ORIGINAL RESEARCH

Limited temporal response of Cerrado mammals to anthropogenic pressure in areas under distinct levels of protection

G. B. Ferreira[1,2,3] (ID), T. Newbold[1], M. J. R. Oliveira[3], H. Pringle[1], M. S. Pinheiro[3], F. F. de Pinho[3,4] (ID), C. Carbone[2,]* & M. Rowcliffe[2,]*

[1]Centre for Biodiversity and Environment Research, University College London, London, UK
[2]Institute of Zoology, Zoological Society of London, London, UK
[3]Instituto Biotrópicos, Diamantina, Brazil
[4]Programa de Pós-graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

Abstract

Anthropogenic pressure has well-documented effects on the spatial distribution of biodiversity but it can also have more subtle effects on wildlife, influencing the time of the day and for how long animals are active. These temporal effects have not received much attention from the scientific and conservation community, despite activity being intrinsically related to crucial aspects in an animal's life. Here we use data from a large-scale camera trap survey (517 survey sites covering more than 1000 km^2) conducted in areas under distinct levels of protection in the Brazilian Cerrado to investigate the effect of anthropogenic pressure on the activity of mammal species >1 kg. We used both circular statistics and GLMMs to investigate whether species would shift activity towards the night in response to disturbance, resulting in a decrease of diurnal activity in areas under lower protection levels and closer to households. Our results revealed that most species investigated did not show a temporal response to anthropogenic pressure, with only two species responding in the way we expected: tamanduas reduced the probability of daytime activity closer to households and collared peccaries reduced diurnal activity slightly in areas under lower protection levels. Our findings also suggest that environmental factors have a greater influence on species' activity than indicators of pressure in the mosaic of protected areas studied. Although stricter levels of habitat protection are known to have a positive and strong influence on the spatial distribution of many mammal species in the study region, we showed here that human pressure has only a modest effect on the period these species were active. This limited temporal response highlights the need for large natural areas under low disturbance that allow mammal species to respond spatially to threats.

Introduction

Anthropogenic pressure has well-documented effects on the spatial distribution of biodiversity (Barlow et al., 2016; Ceballos & Ehrlich, 2002; di Marco & Santini, 2015), 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 (Gaynor, Hojnowski, 2018) and for how long animals are active (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 (Creel & Christianson, 2008; Shamoon et al., 2018), thus potentially affecting reproductive and survival rates. 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 mammal species (Gaynor, Hojnowski, 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 (Oberosler et al., 2017; Reilly et al., 2017). Human activities may also affect animals' activity budget (Marty et al., 2019; Pęksa & Ciach, 2018; Thatcher et al., 2019), which in turn may result in reduced activity levels in areas under greater anthropogenic pressure (Ciuti et al., 2012; Clinchy et al., 2016). However, despite their potential negative effects, changes in activity patterns or in activity levels are not necessarily always detrimental. When a shift in activity does not have a substantial impact on demographic rates, it may be an effective strategy allowing the use of anthropogenic areas that otherwise would be unsuitable. Indeed, a shift from diurnal to nocturnal activity has been shown to enable the use of more disturbed landscapes by a wide variety of mammal species (e.g. Carter et al., 2012; Frey et al., 2020; Gaynor, Branco et al., 2018; Oberosler et al., 2017; Pardo et al., 2021).

In the Neotropics, the effect of distinct types of anthropogenic pressure on mammal activity has been assessed in some studies, revealing shifts in activity patterns but not across all species or regions assessed. For instance, land use intensification was associated with a marked increase in nocturnality for one of four species assessed in the Colombian Llanos (Pardo et al., 2021) and with a slight decrease in diurnal activity in two of four native mesocarnivores investigated in southern Chile (Galvez et al., 2021). In the Ecuadorian Andes, three of seven species assessed changed their activity in response to domestic dogs (Zapata-Ríos & Branch, 2016), whereas all three large herbivores investigated in Argentinean grasslands reduced diurnal activity in the presence of cattle (Di Bitetti et al., 2020). 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 poaching and easier access to humans, but dwarf brocket deer (*M. nana*), jaguarundi (*Herpailurus yagouaroundi*) and margay (*Leopardus wiedii*) did not show a shift in activity (Cruz et al., 2018; Di Bitetti et al., 2008; Paviolo et al., 2009). Human disturbance did not change ocelot (*Leopardus pardalis*) activity in the Peruvian Amazon (Kolowski & Alonso, 2010), but increased its nocturnal activity in the Atlantic Forest (Massara et al., 2018) and the Cerrado (Barcelos et al., in press) of Brazil. Similarly, 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 a large improvement in the knowledge of human impacts on Neotropical mammals' activity patterns, most studies focused on a few species in each locality and on forest ecosystems. Given that environmental factors, such as water availability and canopy cover, also play a role in determining when and for how long animals are active by reducing the thermal stress related to daytime activity (Attias et al., 2018; Cain et al., 2008; Camilo-Alves & Mourão, 2006; Levy et al., 2019; Owen-Smith, 1998), it is important to extend assessments on the effect of anthropogenic

pressure on activity to non-forest ecosystems. Furthermore, despite the establishment of protected areas (PAs) being one of the key interventions adopted worldwide to minimize anthropogenic pressure on biodiversity (Watson et al., 2014), seldom was the effect of habitat protection on activity explicitly investigated in the Neotropics (but see Di Bitetti et al., 2008; Paviolo et al., 2009).

Here, we use data from a large-scale camera trap survey covering more than 1000 km^2 to investigate the effect of anthropogenic pressure on the activity of mammal species >1 kg occurring in a Neotropical savanna, the Brazilian Cerrado. We first compare species' activity patterns and overall activity levels in PAs under two management regimes that provide very distinct levels of protection to anthropogenic pressure. We then assess the effects of protection level and proximity to households on the probability of diurnal activity while accounting for environmental factors that may influence daytime activity. Our study was conducted in a region where strict PAs are known to have a strong positive effect on the spatial distribution of mammal species (Ferreira et al., 2020), we therefore expected that lower levels of protection, as well as proximity to households, would drive some species to shift part of their activity towards the night, reducing the probability of diurnal activity. We expected to observe this response more frequently on diurnal or cathemeral species, as for highly nocturnal species probably only very strong effects would be detected in our analyses (e.g. going from little to no diurnal activity). On the other hand, we did not expect only threatened or persecuted species to respond temporally to pressure, given that changes in activity have also been shown to allow less sensitive species to use disturbed or anthropogenic habitats (e.g. Díaz-Ruiz et al., 2016; Oberosler et al., 2017; Pardo et al., 2021; Reilly et al., 2017). Finally, we did not anticipate a strong effect of protection level on overall activity because the expected shifts in activity patterns would allow species to be active for approximately the same amount of time in both management regimes.

Materials and methods

Study area

We conducted our study at a mosaic of PAs in northern Minas Gerais state (Fig. 1), in a region located within the Brazilian Cerrado, but also encompassing the southern limits of the Caatinga – a xeric ecosystem associated with semi-arid climate. The Sertão Veredas-Peruaçu Mosaic extends over 18 000 km^2 and is formed by 14 PAs of distinct management categories and two indigenous lands. For this study, we surveyed seven PAs under very distinct management regimes: five strict PAs and two large Environmental Protection Areas (herein APAs, according to the Portuguese acronym; Table 1). The strict PAs surveyed include national and state parks (IUCN category II) and a private reserve (RPPN according to the Portuguese acronym; IUCN category IV), all of which have biodiversity conservation as their main goal and similar regulations prohibiting human occupation or direct use of natural resources (Brasil, 2000). On the other hand, APAs (IUCN category V) represent the least restrictive category
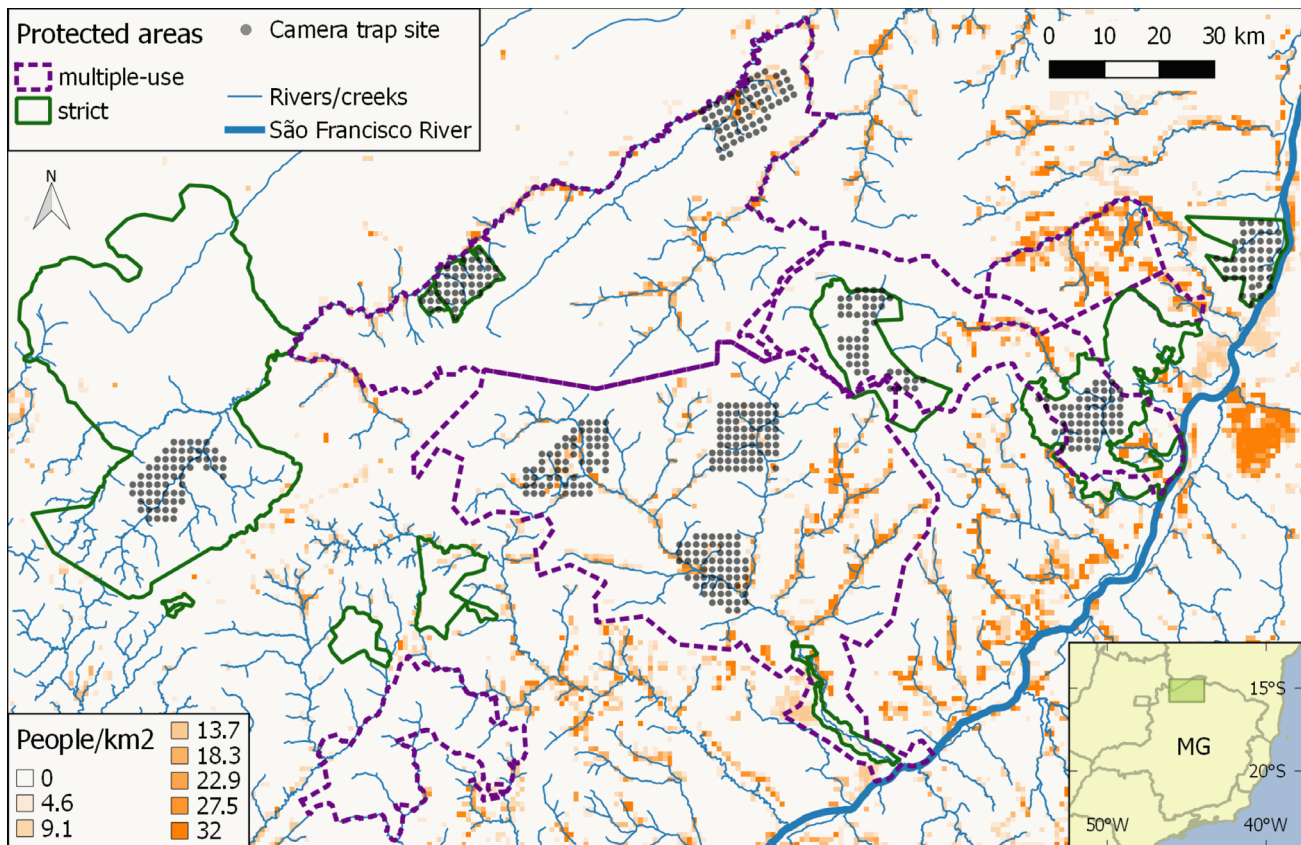
Figure 1 Protected areas, camera trap sites and human density in the Sertão Veredas Peruaçu Mosaic, Brazilian Cerrado. Strict protected areas: IUCN categories I–IV; multiple-use protected areas (include APAs): IUCN categories V–VI. Inset map shows location of study area in southeastern Brazil and Minas Gerais (MG) state.

Table 1 Protected areas surveyed and characteristics of the camera trap arrays deployed in the Sertão Veredas Peruaçu Mosaic, Brazilian Cerrado

Protected Area	IUCN category	Area (km^2)	Camera trap sites	Survey effort (days)	Dist. households (km)[a]	Dist. water (km)[a]	NDVI[a]
Strict protected areas							
Grande Sertão Veredas NP	II	2300	65	3767	12.40	1.35	0.35
Cavernas do Peruaçu NP	II	568	60	2939	3.52	2.58	0.44
Veredas do Peruaçu SP	II	312	50	1826	8.24	4.25	0.34
Mata Seca SP	II	136	46	2085	4.06	2.77	0.44
Porto Cajueiro Private Reserve	IV	90	43	2048	4.01	0.85	0.32
APAs (multiple-use)							
Rio Pandeiros	V	3801					
Array 1			63	3714	1.41	1.19	0.28
Array 2			70	3900	1.71	1.33	0.31
Array 3			60	3302	1.46	1.14	0.34
Cochá Gibão	V	2844	60	2786	1.20	1.18	0.32

NP, National Park; SP, State Park.

[a]Average values across camera trap sites in the same array.

of PA in Brazil, where human settlements and some level of land conversion are permitted (Brasil, 2000; Rylands & Brandon, 2005), and are not effective in avoiding habitat loss in the Brazilian Cerrado (Françoso et al., 2015).

Due to the low levels of restrictions and management interventions, but the high proportion of natural vegetation cover (WWF-Brasil, 2011), the APAs surveyed here provide an adequate counterfactual to investigate the effect of habitat protection

on biodiversity. These APAs have low average human density (2.2 and 1.1 people/km^2; IBGE, 2017) and the population is concentrated in one small town and scattered rural villages connected by unpaved roads. Most local communities engage in small-scale agriculture and cattle ranching, but some properties have converted larger natural areas to pasture (Fig. S1).

Several vegetation formations are found in the study region, from dry forests to savannas with varying densities of trees and shrubs, as well as palm swamps and gallery forests along riparian areas (Fig. S1). The climate is markedly seasonal with a dry season between April and mid-October and a wet season from mid-October to March. The mean average temperature during our core survey period (April to August) was 22.5°C, whereas the mean maximum temperature was 31.4°C – data from INMET (www. inmet.gov.br).

Data collection

Camera trapping

We deployed five camera trap arrays in strict PAs and four arrays in APAs (Fig. 1), adapting a standardized protocol (TEAM Network, 2011). Arrays within APAs were 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 respectively. Additionally, we kept at least 12 km between pairs of camera trap arrays to cover a larger geographic area and minimize spatial non-independence. Only the largest PA had multiple camera trap arrays (Table 1), which surveyed distinct parts of the Pandeiros River basin (Fig. S2).

Each camera trap 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 selected the location deemed most adequate to set up camera traps. Cameras were deployed by only four different researchers to limit variation in deployment, at least 200 m away from households, and only in natural vegetation areas (i.e. pasture or cropland were not surveyed). Due to our systematic distribution of sampling sites, camera trap locations were not biased towards roads or man-made trails.

Overall, we deployed camera traps (Bushnell TrophyCam and Bushnell Agressor) at 517 sampling sites covering approximately 1000 km^2 and totalling 26 367 survey days. Only 8% of the sampling sites were established outside the 50-m buffer due to access conditions, but never more than 200 m away from the pre-determined coordinates. We retained data for analysis from 506 sites where camera traps worked adequately for more than five days (average effort per site: 52 days; 90% surveyed for at least 30 days). Surveys were conducted between 2012 and 2017, always during the dry season, and no lure was used. Camera trap sensitivity was set to 'normal' and a 30-s interval between sequential triggers was observed.

Model covariates

Each survey site was assigned to a management regime according to the PA where it was located: either strict PA or

APA (Fig. 1). To calculate the distance between survey sites and households, we used a spatial layer of human density in 2010 at 1 km^2 resolution (IBGE, 2017) to measure the shortest distance between a camera trap site and the centroid of a cell with human occupation. We could not use human density directly due to the large number of survey sites located in cells with no human occupation, which generated convergence problem in exploratory models. We also used Normalized Difference Vegetation Index (NDVI) and distance to water sources to account for environmental variation that may influence probability of diurnal activity. Mean NDVI of a 500-m buffer around each survey site was calculated from Landsat 8 images following standard formula (Pettorelli et al., 2018). NDVI has been shown to correlate with green cover as well as with vegetation types in the Cerrado (Ferreira et al., 2003). The shortest distance between camera trap sites and water sources was calculated based on a spatial layer of permanent rivers, creeks and lakes (SEMAD, 2017). We could not account for variation in daily temperature because our analysis required data to be aggregated over the camera trap site during the survey and because there is no fine-scale temperature data available for the whole study region. All spatial data were obtained using QGIS (QGIS Development Team, 2017).

Data analysis

Before conducting analysis, we eliminated non-independent records, defined here as sequential records of a species at a single camera trap site with less than 30 min interval between them. We also excluded records for *Dasypus* armadillos as we could not always distinguish between the two species occurring in the region (*D. novemcintus* and *D. septemcinctus*) and they may differ in their activity patterns (Feijó, 2020; Norris et al., 2010). We then used these independent records to investigate the effect of anthropogenic pressure on activity-related parameters using a range of statistical analyses described below and summarized in Table 2.

Daily activity pattern and proportion of time active

To assess the effect of protection level on species activity, we compared daily activity patterns and the proportion of time active (activity level) between strict PAs and APAs for species with at least 25 independent records in each management regime (seven species in total; Table 2 and Table S1). This cut-off point in the number of records is needed to avoid large biases in estimates (Rowcliffe et al., 2014). To assess the overlap in daily activity patterns of a species in each management regime, we used circular kernel density estimation from the 'overlap' package to calculate a coefficient of overlap that ranges from 0 to 1, where 0 indicates completely distinct activity patterns and 1 represents identical patterns (Meredith & Ridout, 2014). Following an assessment from Ridout and Linkie (2009), we adopted Dhat1 as the coefficient when the smallest sample size of the comparison (i.e. strict PAs vs. APAs) was <50 records and Dhat4 for samples >50 records. We then conducted a Watson's two-sample test to determine

Table 2 Parameters and analyses used to investigate the effect of anthropogenic pressure on activity of Cerrado mammals

Parameter	Cut-off	Analysis	References
Daily activity pattern	Species with ≥ 25 records in each management regime (*n* = 7)	Pair-wise comparisons of daily activity patterns in strict PAs and APAs using a Watson's two-sample test to infer statistical difference; estimates of overlap in activity in strict PAs and APAs	Jammalamadaka & SenGupta, 2001; Oliveira-Santos et al., 2013; Ridout & Linkie, 2009
Proportion of time active		Pair-wise comparisons of the proportion of time active in strict PAs and APAs using a Wald test to infer statistical difference	Rowcliffe et al., 2014
Probability of diurnal activity	Species recorded in ≥ 30 camera trap sites (*n* = 14)	GLMs or GLMMs with binomial distribution using the variables: management regime, distance to households, distance to water sources and NDVI	Zuur et al., 2009

whether species' activity patterns were significantly different in strict PAs and APAs (Jammalamadaka & SenGupta, 2001; Oliveira-Santos et al., 2013) via the package 'circular' (Agostinelli & Lund, 2017). To estimate the proportion of time species were active in each management regime, we used the 'activity' package to fit a flexible circular kernel distribution to time-of-detection data followed by a Wald test to check whether the difference between strict PAs and APAs was statistically significant (Rowcliffe et al., 2014).

Probability of diurnal activity

We estimated the probability of diurnal activity for 14 species that were recorded in more than 30 survey sites (Table 2 and Table S1) using generalized linear mixed effects models (GLMMs) with binomial distribution (Zuur et al., 2009) implemented via the package 'lme4' (Bates et al., 2014). We classified each independent record as either diurnal (06:00–17:59 h) or nocturnal (18:00–05:59 h) and modelled probability of diurnal activity as a function of management regime, distance to the nearest household, distance to water sources and NDVI, with camera trap array as a grouping variable determining random intercepts. 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 sunrise and sunset during data collection was minimum (consistently close to 06:00 and 18:00 – NOAA, 2020) and not accounted for in the models.

We started the modelling approach building a global model with the four explanatory variables and with camera trap array determining random intercepts. We first checked estimates of the random component of this model, because mixed-effects models may be unable to estimate the among-population variance if the random variable has less than five levels (Harrison et al., 2018). For 11 out of the 14 species, estimated variance between arrays was very close to 0, indicating the model did not estimate random intercepts and performed as a binomial GLM (Harrison et al., 2018). We also checked this initial global model for convergence and noticed that models for tapir (*Tapirus terrestris*), hoary fox (*Lycalopex vetulus*), yellow armadillo (*Euphractus sexcinctus*) and tamandua (*Tamandua tetradactyla*) had convergence problems. This was due to very

low number of records in one of the management regimes (hoary fox and tapir) or because records at each site were either 100% at night or 100% at daytime (yellow armadillo and tamandua), thus we eliminated management regime from these species' global models.

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. We then selected a top model set for each species including all models up to a summed AICc weight of 0.95 to obtain averaged estimates (Burnham & Anderson, 2002). We implemented model selection and averaging via the package 'MuMIn' (Barton, 2018), and adopted the more conservative approach of averaging estimates across all models in the set (Burnham & Anderson, 2002). All numerical variables were scaled and checked for collinearity before running the models. We also implemented these modelling procedures to estimate the probability of activity in a more restricted period of the day, between 07:00 and 16:00 h (defined as core diurnal activity), when we assumed encounters with people would be more likely.

Finally, we calculated Moran's I values for each species to assess spatial autocorrelation in the data used for the GLMs and GLMMs. There was evidence of spatial autocorrelation only for ocelot and collared peccary, indicating that survey sites were independent for 12 of the 14 species (Table S2). Excluding data from sites ≤2 km away from each other eliminated spatial autocorrelation in the data for ocelot and collared pecary (Table S2) but did not change the interpretation of results (Table S3). We therefore decided to present results using models that relied on the full dataset for all species. All statistical analyses were conducted in R (R Development Core Team, 2018).

Results

Activity under distinct levels of protection

Contrary to our predictions, there was not a clear increase in nocturnality in areas under lower levels of protection for any of the species assessed – although collared peccaries (*Pecari tajacu*) reduced slightly diurnal activity in APAs (Fig. 2).
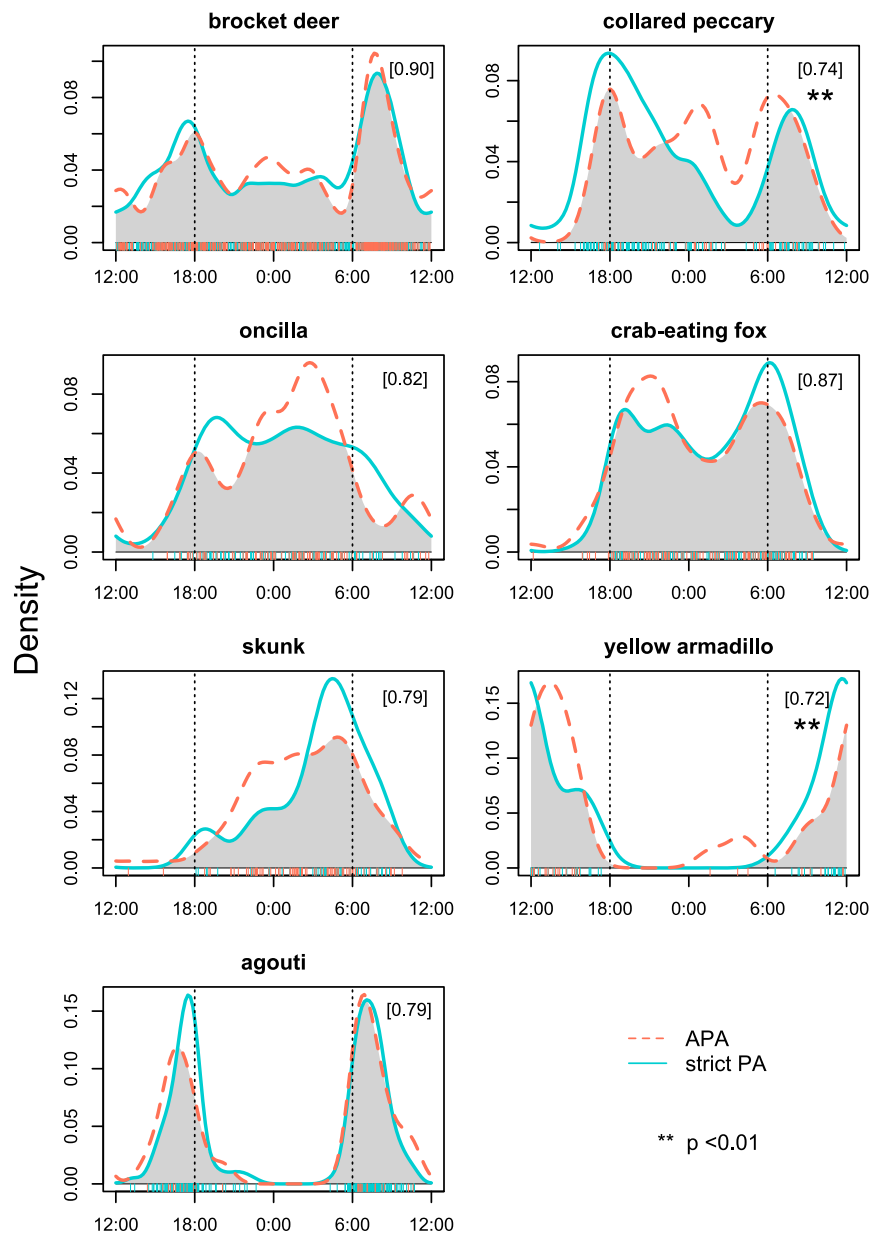
Figure 2 Overlap in daily activity patterns of seven mammal species in areas under distinct levels of protection in the Brazilian Cerrado (APA: red; strict PA: blue). Estimates inside square brackets are the coefficient of overlap (0 indicates no overlap and 1 indicates identical activity pattern). Asterisks indicate p-value of a Watson's two-sample test of homogeneity used to infer whether activity patterns were statistically different between management regimes. Note that plots are centred at midnight (0:00) and dotted lines indicate transition between diurnal and nocturnal periods. See Table S1 for the Latin names for the species.

Daily activity patterns in the two management regimes were similar for five of seven species with enough data to conduct the pair-wise comparisons, with coefficients of overlap around 0.8 or higher. Among those species, grey brocket deer (*Mazama gouazoubira*) and agouti (*Dasyprocta azarae*) had diurnal activity peaks that were virtually at the same time in strict PAs and APAs. Conversely, collared peccary and yellow armadillo (a cathemeral and a diurnal species respectively) had distinct daily activity patterns in each management regime, with lower coefficient of overlap than other species. Collared peccary did show higher levels of activity during the night in APAs, with a third activity peak at around midnight that was not seen in strict PAs (Fig. 2). However, for yellow armadillo the difference seems to be in the peak of activity, which was diurnal in both management regimes but slightly later in APAs (Fig. 2).

On the other hand, confirming our predictions, protection level did not affect the proportion of time species were active (Fig. 3). Oncilla (*Leopardus tigrinus*) was the species with greater variation in activity levels between management regimes, but the difference was not significant (difference: 17.7; Wald test: 3.74 *P*-value: 0.053). For the other six species investigated, the difference between estimates of activity level was less substantial, with brocket deer, crab-eating fox, yellow armadillo and agouti showing very similar activity levels between strict PAs and APAs (Fig. 3).

Probability of diurnal activity

Again, contrary to our predictions, indicators of anthropogenic pressure had very little influence on probability of diurnal activity of 14 mammal species assessed, with the effect of protection level and distance to households often being estimated close to 0 (Fig. 4). Tamandua was the only species that responded to one of the proxies for anthropogenic pressure; it was more likely to be active during daytime further away from households (Fig. 4). At our study region, environmental factors seem to have a greater influence on daytime activity than anthropogenic pressure (Fig. 4). An increase in NDVI, and therefore in vegetation cover, resulted in a higher probability of diurnal activity for agouti and yellow armadillo. Giant anteater (*Myrmecophaga tridactyla*) was more likely to be active during daytime in camera trap sites further away from water sources, whereas the opposite was observed for ocelot.

The additional analysis based on a more restricted diurnal activity (07:00–16:00 h) also revealed little influence of anthropogenic pressure (Fig. S3), with only one species responding to indicators of pressure and not in the direction we anticipated: agouti probability of activity during this core diurnal period was higher closer to households.

Discussion

Effect of anthropogenic pressure on activity

Our results revealed that most mammal species investigated did not change activity due to increased anthropogenic pressure, with protection level and distance to households having little influence on when species were active. Only tamanduas and collared peccaries responded in the way we expected, increasing nocturnal activity in areas under greater pressure. This is very different from findings of a global study showing a consistent increase in nocturnality in mammals as a response to human disturbance (Gaynor, Hojnowski 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 under greater pressure (Cruz et al., 2018; Di Bitetti et al., 2008, 2020; Massara et al., 2018; Norris et al., 2010; Paviolo et al., 2009). Reasons for the limited temporal response observed in our study most likely include the strong spatial response by the local mammal community to protection level (Ferreira et al., 2020), the low diurnal activity
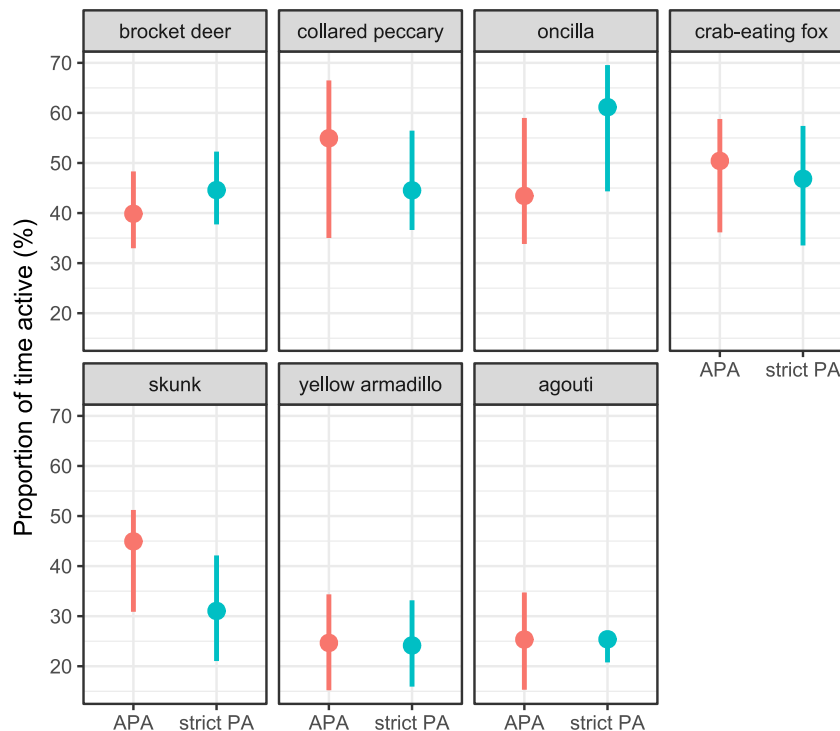

Figure 3 Proportion of time active (activity level) of seven mammal species in areas under distinct levels of protection in the Brazilian Cerrado (APA: red; strict PA: blue). None of the species had a significant difference in activity levels. See Table S1 for the Latin names for the species.
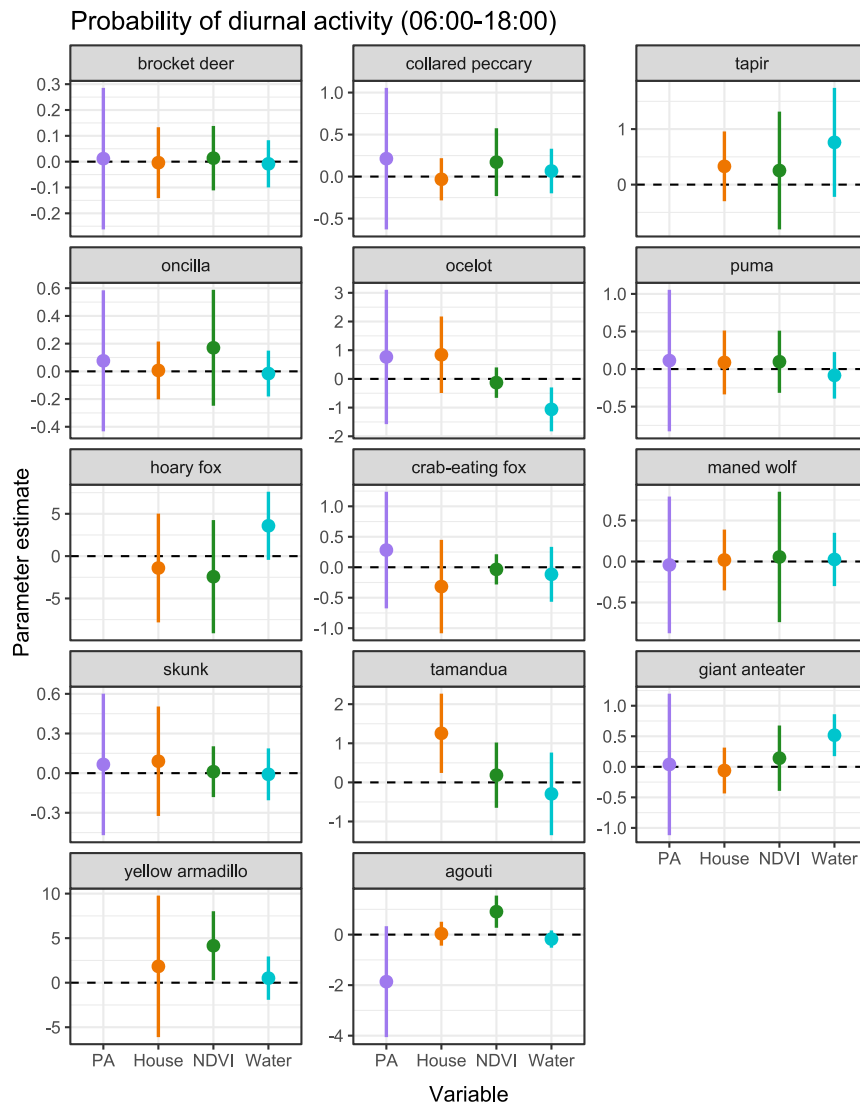
Figure 4 Averaged parameter estimates of models assessing the effect of distinct variables on the probability of diurnal activity (06:00–18:00 h) for 14 mammal species in the Brazilian Cerrado. Positive parameter estimates indicate a higher probability of diurnal activity in strict protected areas (PA), further away from households (House), in sites with greater vegetation cover (NDVI) and further away from water sources (Water). Parameters are on the logit scale and vertical lines represent 95% confidence intervals. Results for brocket deer, crab-eating fox and hoary fox are from a binomial GLMM, whereas for all other species are from a binomial GLM. See Table S1 for the species' Latin names.

among many of the species investigated (overall activity patterns in Fig. S4), and potentially a lack of flexibility in activity pattern in some species due to biological constraints.

The protection level of an area is known to influence greatly the distribution of mammals in the study region and at least six species assessed here (collared peccary, tapir, puma, maned wolf, giant anteater and agouti) have much higher occupancy in strict PAs than in APAs (Ferreira et al., 2020). We believe this spatial response to protection is likely to have contributed to the limited temporal response to anthropogenic pressure. Species that avoided areas under greater anthropogenic pressure (APAs) potentially minimized the need to shift activity pattern

to cope with increased disturbance. The opposite has been reported in several other studies: a shift in species' activity to avoid periods of intense human activity, without changing spatial distribution or abundance (Carter et al., 2012; Oberosler et al., 2017; Ramesh & Downs, 2013; Reilly et al., 2017). There are also instances of species responding both spatially and temporally to human disturbance (Mori, 2017; Shamoon et al., 2018; Zapata-Ríos & Branch, 2016), 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).

Interestingly, hoary fox and probably the crab-eating fox have higher occupancy in the APAs surveyed than in the strict PAs (Ferreira et al., 2020) but they also did not show increased nocturnality in areas under greater human pressure. This could be in part due to their overall low levels of daytime activity, particularly for the former species (Fig. S4). In fact, reduced daytime activity may have also limited the increase of nocturnality in other species in our study: of the 14 species with enough records to investigate the probability of diurnal activity, only grey brocket deer, yellow armadillo and agouti had most of their activity during daytime (Fig. S4). As anticipated, this alone could limit the possibility of observing significant increases in nocturnality in many species – although even the three species with largely diurnal activity did not shift to being more nocturnal under increased anthropogenic pressure. Biological constraints may prevent largely diurnal species becoming more nocturnal as a response to pressure and this may be the case for agouti and yellow armadillo, but not for brocket deer that had substantial nocturnal activity despite the diurnal peaks (Fig. S4).

Although we did not observe consistent changes in activity associated with indicators of anthropogenic pressure, in two cases species changed their activity in response to greater pressure in the way we predicted: tamandua increased the probability of diurnal activity further away from households and collared peccary was moderately more nocturnal in APAs. Collared peccaries are cathemeral animals (Fig. S4), sensitive to anthropogenic pressure (Chiarello, 1999; Urquiza-Haas et al., 2011), they favour strict PAs in the study region (Ferreira et al., 2020), and in one of the national parks surveyed here, their occupancy decreased sharply closer to households (Ferreira, 2018). Cathemeral species may be more flexible in their activity (Galvez et al., 2021) and collared peccary's distinct activity patterns in each management regime (Fig. 2) indicates an additional strategy to cope with anthropogenic pressure, with increased nocturnal activity in APAs. However, the species' probability of diurnal activity was not influenced by anthropogenic factors (Fig. 4) and its strong spatial response to pressure observed previously suggests that a temporal shift in activity may have limited effectiveness in mitigating the negative impacts associated with human presence. Conversely, tamanduas are a non-persecuted species, have a substantial proportion of activity in the night (Fig. S4), and did not respond spatially to protection level in the study region (Ferreira et al., 2020). Nevertheless, their increased nocturnality closer to households also suggests a potential strategy to allow the use of areas under greater human pressure in the study region (but see discussion on Xenarthra activity in the next section). Increasing nocturnal activity close to houses and settlements seems to be a relatively common response in mammals elsewhere and has been reported for many species (Díaz-Ruiz et al., 2016; Gaynor, Branco et al., 2018; Massara et al., 2018; Ohashi et al., 2013; van Doormaal et al., 2015). Finally, in one case activity patterns were significantly different between management regimes, but the species did not respond according to our expectation: yellow armadillos did not increase nocturnal activity in APAs.

Influence of environmental factors on diurnal activity

Environmental factors seem to have a greater influence than human pressure on the probability of mammal species being active during daytime in our study. Greater vegetation cover and availability of water are known to reduce thermal stress in animals (Elmore et al., 2017; Levy et al., 2019; Tuff et al., 2016), which could favour diurnal activity in a region where the daytime temperature reaches around 30°C even in the winter. For example, milder temperatures in areas with greater vegetation cover (Demarchi & Bunnell, 1993; Mourão & Medri, 2007; Pfeifer et al., 2019) may have enabled greater daytime activity in yellow armadillo and agouti. 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, which is not adequately represented by NDVI extracted from a 500-m buffer around the survey site (correlation between NDVI and distance to water: 0.21). In one PA surveyed here, ocelots are known to have unusually high diurnal activity in forest habitats (Barcelos et al., in press). Finally, the probability of daytime activity in giant anteater was also influenced by an environmental factor, but the species increased diurnal activity further away from water, which is contrary to what would have been expected to cope with high temperatures.

Many of the species for which we observed changes in activity are Xenarthras, suggesting this group of species to be more flexible in their activity patterns. All Xenarthras responded to at least one variable in this study and the probability of diurnal activity in two of the three Xenarthra species assessed was influenced by environmental variables. This flexibility could in part be linked to Xenarthra's limited ability to use their metabolism to regulate body temperature (McNab, 1984, 1985) and the adoption of behavioural thermoregulation strategies that include shifts in activity patterns as well as in habitat use in response to variation in air temperature (Attias et al., 2018; Camilo-Alves & Mourão, 2006; Maccarini et al., 2015). However, given the influence of ambient temperature on these species, without fine-scale and daily measurements of temperature we must interpret the shifts in activity presented here cautiously – including tamandua's decrease in diurnal activity closer to households.

Conclusion

We found limited evidence that anthropogenic pressure influenced activity parameters of mammal species in areas under distinct levels of protection in the Brazilian Cerrado. Despite a general global pattern of widespread increases in nocturnality in mammals due to human disturbance (Gaynor, Hojnowski et al., 2018), in our study, only tamanduas and collared peccaries seemed to increase nocturnal activity in areas under greater human influence. At the mosaic of protected areas studied, lower levels of protection have a clear negative impact on the distribution of many mammal species (Ferreira et al., 2020), but we showed here that it has little effect on the period these

species were active. The limited temporal response observed indicates that in some cases activity shifts will not be effective against anthropogenic pressure, highlighting the need for large natural areas under low human pressure that allow mammal species to respond spatially to threats. Our findings also suggest that environmental factors have a greater influence on the probability of diurnal activity than indicators of anthropogenic pressure in the study region. In fact, the relationship between environmental conditions, ambient temperature 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.

Acknowledgements

Conflict of interest

GBF was part of SVP's advisory council between 2010 and 2016 and part of Cavernas do Peruaçu National Park's council between 2014 and 2016; MSP was also a member of this park's council between 2016 and 2018. IDESE manages the private reserve (RPPN) surveyed.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Land use and land cover in the Sertão Veredas-Peruaçu Mosaic. Yellow stars indicate the location of towns.

Figure S2. Plot of a Principal Component Analysis (PCA) using environmental and anthropogenic variables to compare camera trap sites (dots) from three distinct arrays (CL, VB, VPD) deployed in APA Pandeiros. Variables used in the PCA are as follows: NDVI (NDVImean_500 m), distance to water (Dist_water), distance to main roads (Dist_road), distance to city/town (Dist_city), human density (HDens_2 km) and cattle frequency (cattle_freq).

Figure S3. Averaged parameter estimates of models assessing the effect of distinct variables on the probability of activity between 07:00 and 16:00 h (core diurnal activity) for 14 mammal species. Parameters are on the logit scale and vertical lines represent the 95% confidence interval. Positive parameter values indicate a 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, crab-eating fox and skunk are from a binomial GLMM, whereas for all other species are from a binomial GLM. See Table S1 for species' Latin names.

Figure S4. Overall daily activity patterns across all camera trap arrays for mammal species with at least 15 independent records in total. It includes species that did not reach the minimum number of records for analysis. See Table S1 for Latin names.

Table S1. Independent records, occurrence at camera trap sites and at camera trap arrays for 27 mammal species at the Sertão Veredas-Peruaçu Mosaic.

Table S2. Moran's *I* values calculated to assess spatial autocorrelation in camera trap data for species with more than 10 records in the full dataset.

Table S3. Model-averaged coefficients from binomial GLMs for ocelot and collared peccary using a subset of the full data after excluding survey sites to eliminate spatial autocorrelation.