confounding variables because the areas are adjacent, a significant part of the difference can be attributed to their distinct management regimes. Also due to their distinct objectives it was expected that the parameters investigated would have greater values at XIL, but this illustrates the potential changes that may occur if anthropogenic pressure increases in the overlapping area and highlights the need for strict PAs to maintain natural vegetation cover in the region.

This local scale result agrees with recent Cerrado-wide studies showing that although indigenous land usually avoid deforestation, strict PAs are even more effective (Carranza et al., 2014) and that deforestation is lower in strict than in multiple-use PAs, particularly in areas where land tenure issues have been solved (Françoso et al., 2015). Furthermore, subtle habitat degradation that does not result in complete conversion of natural vegetation can have significant impacts on biodiversity (Barlow et al., 2016). Chronic anthropogenic impacts in the Caatinga, such as firewood extraction, selective logging and extensive grazing – all activities likely to happen at the overlapping area of CPNP if direct use is allowed – have been linked to the replacement of old-growth dry forests by shrub-dominated vegetation and to the phylogenetic impoverishment of the flora (Ribeiro et al., 2016, 2015).

To understand the potential effects of increased human pressure on local biodiversity, I used data from a standardized camera trap survey (TEAM Network, 2011) conducted between 22 June and 14 August 2014, in which 60 camera traps (model Bushnell TrophyCam) were deployed at a density of 1 unit per 2 km^2, covering approximately 120 km^2 of the central portion of CPNP. I used the single season occupancy framework (MacKenzie et al., 2006) to investigate the effect of environmental and anthropogenic variables on collared peccaries (*Pecari tajacu*), a species favoured by poachers and hunters throughout the Neotropics (Antunes et al., 2016; Cullen et al., 2000; Urquiza-Haas et al., 2009) and that can be negatively affected if anthropogenic impact is high (Chiarello, 1999; Urquiza-Haas et al., 2011). Occupancy modelling was conducted using the ‘unmarked’ package (Fiske and Chandler, 2011) for R (R Development Core Team, 2015) and following similar procedures as described in Ferreira et al. (2017). To obtain variables for this analysis, I used the software QGIS to extract Euclidian distances from each camera trap site to the nearest river, main road, CPNP’s border and human settlement (regardless of ethnicity). Additionally, I used variables representing cattle frequency at the camera trap site (number of cattle records divided by survey effort) and describing the broad vegetation type of each site (savanna, dense savanna, dry forest). Location of settlements (mostly small rural households) was obtained from data on the Brazilian population in 2010 at 1 km^2 resolution (IBGE, 2017), whereas all other spatial layers were obtained from the economic and ecological zoning platform of Minas Gerais state (SEMAD, 2017).

At CPNP collared peccary occupancy (a measure of probability of using a location) approached zero close to human settlements and increased sharply at sites further away from houses and villages, indicating a negative effect of human presence (Fig. 2). In fact, distance from settlements was the most important factor influencing the species: this variable was present in three of the four top-ranked models explaining the species occupancy. This clear negative anthropogenic effect may be at least partly caused by hunting pressure, an activity that happens in CPNP (pers. obs.), and presumably within XIL. However, the mere presence of humans and the associated noises and smells, as well the presence of domestic dogs, may be enough to create an unfavourable buffer zone for collared peccaries around settlements, in practice reducing the amount of habitat available for the species. I acknowledge that not all species will respond similarly to anthropogenic pressure, but the effect on collared peccary is a plausible model of what may be happening to rare and threatened mammal species that occur in the region, such as white-lipped peccary (*Tayassu pecari*), giant anteater (*Myrmecophaga tridactyla*), and bush dog (*Speothos venaticus*) (Ferreira et al., 2017; Ferreira and Oliveira, 2014), but for which there was not enough data for analysis.

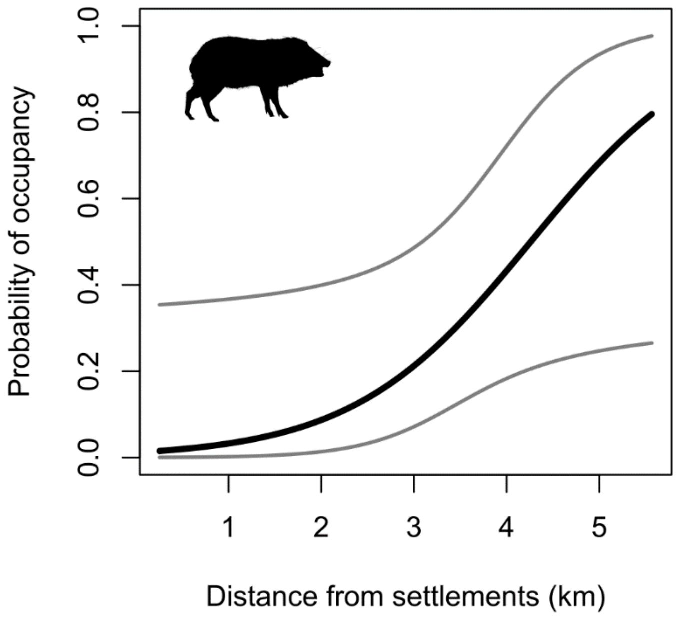

Figure 2: Effect of distance from human settlements on collared peccary occupancy at Cavernas do Peruaçu National Park.

These results indicate that expanding the indigenous land over CPNP has the potential to negatively impact vegetation cover and local biodiversity, influencing the national park's conservation effectiveness. A key assumption, however, is that similar land uses currently happening at XIL would also take place at the overlapping area. Despite the possibility of many levels of natural resource use on indigenous land, this assumption is not unrealistic considering the land use and activities usually developed by the Xacriabás (Clementino and Monte-Mór, 2006; Paraiso, 1987) and that XIL is among the indigenous land with the largest loss of native vegetation in the Cerrado (MMA, 2014) – although FUNAI and the Xacriabás have stated that there is no intention to occupy or use the overlapping area (ICMBio, 2017b). While this commitment is appealing, it is uncertain how feasible it is to be fulfilled given the dynamic nature of human communities and the extent to which the Xacriabás rely on agriculture and cattle ranching. A single disagreement between some of the indigenous leadership could result in a group demanding direct use of the overlapping area, ultimately compromising their conservation commitment.

In case that the disputed area is eventually designated as indigenous land (after the full legal process), a co-management agreement between ICMBio and Xacriabás seems to be the approach favoured by FUNAI and at least some of the indigenous leadership (ICMBio, 2017b). Although such an agreement is possible in theory (e.g. Cundill et al., 2013), it is likely to be extremely challenging in practice due to the distinct objectives of an indigenous land and a national park, as well as the contrasting levels of natural resource use and human occupation allowed in those areas – not to mention two different governmental agencies under different ministries. For instance, Zanatto (2016) reports that formal agreements to manage fisheries and regulate cattle ranching in an overlapping area between indigenous land and Araguaia National Park in central Brazil is not being followed by any of the stakeholders involved. A hint on how challenging an agreement at CPNP would be comes from the report characterising the Xacriabá claim (FUNAI, 2014): it mentions the potential for a joint administration of the area overlapping CPNP, as long as the uses and traditions of the Xacriabás are considered. However, most, if not all, direct uses would immediately clash with the national park regulations (Brasil, 2000), restricting the breadth of activities allowed in the area. In view of this, a co-management solution where the national park objectives are achieved and the Xacriabá uses and traditions are implemented seems to be an extremely optimistic win-win situation, which would not only be hard to achieve, but could also generate conflicts and be harmful to the current respectful relationship between ICMBio, FUNAI and the Xacriabás.

3. Final remarks and recommendations

The number of overlap cases between strict PAs and indigenous land in Brazil (Madeira et al., 2015) suggests that several managers and organizations have faced similar issues as the ones currently affecting CPNP. Useful lessons should be learnt from these situations, so that future decisions are based on past experiences and evidence. However, the existing literature on this topic focus largely on describing the anthropological and legal aspects of individual cases, with very few broadly applicable recommendations. Systematic assessments of environmental changes (particularly in vegetation, given the availability of satellite images) in consolidated or ongoing land claims over PAs would help to understand the trade-offs involved and, more importantly, could objectively inform in which context negative consequences for biodiversity are more likely to happen. Without adequate and objective information the debate will be based on big assumptions and wishful thinking, frequently becoming ideological and making it hard to reach a compromised solution. Furthermore, to achieve solutions and avoid future overlap cases, communications between conservation and indigenous agencies must be improved so they can act synergistically, instead of competing for the same piece of land. Finally, in cases where the geographical overlap exists and there is also an overlap of objectives (for instance, ICMBio, FUNAI and Xacriabá leaders all agree that the overlap area at CPNP should be protected and not have direct use – ICMBio, 2017b), the solution most likely to achieve the common goal should be adopted. At CPNP it seems that the most effective solution to safeguard native vegetation and biodiversity is to maintain the national park's integrity without overlap with indigenous land.

Impacts caused by indigenous peoples are certainly not the main reason behind the dire status of many species and ecosystems in Brazil. However, in a context of widespread conversion of natural areas (such as in the Cerrado, Caatinga and Atlantic Forest) and of indigenous groups adopting productive techniques of the non-indigenous society, their impacts on the ecosystem become significant and a trade-off between the use of natural resources and biodiversity conservation will often exist in land claims over strict PAs. I am not here questioning the legitimacy of expanding and creating indigenous land, neither its overall relevance in avoiding deforestation and holding back the agricultural frontier (e.g. Carranza et al., 2014; Nepstad et al., 2006). Also, I am not arguing that lands managed by Xacriabás are devoid of conservation value; the currently designated XIL still holds a fair amount of native vegetation cover and have a role to play in the regional conservation context. However, expanding this indigenous land over CPNP is likely to negatively impact the national park. The data I presented here strongly suggest that an intensification of human activity or presence in the overlapping area between CPNP and the new Xacriabá claim will result in loss of native vegetation, increase in the number of fires and, will possibly have a negative effect on populations of more sensitive species, such as the collared peccary. In fact, similar impacts have been observed following the establishment of indigenous lands over other strict PAs in Brazil, such as fires negatively affecting the natural vegetation at Araguaia National Park (Zanatto, 2016), clearing of old growth forests at Monte Pascoal National Park (Timmers, 2004), and negative impact on large mammals and birds at Ilha do Cardoso State Park (Olmos et al., 2004).

Given the potential negative effects and the prospects of a challenging co-management between ICMBio and the Xacriabás, I argue against expanding the indigenous land at the expense of the already reduced area under strict protection in the Cerrado and Caatinga (3.1 and 2%, respectively - Brandão and Françoso, 2017; MMA, 2017). A mix of policies have recently been proposed to avoid the collapse of Cerrado's biodiversity (Strassburg et al., 2017) and key among them is the extension of the PA network, which is also one of the main objectives of an inter-ministry action plan for preventing deforestation and fires in the Cerrado (MMA, 2014). Therefore, putting CPNP at risk is certainly not contributing towards these long-term goals and is unlikely to be a sound decision for the conservation of biodiversity in northern Minas Gerais, or elsewhere in the Cerrado and Caatinga.

Conflicts of interest

The author used to be member of CPNP's advisory council representing Instituto Biotrópicos, which still composes the council.

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References

Antunes, A.P., Fewster, R.M., Venticinque, E.M., Peres, C.A., Levi, T., Rohe, F., Shepard, G.H., 2016. Empty forest or empty rivers? A century of commercial hunting in Amazonia. Sci. Adv. 2.

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M., Manica, A., 2009. A global perspective on trends in nature-based tourism. PLoS Biol. 7, e1000144. doi:10.1371/journal.pbio.1000144

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, Thomson, J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C. de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature. doi:10.1038/nature18326

Bernard, E., Penna, L.A.O., Araújo, E., 2014. Downgrading, downsizing, degazettement, and reclassification of protected areas in Brazil. Conserv. Biol. 28, 939–50. doi:10.1111/cobi.12298

Brandão, R.A., Françoso, R.D., 2017. Unidades de Conservação e garantias à preservação da biodiversidade no Bioma Caatinga: Uma Introdução, in: Valtuille, T., Ubaid, F.K., Santana, M.L.C., Castro, S.V., Brandão, R.A., Françoso, R.D., Cavalcanti, R.B., Carquejo, J., Abrão, L. (Eds.), Conservação Do Jacu Do Nordeste: Um Estudo Na Caatinga Brasileira. SAMEC, Florianópolis, Brazil, pp. 21–39.

Brasil, 2000. SNUC – Sistema Nacional de Unidades de Conservação da Natureza: Lei nº 9.985, de 18 de julho de 2000.

Carranza, T., Balmford, A., Kapos, V., Manica, A., 2014. Protected Area Effectiveness in Reducing Conversion in a Rapidly Vanishing Ecosystem: The Brazilian Cerrado. Conserv. Lett. 7, 216–223. doi:10.1111/conl.12049

Chiarello, A.G., 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol. Conserv. 89, 71–82. doi:10.1016/S0006-3207(98)00130-X

Clementino, A.M., Monte-Mór, R.L., 2006. Xakriabás - economia, espaço e formação de identidade, in: XV Encontro Nacional de Estudos Populacionais. Caxambú, Brazil.

Coetzee, B.W.T., Gaston, K.J., Chown, S.L., 2014. Local scale comparisons of biodiversity as a test for global protected area ecological performance: a meta-analysis. PLoS One 9, e105824. doi:10.1371/journal.pone.0105824

Cullen, L., Bodmer, R.E., Valladares Pádua, C., 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. Biol. Conserv. 95, 49–56. doi:10.1016/S0006-3207(00)00011-2

Cundill, G., Thondhlana, G., Sisitka, L., Shackleton, S., Blore, M., 2013. Land claims and the pursuit of co-management on four protected areas in South Africa. Land use policy 35, 171–178. doi:10.1016/J.LANDUSEPOL.2013.05.016

de Almeida, R.H., 2006. Xakriabá – cultura, história, demandas e planos. Rev. Estud. e Pesqui. 3, 9–39.

do Monte, B.G.O., Gallão, J.E., von Schimonsky, D.M., Bichuette, M.E., 2015. New records of two endemic troglobitic and threatened arachnids (Amblypygi and Opiliones) from limestone caves of Minas Gerais state, southeast Brazil. Biodivers. data J. e5260. doi:10.3897/BDJ.3.e5260

Ferreira, G.B., Ahumada, J.A., Oliveira, M.J.R., de Pinho, F.F., Barata, I.M., Carbone, C., Collen, B., 2017. Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado. Biotropica 49, 734–744. doi:10.1111/btp.12450

Ferreira, G.B., Oliveira, M.J.R., 2014. Descobrindo os mamíferos – um guia para as espécies do norte de Minas Gerais/Discovering mammals – a guide to the species of northern Minas

Gerais, 1st ed. Biografa, Januária, Brazil.

Fiske, I.J., Chandler, R.B., 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23. doi:10.1002/wics.10

Françoso, R.D., Brandão, R., Nogueira, C.C., Salmona, Y.B., Machado, R.B., Colli, G.R., 2015. Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. Nat. Conserv. 13, 35–40. doi:10.1016/j.ncon.2015.04.001

FUNAI, 2018. Índios no Brasil [WWW Document]. URL http://www.funai.gov.br/index.php/indios-no-brasil/terras-indigenas (accessed 1.29.18).

FUNAI, 2014. Resumo do relatório circunstanciado de reestudo de limites da Terra Indígena Xacriabá. Diário Of. da União 192, 06 Oc, 30–36.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol. Conserv. 161, 230–238. doi:10.1016/j.biocon.2013.02.018

Geoclock, 2005. Plano de Manejo do Parque Nacional Cavernas do Peruaçu. Brasília, Brazil.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat. Commun. 7, 12306. doi:10.1038/ncomms12306

IBGE, 2017. Downloads IBGE [WWW Document]. URL https://downloads.ibge.gov.br/ (accessed 7.5.17).

ICMBio, 2017a. Ata da VIII reunião ordinária do conselho consultivo da Área de Proteção Ambiental Cavernas do Peruaçu e do Parque Nacional Cavernas do Peruaçu.

ICMBio, 2017b. Ata da II reunião extraordinária do conselho consultivo da Área de Proteção Ambiental Cavernas do Peruaçu e do Parque Nacional Cavernas do Peruaçu.

ISA, 2018a. Terras Indígenas no Brasil [WWW Document]. URL https://terrasindigenas.org.br/ (accessed 1.29.18).

ISA, 2018b. Povos Indígenas no Brasil [WWW Document]. URL https://pib.socioambiental.org/pt (accessed 1.29.18).

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy estimating and modeling – inferring patterns and dynamics of species occurrence. Elsevier Academic Press, London, UK.

Madeira, J.A., Abirached, C.F. de A., Francis, P. de A., Castro, D. de M.P. de, Barbanti, O., Cavallini, M.M., Melo, M.M. de, 2015. Interfaces e sobreposições entre Unidades de Conservação e territórios de povos e comunidades tradicionais: dimensionando o desafio, in: VII Seminário Brasileiro Sobre Áreas Protegidas E Inclusão Social. Florianópolis, Brazil, pp. 617–626.

Mascia, M.B., Pailler, S., 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. Conserv. Lett. 4, 9–20. doi:10.1111/j.1755-263X.2010.00147.x

MCTI/INPE, 2017. Plataforma digital para monitoramento e alerta de fogo na vegetação no Cerrado brasileiro [WWW Document]. URL https://prodwww-queimadas.dgi.inpe.br/bdqueimadas# (accessed 9.11.17).

MMA, 2017. Cadastro Nacional de Unidades de Conservação [WWW Document]. URL www.mma.gov.br/cadastro_uc (accessed 9.11.17).

MMA, 2014. Plano de Ação para Prevenção e Controle do Desmatamento e das Queimadas no Cerrado. Brasília, Brazil.

Nepstad, D., Schwartzman, S., Bamberger, B., Santilli, M., Ray, D., Schlesinger, P., Lefebvre, P., Alencar, A., Prinz, E., Fiske, G., Rolla, A., 2006. Inhibition of Amazon Deforestation and Fire by Parks and Indigenous Lands. Conserv. Biol. 20, 65–73. doi:10.1111/j.1523-1739.2006.00351.x

Olmos, F., São Bernardo, C.S., Galetti, M., 2004. O impacto dos Guarani sobre Unidades de Conservação em São Paulo, in: Fany, R. (Ed.), Terras Indígenas & Unidades de Conservação Da Natureza: O Desafio Das Sobreposições. ISA, São Paulo, Brazil, pp. 246–261.

Paraiso, M.H.B., 1987. Identidade étnica dos Xakriabá - Laudo antropológico. Salvador, Brazil.

R Development Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B., 2010. Biodiversity conservation: challenges beyond 2010. Science 329, 1298–1303. doi:10.1126/science.1189138

Ribeiro, E.M.S., Arroyo-Rodriguez, V., Santos, B.A., Tabarelli, M., Leal, I.R., 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. J. Appl. Ecol. 52, 611–620. doi:10.1111/1365-2664.12420

Ribeiro, E.M.S., Santos, B.A., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G., Leal, I.R., 2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology 97, 1583–1592. doi:10.1890/15-1122.1

SEMAD, 2017. Zoneamento Ecológico-Econômico de Minas Gerais [WWW Document]. URL http://geosisemanet.meioambiente.mg.gov.br/zee/ (accessed 8.19.17).

Soares-Filho, B., Moutinho, P., Nepstad, D., Anderson, A., Rodrigues, H., Garcia, R., Dietzsch, L., Merry, F., Bowman, M., Hissa, L., Silvestrini, R., Maretti, C., 2010. Role of Brazilian Amazon protected areas in climate change mitigation. Proc. Natl. Acad. Sci. U. S. A. 107, 10821–6. doi:10.1073/pnas.0913048107

Strassburg, B.B.N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A.E., Oliveira Filho, F.J.B., Scaramuzza, C.A. de M., Scarano, F.R., Soares-Filho, B., Balmford, A., 2017. Moment of truth for the Cerrado hotspot. Nat. Ecol. Evol. 1, 99. doi:10.1038/s41559-017-0099

TEAM Network, 2011. Terrestrial vertebrate (camera trap) monitoring protocol, v.3.1. Arlington, USA.

Timmers, J.-F., 2004. Respeitar a vida e o ser humano: a preservação do meio ambiente com e pelos índios evita a definitiva condenação da biodiversidade, in: Ricardo, F. (Ed.), Terras Indígenas & Unidades de Conservação Da Natureza: O Desafio Das Sobreposições. ISA, São Paulo, Brazil, pp. 174–187.

Trajano, E., Gallão, J.E., Bichuette, M.E., 2016. Spots of high diversity of troglobites in Brazil: the challenge of measuring subterranean diversity. Biodivers. Conserv. 25, 1805–1828. doi:10.1007/s10531-016-1151-5

Urquiza-Haas, T., Peres, C.A., Dolman, P.M., 2011. Large vertebrate responses to forest cover and hunting pressure in communal landholdings and protected areas of the Yucatan Peninsula, Mexico. Anim. Conserv. 14, 271–282. doi:10.1111/j.1469-1795.2010.00426.x

Urquiza-Haas, T., Peres, C.A., Dolman, P.M., 2009. Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico. Biol. Conserv. 142, 134–148. doi:10.1016/j.biocon.2008.10.007

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67–73. doi:10.1038/nature13947

WWF-Brasil, 2014. Alteracão do Uso e Cobertura do solo - Mosaico Sertão Veredas Peruaçu/MG. Brasília, Brazil.

WWF-Brasil, MMA, 2015. Áreas prioritárias para conservação da biodiversidade no Cerrado e Pantanal. Brasília, Brazil.

Zanatto, V.G., 2016. Conflitos entre Unidades de Conservação e Terras Indígenas: o caso da ilha do Bananal - TO. Meridiano - Rev. Geogr. 5, 145–164.

Appendix 2: First ever record of a black-coloured maned wolf

This appendix reports on the first records of a black-coloured maned wolf (*Chrysocyon brachyurus*) obtained through camera trapping at the Veredas do Acari Sustainable Reserve, part of the Sertão Veredas-Peruaçu mosaic. It has been published as:

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First ever record of a black-coloured maned wolf

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Abstract

Records of atypical black individuals of Neotropical canids are extremely rare. Here we report the first record ever of a black-coloured maned wolf (*Chrysocyon brachyurus*), either wild or in captivity. Using camera traps to survey a protected area in the Brazilian Cerrado we obtained 30 maned wolf photographic records, 25 in its common reddish colour and five (16.6% of the records) in the previously unknown black phenotype. We suggest this is possibly an independent event of melanism in canids, discuss its potential evolutionary benefits and give recommendations for further research.

Keywords

Maned wolf; *Chrysocyon brachyurus*; black phenotype; melanism; coat colour; Brazil; Minas Gerais; Cerrado; camera trap

Article

Colouration in animals has many functions and is often influenced by genetic and environmental factors (Hubbard et al. 2010). According to Caro (2005), it has three primary purposes: concealment, communication, and regulation of physiological processes. Despite colouration`s vital role for species, individuals of unusual colours can arise in a population. If this atypical coloured specimens perform in the same way or better than the regular coloured individuals, the new colouration may be retained in the population for several generations and become relatively common, such as in the melanistic wolves (*Canis lupus*) of western North America (Musiani et al. 2007) and leopards (*Panthera pardus*) in south-east Asia (Kawanishi et al. 2010).

Descriptions of atypically coloured specimens of carnivores are frequent in the literature (Delibes et al. 2013), and melanism has been observed in species of the canid (Apollonio et al. 2004), felid (Eizirik et al. 2003), viverrid (Gaubert and Mézan-Muxart 2010) and mustelid (Hosoda et al. 2005) families. For Neotropical carnivores, black phenotypes have been reported for several felid species (Eizirik et al. 2003; Schneider et al. 2012), however, apart from the report of near-melanistic hoary foxes (*Lycalopex vetulus* - Cabrera 1931; Vieira 1946), there is no record of atypical black individuals for Neotropical canids (Sillero-Zubiri et al. 2004).

The maned wolf (*Chrysocyon brachyurus* Illliger, 1815) is a Near-Threatened omnivorous and generally solitary canid that inhabits grasslands and savannas in central South America (Dietz 1985; Paula & DeMatteo 2015). The species has a unique appearance, with a distinctive reddish coat colour, slender and tall body, short tail, long legs and ears. The typical maned wolf colouration is so characteristic that the species' Latin name makes reference to it (*Chrysocyon*: golden dog). Here we report what is, to the best of our knowledge, the first ever record of a black-coloured maned wolf, either wild or in captivity.

Located in northern Minas Gerais state, in Brazil, Veredas do Acari Sustainable Reserve (VASR – Fig. 1) protects 600 km2 of savanna vegetation (typical Cerrado ecosystem physiognomy; sparse trees and large shrubs about 2-8 m tall with a grass layer at the ground level – Ratter et al. 1997) and veredas (humid grasslands along water courses and dominated by the palm species Mauritia flexuosa). Inside the reserve there are also some anthropogenic habitats created prior to its establishment. In 2013, three VASR rangers were trained on the basic use of camera traps with the objective of conducting a preliminary survey of medium- and large-sized mammal species in the protected area. They deployed six 35mm film camera traps with passive infrared sensor (model Tigrinus 6.0c) on internal roads and animal trails within the two major vegetation types found at the protected area. Camera traps were attached to trees at 25-30 cm from the ground and no bait was used to attract animals. Each camera trap site was surveyed for at least one month, after which park rangers were free to move the unit to another sampling site or to leave it for another 30-days period in the same location.

Camera trapping was conducted from May to December 2013 and overall 20 different sites were surveyed (Fig. 1). The maximum distance between camera trap sites was 22 km, whereas the minimum was 0.4 km. Due to the limited training given to park rangers and the fairly complex camera trap model used (date and time of the photo is stored in a data logger, not printed on the film) we could not retrieve information about date and time of the photographic records. Similarly, although reserve rangers recorded the geographic coordinates of each camera trap site, we were unable to accurately link each photo with its exact location due to missing information on field forms. Nevertheless, we were still able to associate each photograph film with a broad geographic portion of the reserve and also, based on the background of the photo, to identify records from the same sampling site. While this situation is not ideal, it does not compromise the main objective of this manuscript: report the first record of a black maned wolf.

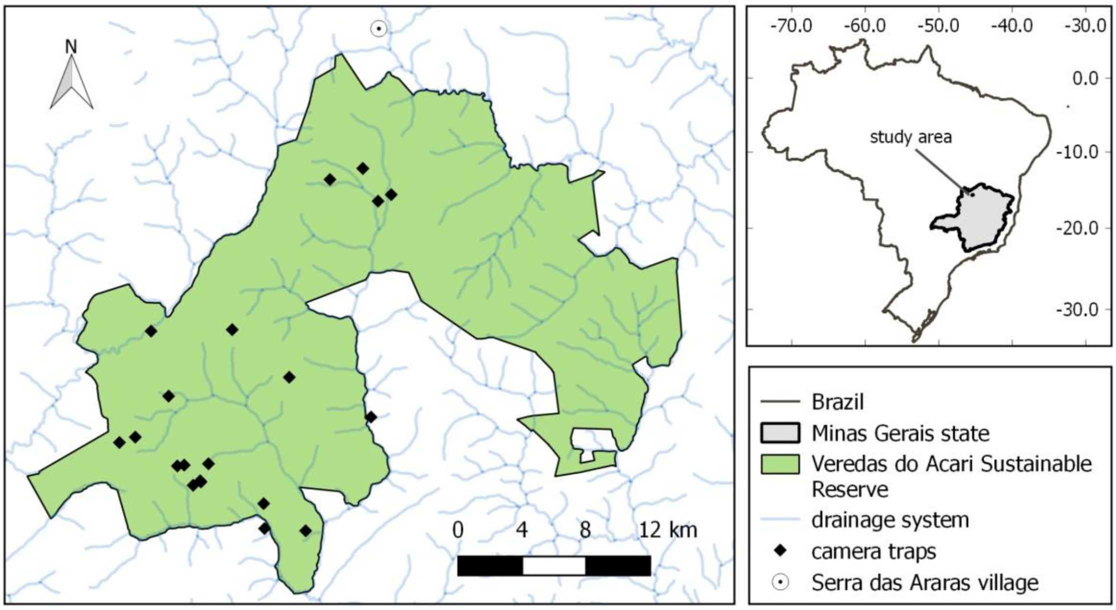

Figure 1: Camera trap sites surveyed at Veredas do Acari Sustainable Reserve, south-eastern Brazil. Inset shows study area location in northern Minas Gerais state, Brazil.

Ten species of medium- and large-sized mammals were recorded at VASR during the study (Table 1), including records of the unusually coloured maned wolf (Fig. 2a, b). Maned wolves were recorded in 30 photographs, 25 in its common reddish colour (Fig. 2c) and five in the previously unknown black phenotype (Fig. 2a, b), which represents 16.6% of the species' photographic records. The species is frequently recorded in northern Minas Gerais (Fundação Pró-Natureza 2003; Ferreira et al. 2017), including a private reserve close to VASR (Ferreira and Oliveira 2014), and in other regions of the Cerrado (Rodden et al. 2004), but a black maned wolf had never been recorded before, either by camera trap or any other means. In the past, few reports of local people described the observation of a black maned wolf roaming in the region, but these reports were never confirmed.

The black-coloured animal in the camera trap photographs has all the distinctive morphological characteristics of a typical maned wolf. However, its coat is very dark and relatively homogenously coloured, varying from dark brown to black, with the reddish colouration totally absent (Fig. 2a, b). The white patch on the throat is also absent, although the tip of the tail is still white (Fig. 2b). As in regular-coloured maned wolves (Fig. 2c), the legs appear to be darker than the rest of the body. Interestingly, a similar colouration pattern is observed on maned wolf cubs in their first weeks: an entirely dark brown/blackish coat (Dietz 1985).

Camera trap records of the black-coloured maned wolf were obtained in five different sampling sites located in the central and south-western portions of the reserve, always at night time (or at least with minimal sunlight since the camera flash was triggered in all records). Considering the maximum distance between camera trap sites, the species relatively large home-range (Jácomo et al. 2009) and the presence of a single animal in each photo, it is possible that all photographic records came from the same individual. Therefore, at this stage we cannot say that there was more than one black maned wolf living at VASR at the time of our survey. Records of regular-coloured and black animals in the same location happened in two camera trap sites, showing that both forms used the same area.

Table 1: Mammal species recorded using camera traps at Veredas do Acari Sustainable Reserve, south-eastern Brazil.

Scientific name	Common name
Pilosa	
Myrmecophaga tridactyla	Giant anteater
Carnivora	
Leopardus pardalis	Ocelot
Leopardus tigrinus	Oncilla
Puma concolor	Puma
Cerdocyon thous	Crab-eating fox
Chrysocyon brachyurus	Maned wolf
Perissodactyla	
Tapirus terrestris	Lowland tapir
Artiodactyla	
Pecari tajacu	Collared peccary
Mazama gouazoubira	Gray brocket deer
Ozotoceros bezoarticus	Pampas deer

Figure 2: Camera trap photographs of maned wolves (*Chrysocyon brachyurus*) with different coat colours at Veredas do Acari Sustainable Reserve, south-eastern Brazil. **a** and **b** records of a black maned wolf, in **b** it is possible to note a lighter-coloured patch in the tip of the tail; **c** regular-coloured maned wolf, highlighting the darker legs in relation to the body.

In spite of the large number of melanistic carnivore species, unusual black individuals in canids are known mostly for the *Canis* genus, such as wolf (Anderson et al. 2009), coyote (*Canis latrans* – Mowry and Edge 2014) and golden jackal (*C. aureus* – Ambarli and Bilgin 2013).

For *C. lupus* and *C. latrans*, molecular evidence suggests the mutation for melanism occurred first in domestic dogs with later introgression to wild animals through hybridization (Anderson et al. 2009). This mutation happened possibly around 45,000 years ago (Anderson et al. 2009), millions of years after the divergence between maned wolf and grey wolf (Wang et al. 2004), indicating possible independent events of melanism mutations. Interestingly, independent melanism events have been confirmed in Felidae, with at least four independent genetic origins in this family (Eizirik et al. 2003). Due to the phylogenetic distance between *Canis lupus* and maned wolves (Wang et al. 2004; Prevosti 2010), a recent (<15,000 ybp) mutation introgression from domestic dogs to the South American canid through hybridization is unlikely – and despite rumours, a hybrid between those two species has never been recorded. A more feasible explanation for the black coat in maned wolf is an independent genetic mutation for melanism, which could, among other possibilities, involve a mutation that favours the retention of the cub colour in an adult individual.

Melanism has clearly adaptive value for some species. The appearance or proliferation of melanic forms of some insects since industrialization is probably one of the best examples of Darwinian evolution in the wild (Majerus and Mundi 2003). Correlations between coat pattern and habitat have also been observed for some mammals (Dice 1947; Hoekstra et al. 2005; Musiani et al. 2007), indicating that colouration has adaptive value by either decreasing the probability of being detected by predators or increasing predation efficiency. In felids, Eizirik et al. (2003) suggested that in certain ecological circumstances melanistic individuals may have an adaptive advantage over their regular-coloured conspecifics. For the black maned wolf, however, it is unclear if the dark colouration has any adaptive value and we can only speculate the potential advantages of such colour.

The individual photographed is an adult and apparently healthy specimen. Thus, the uniform black coat did not prevent it from achieving adulthood – though this observation does not prove that the survival rate of black maned wolves is similar to the regular coloured individuals. Because roughly 50% of the maned wolf diet is composed of vertebrates, especially rodents, armadillos and terrestrial birds (Motta-Júnior et al. 1996; Jácomo et al. 2004; Rodrigues et al. 2007), hunting is an important activity in the species' life. The dark coat may give some advantage when preying upon small preys at night, since against the dark background a darker maned wolf may appear more inconspicuous than a reddish one. Furthermore, as it has been recently observed for oncilla (*Leopardus tigrinus*) (Graipel et al. 2014), melanistic maned wolves may be more active during bright nights than regular-coloured individuals. This would allow black individuals to have longer hunting periods, possibly giving them a slight competitive advantage. To a lesser extent, a black coat may also give adaptive advantage by helping avoid predation by the mostly nocturnal puma (*Puma concolor*), that can prey on maned wolves in some circumstances (Dr. Flavio Henrique Guimarães Rodrigues, pers. comm.). However, predation is probably not a major evolutionary pressure for maned wolves. In any case, we must highlight that these are potential advantages only and we have no data to corroborate them at this point. In fact, the rarity of the black phenotype in maned wolves does not indicate that this form has a higher adaptive value than the typical reddish-coloured animal.

Understanding the evolutionary and ecological implications of the black colouration in maned wolves will only be possible through systematic ecological studies assessing the differences between the two phenotypes. Similarly, only the collection of samples from black maned wolves will elucidate the molecular bases and the mechanism responsible for the black phenotype in this Neotropical canid. We, thus, recommend VASR to be considered a priority site for future studies of maned wolf ecology and genetics, and suggest that this population should be regarded as extremely important for the genetic diversity of the species.

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References

Ambarli, H. and Bilgin, C. 2013. First record of a melanistic golden jackal (*Canis aureus*, Canidae) from Turkey. *Mammalia 77*(2):219-222.

Anderson, T.M., Candille, S.I., Musiani, M., Greco, C., Stahler, D.R., Smith, D.W., Padhukasahasram, B., Randi, E., Leonard, J.A., Bustamante, C.D. and Ostrander, E.A. 2009. Molecular and evolutionary history of melanism in North American gray wolves. *Science* 323(5919): 1339-1343.

Apollonio, M., Mattioli, L. and Scandura, M. 2004. Occurrence of black wolves in the Northern Apennines, Italy. *Acta theriologica* 49(2): 281-285.

Cabrera, A. 1931. On some South American canine genera. *Journal of Mammalogy* 12(1): 54-67.

Caro, T. 2005. The adaptive significance of coloration in mammals. *BioScience* 55(2): 125-136.

Delibes, M., Mézan-Muxart, V. and Calzada, J. 2013. Albino and melanistic genets (*Genetta genetta*) in Europe. *Acta Theriologica* 58(1): 95-99.

Dice, L.R. 1947. Effectiveness of selection by owls of deer mice (*Peromyscus maniculatus*) which contrast with their back-ground. *Contributions from the Laboratory of Vertabrate Biology, University of Michigan* 34: 1–20.

Dietz, J.M. 1985. *Chrysocyon brachyurus*. *Mammalian Species* 234: 1-4.

Eizirik, E., Yuhki, N., Johnson, W.E., Menotti-Raymond, M., Hannah, S.S. and O'Brien, S.J. 2003. Molecular genetics and evolution of melanism in the cat family. *Current Biology* 13(5): 448-453.

Ferreira, G.B., Ahumada, J.A., Oliveira, M.J., Pinho, F.F., Barata, I.M., Carbone, C. and Collen, B. 2017. Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado. *Biotropica* 49(5): 734-744.

Ferreira, G.B. and Oliveira, M.J.R. 2014. *Discovering mammals: a guide to the species of northern Minas Gerais*. Biografa, Januária, Brazil.

Fundação Pró-Natureza. 2003. *Plano de Manejo do Parque Nacional Grande Sertão Veredas*. Ministério do Meio Ambiente, Brasília, Brazil.

Gaubert, P. and Mézan-Muxart, V. 2010. Where have the ‘black genets’ gone? A likely restriction of melanistic cases of the common genet (*Genetta genetta*) to its introduced range. *Mammalian Biology* 75:353–357.

Graipel, M.E., Oliveira-Santos, L.G.R., Goulart, F.V.B., Tortato, M.A., Miller, P.R.M. and Cáceres, N.C. 2014. The role of melanism in oncillas on the temporal segregation of nocturnal activity. *Brazilian Journal of Biology* 74(3): 142-145.

Hoekstra, H.E., Krenz, J.G. and Nachman, M.W. 2005. Local adaptations in the rock pocket mouse (*Chaetodipus intermedius*): natural selection and phylogenetic history of populations. *Heredity* 94:217-228.

Hosoda, T., Sato, J.J., Shimada, T., Campbell, K.L. and Suzuki, H. 2005. Independent nonframeshift deletions in the MC1R gene are not associated with melanistic coat coloration in three mustelid lineages. *Journal of Heredity* 96(5): 607-613.

Hubbard, J.K., Uy, J.A.C., Hauber, M.E., Hoekstra, H.E. and Safran, R.J. 2010. Vertebrate pigmentation: from underlying genes to adaptive function. *Trends in Genetics* 26(5): .231-239.

Jácomo, A.T.A., Silveira, L. and Diniz-Filho, J.A.F. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. *Journal of Zoology* 262(1): 99-106.

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(1): 150-157.

Kawanishi, K., Sunquist, M.E., Eizirik, E., Lynam, A.J., Ngoprasert, D., Wan Shahruddin, W.N., Rayan, D.M., Sharma, D.S.K. and Steinmetz, R. 2010. Near fixation of melanism in leopards of the Malay Peninsula. *Journal of Zoology* 282(3): 201-206.

Majerus, M. E. and Mundy, N.I. 2003. Mammalian melanism: natural selection in black and white. *Trends in Genetics* 19(11): 585-588.

Motta-Junior, J.C., Talamoni, S.A., Lombardi, J.A. and Simokomaki, K. 1996. Diet of the maned wolf, *Chrysocyon brachyurus*, in central Brazil. *Journal of Zoology* 240(2): 277-284.

Mowry C.B. and Edge, J.L. 2014. Melanistic Coyotes in Northwest Georgia. *Southeastern Naturalist* 13(2): 280-287.

Musiani, M., Leonard, J.A., Cluff, H., Gates, C.C., Mariani, S., Paquet, P.C., Vilà, C. and Wayne, R.K. 2007. Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Molecular Ecology* 16(19): 4149-4170.

Paula, R.C. and DeMatteo, K. 2015. *Chrysocyon brachyurus*. *The IUCN Red List of Threatened Species 2015*: e.T4819A88135664. Downloaded on 06 July 2017.

Prevosti, F.J. 2010. Phylogeny of the large extinct South American canids (Mammalia, Carnivora, Canidae) using a “total evidence” approach. *Cladistics* 26(5):456-481.

Ratter, J.A., Ribeiro, J.F. and Bridgewater, S. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. *Annals of Botany* 80: 223-230.

Rodden, M., Rodrigues, F.H.G and Bestelmeyer, S. 2004. Maned wolf (*Chrysocyon brachyurus*). Pp. 38-44 in C. Sillero-Zubiri, M. Hoffmann, D.W. Macdonald (eds.), *Canids: Foxes, Wolves, Jackals and Dogs, Status Survey and Conservation Action Plan.* IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK.

Rodrigues, F.H., Hass, A., Lacerda, A.C., Grando, R.L., Bagno, M.A., Bezerra, A.M. and Silva, W.R. 2007. Feeding habits of the maned wolf (*Chrysocyon brachyurus*) in the Brazilian Cerrado. *Mastozoología Neotropical* 14(1): 37-51.

Schneider, A., David, V.A., Johnson, W.E., O'Brien, S.J., Barsh, G.S., Menotti-Raymond, M. and Eizirik, E. 2012. How the leopard hides its spots: ASIP mutations and melanism in wild cats. *PloS one* 7(12): e50386.

Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. 2004. *Canids: Foxes, Wolves, Jackals and Dogs, Status Survey and Conservation Action Plan.* IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK.

Vieira, C. 1946. Carnívoros do estado de São Paulo. *Papéis Avulsos de Zoologia* 5:1-553

Wang, X., Tedford, R.H., Van Valkenburgh, B., Wayne, R.K. 2004. Evolutionary history, molecular systematics, and evolutionary ecology of Canidae. Pp 39-54 in D.W. Macdonald and C. Sillero-Zubiri (eds.), *Biology and conservation of wild canids*. Oxford University Press, Oxford, UK.

Appendix 3: List of publications

List of published materials during the period I held a PhD scholarship from CNPq (funding agency of Brazil's Ministry of Science):

Newbold T, Adams GL, Robles GA, Boakes EH, Ferreira GB, Chapman AS, Etard A, Gibb R, Millard J, Outhwaite CL, Williams, JJ. 2019. Climate and land-use change homogenise terrestrial biodiversity, with consequences for ecosystem functioning and human well-being. *Emerging Topics in Life Sciences* 3(2):207-219.

Santos PM, Bocchiglieri A, Chiarello AG, Paglia AP,[…] Ferreira GB, et al. 2019. NEOTROPICAL XENARTHRANS: a data set of occurrence of xenarthran species in the Neotropics. *Ecology*. Apr 23:e02663.

Barata IM, Griffiths RA, Ferreira GB. 2018. Activity pattern and behavior of an endemic bromeliad frog observed through camera trapping. *Herpetological Review* 49:432–438.

Coelho EDR, Paglia AP, Viana-Junior AB, Falcão LAD, Ferreira GB. 2018. Species richness, abundance and functional diversity of a bat community along an elevational gradient in the Espinhaço Mountain Range, southeastern Brazil. *Acta Chiropterologica* 20:129–138.

Ferreira GB. 2018. When the blanket is too short: Potential negative impacts of expanding indigenous land over a national park in a high priority area for conservation. *Land Use Policy* 76:359–364.

Pinho FF, Ferreira GB, Barata IM. 2018. Feeding ecology and spraint deposition sites of the Neotropical otter (*Lontra longicaudis*) at Cavernas do Peruaçu National Park, Brazil. *IUCN Otter Specialist Group Bulletin* 35:11–21.

Ferreira GB, Ahumada JA, Oliveira MJR, de Pinho FF, Barata IM, Carbone C, Collen B. 2017. Assessing the conservation value of secondary savanna for large mammals in the Brazilian Cerrado. *Biotropica* 49:734–744.

Ferreira GB, Barros CS, Costa AB, Dias TS, Oliveira MJRR. 2017. First ever record of a black-coloured maned wolf. *Canid Biology & Conservation* 20:42–45.

Pinho FF, Ferreira GB, Paglia AP. 2017. Influence of vegetation physiognomy, elevation and fire frequency on medium and large mammals in two protected areas of the Espinhaço range. *Zoologia* 34:e11921.

Fernandes GW, Pedroni F, Lacerda MS, Scariot A, Aguiar LMS, Ferreira GB, […] Muniz F. 2016. *Cerrado: em busca de soluções sustentáveis*. 211p. ISBN: 978-85-63100-09-2

Barata IM, Correia CM, Ferreira GB. 2016. Amphibian species composition and priorities for regional conservation at the Espinhaço mosaic, Southeastern Brazil. *Herpetological Conservation and Biology* 11:293–303.

Barata IM, Uhlig VM, Silva GH, Ferreira GB. 2016. Downscaling the gap: Protected areas, scientific knowledge and the conservation of amphibian species in Minas Gerais, southeastern Brazil. *South American Journal of Herpetology* 11:34–45.

Aguiar LMS, Machado RB, Françoso RD, Neves AC, Fernandes GW, Pedroni F, Lacerda MS, Ferreira GB, Silva JA, Bustamante M, Diniz S. 2015. Cerrado: Terra incógnita do século 21. Ciência Hoje 55:32–37