

The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado

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Abstract The impact of deforestation and fragmentation upon ecologically important and poorly known groups is currently an important issue for conservation biology. Herein we describe xenarthran communities across the Brazilian Cerrado and study the effects of habitat fragmentation on occupancy and activity patterns on these assemblages. Our hypothesis was that larger and specialized species would be more ecologically sensitive, and likely to exhibit shifts in their activity patterns in more deforested areas as a way of dealing with the myriad of effects involved in the fragmentation process. The study was conducted by camera trapping in ten Cerrado sites. Five species were analyzed: *Priodontes maximus*, *Euphractus sexcinctus*, *Dasypus novemcintus* (Order Cingulata), *Tamandua tetradactyla* and *Myrmecophaga tridactyla* (Order Pilosa). Fragmentation was quantified by landscape metrics, calculated on scales that matched

the species' home ranges. Occupancy and detection probability analyses were conducted to test for shifts in occupancy under different fragmentation conditions. A mixed-effects model analysis was conducted to test for shifts in species' frequency of records related to time of day, controlling for spatial autocorrelation by means of eigenvector-based spatial filters for the models' residuals. There were no changes in activity pattern between more and less fragmented areas, so that our behavioural plasticity hypothesis was not corroborated for this group. The lack of changes in the patterns could be explained by a species' time-lag response, or by the lack of a wide enough fragmentation gradient in our study.

Keywords Activity pattern · Ecological sensitivity · Habitat fragmentation · Landscape ecology · Xenarthra

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Introduction

Deforestation causes several types of impacts, and one of the most significant is habitat fragmentation, which in a broad sense involves not only the loss of native vegetation area, but also the growing isolation of the remaining patches (Pires et al. 2002; Fahrig 2003). The study of the impact of fragmentation on biodiversity is presently being conducted in the light of landscape ecology, which works with a complex range of elements and variables that characterize landscape

structure (e.g., Andr n 1994; Chiarello 1999; Pires et al. 2002; Pardini et al. 2005). Not only the size, but also the distance between patches, their shape and orientation, as well as the type of matrix where they are inserted are considered (Fahrig 2003). The scale considered for the study can also influence the patterns observed and studies should use a scale that is relevant to the species and the phenomena analyzed (Wiens 1989). The exact scale perceived by the species is generally unknown, although it is commonly stated that the scale on which an organism perceives its environment corresponds to the scale of its home range (Wiens 1989; Tews et al. 2004; Gardner et al. 2009).

The central Brazilian Cerrado is a tropical savannah, covering over 2 million square kilometers. It consists of a mosaic of vegetation formations, from open grasslands to closed riverine forests (Eiten 1972; Ab’Saber 1983). Because of its high degree of endemism and high destruction rate, it is considered one of the 34 global ‘hotspots’ for biodiversity (Mittermeier et al. 2004). It harbours 10 out of the 23 Neotropical terrestrial xenarthrans (Orders Cingulata and Pilosa, Mammalia) (Wetzel 1985a, b; Eisenberg and Redford 1999), three of which are considered “vulnerable” according to the Brazilian list of endangered mammals (Machado et al. 2008): the giant armadillo (*Priodontes maximus*), the three-banded armadillo (*Tolypeutes tricinctus*) and the giant anteater (*Myrmecophaga tridactyla*). This group is endemic to the Neotropics, where it is known for playing an important ecological role (Eisenberg and Thorington 1973; Redford 1985). They are believed to be important in the nutrient cycling in the natural ecosystems where they occur (Eisenberg and Thorington 1973; Redford 1985), and also as prey for top predators, such as canids and felids (Encarna o 1986; Juarez and Marinho-Filho 2002; Miranda 2004).

Surprisingly few studies up to date have evaluated the effect of habitat fragmentation on terrestrial xenarthran ecology (Chiarello 1999; Norris et al. 2010). Most studies focus on describing species’ natural history aspects (Encarna o 1986; Anacleto and Marinho-Filho 2001; Medri et al. 2003; Miranda 2004; Anacleto 2007; Silveira et al. 2009). Xenarthrans have mostly nocturnal habits, except for the yellow armadillo (*Euphractus sexcinctus*), which is mostly diurnal (Meritt 1985; Montgomery 1985a, b;

Encarna o 1986; Eisenberg and Redford 1999). There are highly specialized species (insectivores: *M. tridactyla*, *Tamandua tetradactyla*, *P. maximus*, *Cabassous unicinctus*, *Cabassous tatouay*, *T. tricinctus*, *Tolypeutes matacus*) and generalist species (generalist-insectivores: *Dasypus novemcinctus*, *Dasypus septemcinctus*; carnivore-omnivores: *E. sexcinctus*) (Redford 1985). The specialist-insectivores depend on resources that are energetically poor (McNab 1985), and large-bodied species such as the *M. tridactyla* and *P. maximus*, both weighing between 20 and 30 kg, require large areas for their survival (Encarna o 1986; Anacleto and Marinho-Filho 2001; Medri et al. 2003; Miranda 2004). The sum of these factors can contribute to their sensitivity to habitat fragmentation (Crooks 2002; Swihart et al. 2003; Henle et al. 2004).

However, a factor that has received little attention is the possibility that species may deal with the fragmentation of their environments by altering their dietary or activity patterns, among other behaviours (Garcia-Chiarello 1993; Estrada et al. 1999; Onderdonk and Chapman 2000; Jepsen and Topping 2004). For instance, species may widen their activity periods to compensate for the lack of suitable resources and of adequate foraging areas in a degraded landscape, or nocturnal species may concentrate their activities as a way of avoiding negative interactions with humans and domestic animals during the day. Either way this should indicate a behaviour plasticity that could be critical for a species dealing with habitat fragmentation and degradation (Jepsen and Topping 2004). This kind of strategy has already been documented in the Amazon region for *Dasypus novemcinctus*, a nocturnal species that was more often recorded during the day in forest patches smaller than 1000 ha (Norris et al. 2010).

Herein we describe xenarthran communities across the Brazilian Cerrado and study the effects of habitat fragmentation on occupancy and activity patterns on these assemblages. We hypothesized that specialist species with large area requirements (namely, *M. tridactyla* and *P. maximus*) should have their patterns of occurrence and activity changed in more degraded areas. Based on the idea that the species respond better to processes operating at a scale corresponding to their home ranges, we conducted the analyzes at two scales, one that was close to the home ranges of the species with smaller area requirements and the other that was

close to the home ranges of those species with large area requirements.

Methods

Study areas

In this study, we analyzed ten sites sampled within projects conducted by the Jaguar Conservation Fund (Instituto Onça-Pintada), a Brazilian NGO for the conservation of jaguars. All study sites are located in the Cerrado domain in Central Brazil (Fig. 1). The projects were conducted in the following sites, Brazilian states and time periods: (1) ARA (headwaters of the Araguaia River, along the border of Goiás-GO and Mato Grosso-MT states), 2008; (2) ARU (Aruanã municipality, GO), 2008; (3) ENC (Encantado Environmental Protection Area, GO), 2008; (4) PNE (Emas National Park, GO), 2001–2008; (5) ENT (areas adjacent to the Emas National Park, GO and MT), 2001–2007; (6) COR (Emas-Taquari ecological corridor, GO, MT and Mato Grosso do Sul-MS state), 2001–2003; (7) PAR (Nascentes do Parnaíba National Park, Piauí-PI state), 2007–2008; (8) URU (Uruçuí-Una Ecological Station, PI), 2007–2008; (9) CAN (Cantão State Park and the private reserve of an adjoining cattle ranch, Tocantins-TO e Pará-PA states), 2002–2007; and (10) COC (Cocos municipality, Bahia-BA state), 2006. These areas comprise both legally protected (parks, reserves and ecological stations) and unprotected areas. A brief description of each area is included in the Supplementary Material.

Sampling procedures

Camera-trapping surveys were conducted in each of these areas in accordance with the protocol by Silver (2004), indicated for jaguars (*Panthera onca*). This procedure involves the placement of cameras, which are triggered by an infrared sensor, in dirt roads and trails, forming a grid that comprises the whole area sampled. The traps are deployed observing a minimum distance of 2–3 km between each of them, so as to ensure spatial independence of records for jaguars. Also, an hour was considered the minimum interval for considering two records of the same species as independent events (Silver 2004). This, in turn,

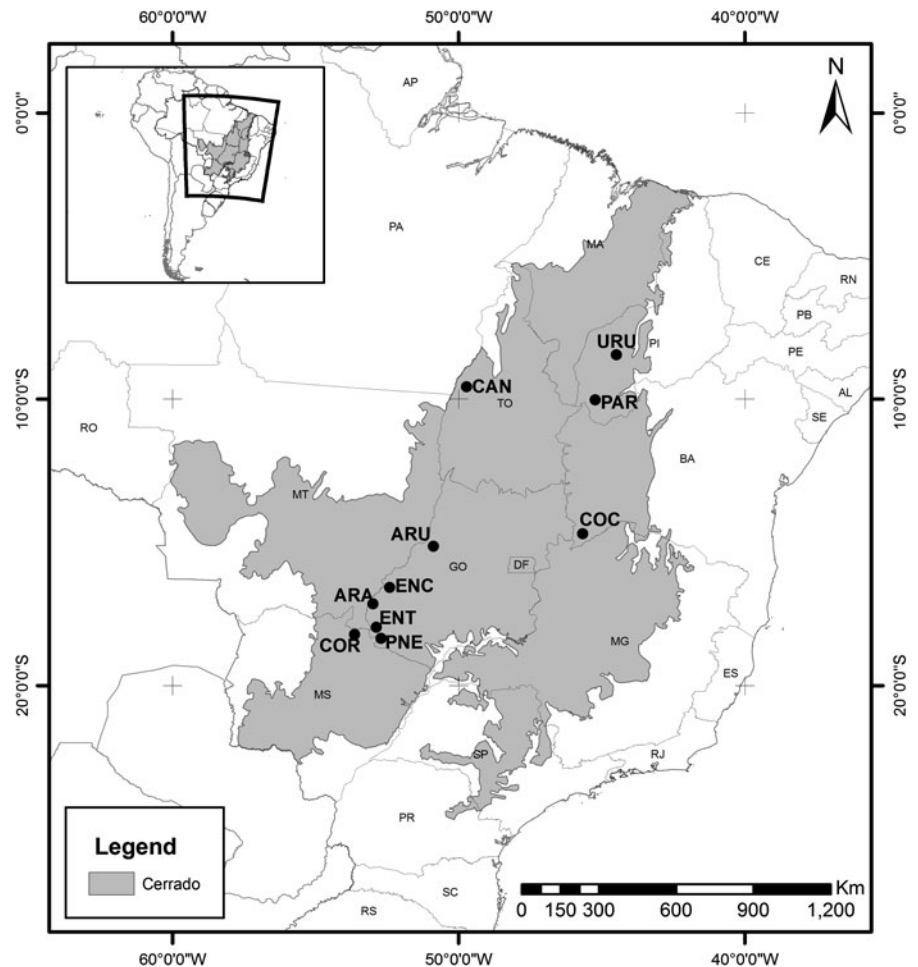
provides spatial independence for the records of smaller species with smaller home-ranges, which are the case here. The records obtained provide the following information: the species recorded, location (vegetation form and geographic coordinates of the trap), time of the record and overall photographic frequency for each species (defined as the number of independent records obtained in a trap, divided by the total sampling effort of that trap; O'Brien et al. 2003). Only those records from cameras that sampled continuously through time (cameras that were on 24 h a day) were considered.

There is considerable discussion about the use of record frequency in camera trapping protocols as a relative abundance index, since it is commonly used to estimate population densities in mark-recapture experiments for species with identifiable individuals (Karanth and Nichols 1998; Karanth et al. 2004). It is however argued that this index can be valuable in the sampling of other species' relative abundances (Carbone et al. 2001, 2002; O'Brien et al. 2003), despite being subject to a potential detectability bias for each species and each study area analyzed (Jennelle et al. 2002; MacKenzie et al. 2003). In our case, because the traps were placed in roads and trails, species that avoid open trails may have been underestimated (Harmsen et al. 2010). Also, considering that our study is conducted by large-scale sampling in different periods, we also had to consider the possibility of temporal and spatial variation in the detectability of each species in different sites (Boulinier et al. 1998). For these reasons, detectability was taken into account in estimating occupancy (described below).

Landscape data

We performed the fragmentation analyzes and the evaluation of the current status of the natural vegetation cover based on two 30-m resolution maps produced by the remote sensing centre of the Brazilian environmental agency (Centro de Sensoriamento Remoto do Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis—CSR-IBAMA 2009). These maps were produced within the Satellite Monitoring of Deforestation of the Brazilian Biomes Project—PMDBBS (http://siscom.ibama.gov.br/monitor_abiomas/), and present the situation for the Cerrado in 2002 and 2008. An additional map for 2008 was produced by the Conservation Planning Lab of the Zoology

Fig. 1 Sampled sites in the Brazilian Cerrado: *ARA* headwaters of the Araguaia River; *ARU* Aruanã municipality; *ENC* Encantado Environmental Protection Area; *PNE* Emas National Park; *ENT* areas adjacent to the Emas National Park; *COR* Emas-Taquari ecological corridor; *PAR*, Nascentes do Parnaíba National Park; *URU* Uruçuí-Una ecological station; *CAN* Cantão State Park and adjoining areas; *e* *COC* Cocos municipality. Cerrado biome map obtained from IBGE (2004)



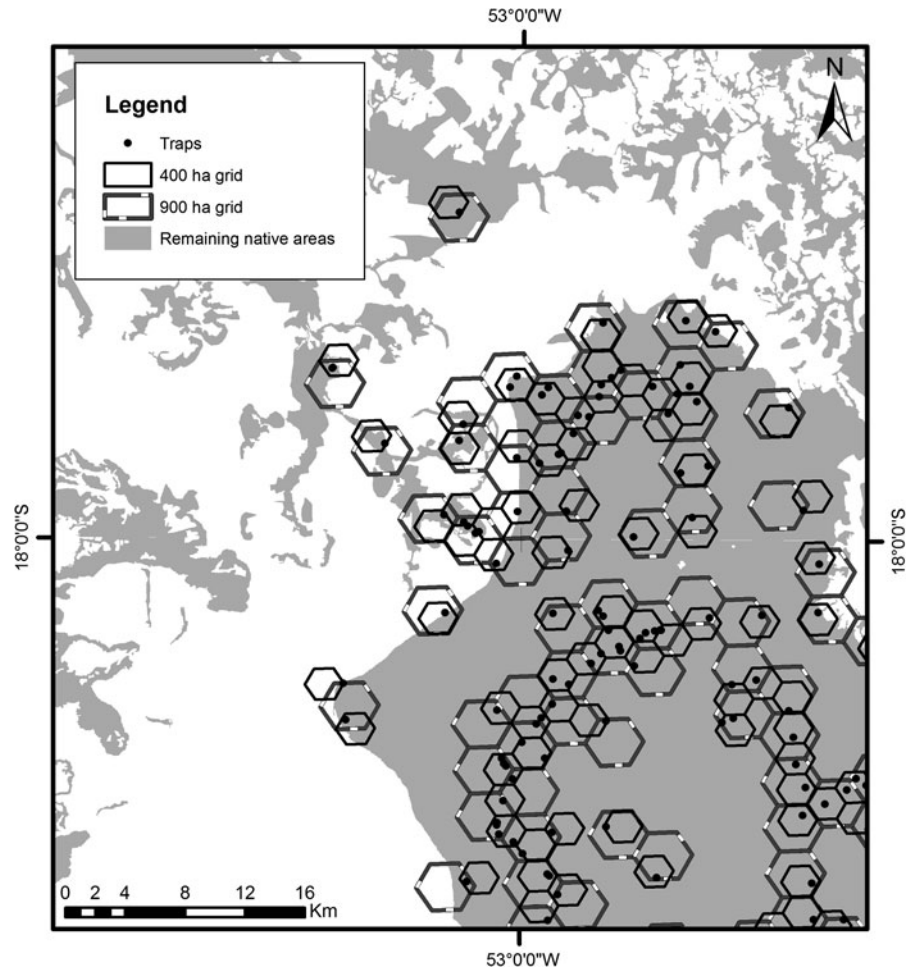
Department, Universidade de Brasília (UnB), to cover an area not included in the PMDBBS project, namely, a portion along the left margin of the Araguaia River, in the state of Pará. The campaigns that took place between the years 2001–2004 were associated with the 2002 vegetation cover map, and the campaigns that took place between 2005 and 2008 were associated with the 2008 map. The association between maps and campaigns in different years is not ideal, but the rate of change in the areas sampled was not high, so we believe this mismatch should not affect our analyses strongly.

We processed both vector files in the ArcGIS v.9.3.1 software (ESRI 2009). We created two spatial grids for each area, consisting of hexagonal cells (sample units—SUs) of 400 and 900 ha respectively (Fig. 2), using the ArcGIS Extension Hawth's Analysis Tools (Beyer 2004). The 400 ha grid corresponded to the home range areas for the species with smaller area requirements

(*T. tetradactyla*: 300 ha; *D. novemcinctus*: 400 ha; Encarnação 1986), and the 900 ha grid corresponded to those with larger area requirements (*Euphractus sexcinctus*: 900 ha; *P. maximus*: 700 ha; *M. tridactyla*: 1000 ha; Encarnação 1986; Medri et al. 2003; Miranda 2004). For the fragmentation analysis, all the traps (records and sampling effort) contained within a single SU were combined. As the frequency of records are calculated by dividing number of records by sampling effort of a single trap, the difference of sampling effort between traps, as well as between SUs are taken into account.

The patches of remaining native habitat map inside each SU were evaluated using four landscape metrics, calculated by the ArcGIS extension package Patch Analyst 3.0 (Rempel 2006): (1) Class area (CA); (2) Number of patches (NumP); (3) Mean patch size (MPS); (4) Mean nearest-neighbor distance (MNN).

Fig. 2 Example of the grid structures in the Emas National Park (*PNE*), in areas adjacent to the Emas National Park (*ENT*) and in the Emas-Taquari ecological corridor (*COR*). Remaining native vegetation map obtained from IBAMA (2009)



The first three metrics relate to the amount (number and size) of remaining native vegetation, while the last metric relates to the connectivity between pairs of patches. A Pearson correlation analysis between each pair of metrics was performed, and the results indicated a high degree of correlation between some of them, on both scales. The highest correlation observed was between the variables CA and NumP ($r = 0.96$ on the 400 ha scale, and $r = 0.94$ on the 900 ha scale).

Also, because our analyses were conducted at such large scale, three variables were chosen to evaluate the effect of environmental variation in the ecological patterns observed: altitude, annual temperature, and annual precipitation. These variables were obtained in the Wordclim database (<http://www.worldclim.org>) for the year 2000, at a resolution of 1 km. For each SU, we extracted the mean values for each variable.

Statistical analyses

Due to the correlation between variables described above, we ran a principal component analysis (PCA) with the four landscape metrics, using a correlation matrix. We used the first component's scores to classify the SUs in a continuous gradient of habitat fragmentation, so that we ended up with only one variable, which described the landscape structure and minimized the effect of the correlation between the original variables. The PCA was drawn for both grid resolutions.

In order to investigate the influence of fragmentation in each SU on the species' occurrence (MacKenzie et al. 2003), we estimated occupancy using the program PRESENCE 3.1 (Hines 2006). This approach models the effects of fragmentation status, time, and site on the detection (p) and occupancy probabilities (Ψ), based on the occurrence history in each SU as

proposed by MacKenzie et al. (2006). PCA scores, as described above, defined the fragmentation status variable; time was divided in months during the entire sampling period for each SU; and the site variable are the ten studied sites. Model selection was based on the Akaike's information criterion (AIC) (Burnham and Anderson 2002). The best model is the one with the lowest AIC and the largest AIC weight (wAIC). We considered more than one model as best, if the delta AIC (Δ AIC), which compares the AIC values of a given model to the best model, was less than 2 (Burnham and Anderson 2002).

In order to analyze whether the species' activity patterns (record frequency at day and night time) differ according to the fragmentation status, we performed a linear mixed-effects model analysis adjusted by restricted maximum likelihood, using the *nlme* package (Pinheiro et al. 2011) in the software R 2.10.1 (R Development Core Team 2009). In these models, fixed factors, or the explanatory variables, are analyzed without the influence of covariates, or random factors (Bennington and Thayne 1994; Pinheiro and Bates 2000), which take into account a possible temporal and spatial pseudo-replication in a single trap. In this case, therefore, the 'record frequency' was related to the fixed factors: fragmentation status, time of day, divided in day (06:01–18:00 h) and night (18:01–06:00 h), the three environmental variables, and the interaction between the terms. Camera trapping record frequency could be related to the detection probability (tested above), but even if there is such an effect, our comparison between day and night frequency would not be influenced. Also, eigenvector-based filters were included in the model as fixed factors, whenever a significant spatial autocorrelation in the model's residuals was detected, based on the Moran's I (Diniz-Filho and Bini 2005). This was tested using SAM 4.0 (Rangel et al. 2010). The random factors were built including the identity of the cell or the sampling site, and the best structure was chosen based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002). In cases where models did not present significant interactions between the fixed factors, each non-significant interaction term was removed, following the model simplification procedure (Zuur et al. 2009). A Pearson residuals test was also performed to verify the presence of outliers, based on a significance level of 0.01. The outliers found were then removed only once

and the modelling procedures repeated. A significance level of 95 % was considered for all other statistical analyses.

Results

In a total sampling effort of 29,618 trap*days, 688 xenarthran records were obtained. Seven species were recorded: *Priodontes maximus* (giant armadillo; $n = 98$), *Euphractus sexcinctus* (yellow armadillo; $n = 55$), *Dasyopus novemcinctus* (nine-banded armadillo; $n = 75$), *Cabassous unicinctus* (naked-tail armadillo; $n = 1$), *Tolypeutes tricinctus* (three-banded armadillo; $n = 1$), *Tamandua tetradactyla* (collared anteater; $n = 31$) and *Myrmecophaga tridactyla* (giant anteater; $n = 427$). The species that were recorded only once could not be used in the analyses. The 400 ha grid comprised in total 165 SUs, and the 900 ha grid comprised 147 SUs. The scores of the first principal component formed the fragmentation status variable, which was to be included in the model. In the PCA performed for both grid resolutions, the landscape metrics behaved the same way. Negative scores of the first axis described better preserved SUs, which presented more total native vegetation (higher CA), larger patches (higher MPS), smaller distances between patches (lower MNN), and less fragmented landscapes (lower NumP). Positive scores of the first axis described less preserved SUs, which presented the opposite relationship with the landscape metrics (Table 1).

Table 1 Correlation between the landscape metrics characterizing fragmentation in each sampling unit in the Brazilian Cerrado and the two first principal components (PC1 and PC2), which resulted from the analysis in both grid resolutions (400 and 900 ha); and the cumulative proportion of variance explained by the components

Variable	400 ha		900 ha	
	PC1	PC2	PC1	PC2
MNN	0.77	0.42	0.67	0.71
CA	-0.90	0.42	-0.92	0.08
NUMP	0.77	0.38	0.76	-0.40
MPS	-0.96	0.24	-0.96	0.10
Cumulative proportion	73.4 %	87.3 %	69.7 %	86.8 %

MNN mean nearest-neighbour distance; *CA* class area; *NumP* number of patches; and *MPS* mean patch size

Table 2 Total sampling effort (days) and sampling success for each species (total number of xenarthran records multiplied by 100 and divided by total sampling effort) in each site, and the first principal component (PC1) scores obtained by the Principal Component Analysis as a descriptor of fragmentation status

Site	Sampling effort (days)	<i>Myrmecophaga tridactyla</i>	<i>Tamandua tetradactyla</i>	<i>Priodontes maximus</i>	<i>Euphractus sexcinctus</i>	<i>Dasybus novemcinctus</i>	PC1 400 ha	PC1 900 ha
ARA	624	1.92	0.96	0.32	0.64	2.08	0.93 ± 1.37	1.33 ± 1.33
ARU	2,797	0.46	0.04	0.11	0	0	1.60 ± 2.63	1.21 ± 1.69
ENC	374	3.21	0.27	0.27	0.53	0	0.20 ± 2.64	-0.19 ± 1.41
PNE	8,112	3.74	0.10	0.89	0.54	0.26	-0.58 ± 1.01	-0.54 ± 1.31
ENT	1,726	1.85	0.17	0.17	0.06	1.04	0.95 ± 1.84	0.66 ± 1.66
COR	1,926	1.04	0.05	0.10	0.62	0.67	1.06 ± 2.09	0.63 ± 1.65
URU	879	0.34	0.11	0	0	0	-1.04 ± 0.02	-1.15 ± 0.05
PAR	2,329	0	0	0	0	0.04	-1.04 ^a	-1.18 ^a
COC	681	0	0	0.15	0	0	1.02 ^a	-1.11 ^a
CAN	10,170	0.06	0.03	0.15	0	0.08	0.45 ± 2.37	0.88 ± 2.39
Total	29,618	1.35	0.08	0.33	0.21	0.25	0.00 ± 1.72	0.00 ± 1.67

Higher PC1 scores indicate more fragmented areas

ARA headwaters of the Araguaia River; ARU Aruanã municipality; ENC Encantado Environmental Protection Area; PNE Emas National Park; ENT areas adjacent to the Emas National Park; COR Emas-Taquari ecological corridor; PAR Nascentes do Parnaíba National Park; URU Uruçuí-Una ecological station; COC Cocos municipality; CAN Cantão State Park and adjoining areas

^a No standard deviation available, since there is only one sampling unit

Table 3 Models selected in the occupancy analysis by the Akaike information criterion (AIC) for the xenarthran species in each sampling unit (SU) in the Brazilian Cerrado

Species	Model	AIC	w	ΔAIC	-2Log (L)	K
<i>M. tridactyla</i>	Ψ(.) p(t)	998.65	0.46	0.00	872.65	63
	Ψ(.) p(site + t)	999.75	0.26	1.10	855.75	72
	Ψ(.) p(PC1 + t)	1000.64	0.17	1.99	872.64	64
<i>T. tetradactyla</i>	Ψ(.) p(.)	187.79	0.52	0.00	183.79	2
<i>P. maximus</i>	Ψ(PC1) p(.)	497.53	0.56	0.00	493.53	2
	Ψ(.) p(.)	498.19	0.40	0.66	494.19	2
<i>D. novemcinctus</i>	Ψ(.) p(PC1 + site)	276.96	0.66	0.00	254.96	11
<i>E. sexcinctus</i>	Ψ(.) p(site)	313.56	0.45	0.00	293.56	10
	Ψ(.) (PC1 + site)	315.28	0.19	1.72	293.28	11

Only the best models ($\Delta AIC < 2.0$) are presented. The variables included in the models are: sampled site (site), time divided by sampling month (t) and fragmentation status (PC1) for each SU. The variable 'Ψ' defines the occupancy probability, and 'p', the detection probability of a species in a sampling unit. Variables presented with a '.' define constant parameters among SUs

w Akaike weight; ΔAIC the difference in AIC value relative to the best model; $-2Log(L)$ twice the negative log-likelihood value; K number of parameters in the model (Burnham and Anderson 2002)

Sampling success varied greatly among areas (Table 2). Sampling success was high in some areas with low sampling effort (e.g. ARA, ENC). COR was the area with the greatest observed richness (presented the only record obtained for *C. unicinctus*), despite a relatively smaller sampling effort. It is easily noted that more preserved sites (lower PC1 scores) are

protected areas, namely PNE, ENC, PAR and URU. Although CAN encompassed a protected area, in this site sampling took place outside the reserve as well, so that its scores were relatively high. *M. tridactyla* and *P. maximus* were the species most frequently recorded overall, while *T. tetradactyla* was generally rare, which can be explained in part by the fact that this

species has a scansorial habit. *P. maximus* occurred most often in PNE, while there are *M. tridactyla* records in both fragmented and unfragmented sites (PNE, ENC, but also ARA and ENT). The other species presented high frequency of occurrence in ARA compared with all other sites, but there was not a clear pattern regarding fragmentation status and sampling success.

There was an indication of differing occupancy probability (parameter Ψ) among SUs only for *P. maximus*, and this difference was negatively related to the fragmentation status (PC1) inside the SUs (linear equation obtained: $\Psi = 0.75 - 0.01 * PC1$). However, since ΔAIC between concurrent models is low, we cannot safely state that fragmentation status actually influences *P. maximus* occupancy. *M. tridactyla*, *E. sexcinctus* and *D. novemcinctus* presented an influence of some of the variables and their interactions only on their probability of detection (parameter p), namely fragmentation status and site. *T. tetradactyla* did not exhibit any response of occupancy or detection patterns to the variables modelled (Table 3).

Small significant auto-correlation was detected in the model residuals for *M. tridactyla* and *P. maximus*. Eigenvector-based filters were thus included in the mixed-effects models these species, so that these spatial patterns were minimized. The first models produced, which included the interaction term between time of day and SU fragmentation status, did not indicate a significant response of any of the species' relative abundance (frequency of records) to this interaction. The final models, derived by simplification, revealed a significant difference only in the number of records between each time class. No species presented an influence of the environmental variables on relative abundance (Table 4).

Discussion

Our results indicated that our initial hypothesis that large-bodied and specialist species are more sensitive to habitat fragmentation could not be corroborated. We cannot safely conclude that fragmentation status actually influences *P. maximus* occupancy, and the other species expected to present such a response, the giant anteater (*Myrmecophaga tridactyla*), did not present such an effect. The generalization of patterns of sensitivity is a research goal in ecology, as the

Table 4 Results of the significance tests for the mixed-effects models' for each xenarthran species

Factors	df	t	p
<i>M. tridactyla</i>			
Status × Time of day	272	−1.044	0.297
Time of day	272	2.985	0.003
Temperature	272	−0.050	0.960
Precipitation	272	0.416	0.678
Altitude	272	0.089	0.929
<i>T. tetradactyla</i>			
Status × Time of day	305	−0.411	0.681
Time of day	305	2.393	0.017
Temperature	305	0.235	0.814
Precipitation	305	−0.022	0.983
Altitude	305	0.243	0.808
<i>P. maximus</i>			
Status × Time of day	276	0.194	0.847
Time of day	276	0.346	<0.001
Temperature	276	0.679	0.498
Precipitation	276	0.724	0.470
Altitude	276	1.082	0.280
<i>D. novemcinctus</i>			
Status × Time of day	162	0.891	0.374
Time of day	162	2.438	0.016
Temperature	159	−0.506	0.072
Precipitation	159	0.271	0.846
Altitude	159	−0.850	0.397
<i>E. sexcinctus</i>			
Status × Time of day	277	−0.202	0.840
Time of day	277	−3.267	0.001
Temperature	277	−1.521	0.129
Precipitation	277	−0.349	0.727
Altitude	277	−1.307	0.192

Status × Time of day = interaction term between fragmentation status of the area inside the cell and time of the record; Time of day = single fixed factor, defined as day (06:01–18:00 h) and night (18:01–06:00 h); Temperature = annual mean temperature; Precipitation = mean annual precipitation. In bold font, 'p' values smaller than $\alpha = 0.05$

df degrees of freedom

identification of focal groups for the optimization of conservation efforts is necessary (Bierregaard et al. 1997; Simberloff 1998; Crooks 2002). In this sense, ecological sensitivity related to body size has received varying support over the years (Crooks 2002; Swihart et al. 2003; Henle et al. 2004; Uezu et al. 2005; Gardner et al. 2009). We thus emphasize with our

results the idiosyncratic nature of the species' response patterns in the face of habitat fragmentation, compared to other studies (e.g. Uezu et al. 2005; Gardner et al. 2009), and recommend caution when applying the use of individual species traits as indicators of ecological sensitivity.

The hypothesis that the animals alter their activity patterns in the face of degradation as a way of dealing with its effects was also not corroborated. Only the patterns already noted in the literature were observed: all species are predominantly nocturnal, with the exception of *E. sexcinctus*, which presents mainly diurnal activity (Merritt 1985; Montgomery 1985a, b; Encarnação 1986; Eisenberg and Redford 1999; Trolle 2003). Theoretically, behaviour plasticity can help species cope with the deleterious effects of fragmentation (Garcia-Chiarelo 1993; Estrada et al. 1999; Onderdonk and Chapman 2000; Jepsen and Topping 2004), but our results did not demonstrate such a strategy from the species analyzed.

Our results were apparently not influenced by geographic variations in the environment, since neither altitude, precipitation, nor temperature proved significant in our models. These variables are generated by interpolation of values across a wide geographic region (Hijmans et al. 2005), so their importance may be mostly associated with regional patterns, rather than local ones, as is the case here. In any case, we observe that activity patterns do not seem to vary geographically, and do not confound the results observed.

The absence of an observed effect of fragmentation on the occupancy probabilities for these species might suggest that these species do not suffer from the impact of habitat fragmentation, but this should be interpreted with care. Clearer effects of habitat loss and fragmentation on occupancy and relative abundance would be more visible if a larger array of fragmented conditions was tested. Although sampling took place in both protected and unprotected sites, camera traps were installed preferably in more preserved areas within each site. Therefore future sampling in both extremes of the landscape fragmentation process may present a variation wide enough for observing shifts in the species relative abundances, occupancy patterns, and activity patterns.

Lastly, we would like to reinforce the apparent importance of the ARA site, which is a strip of legally protected area along the Araguaia River, known as

Permanently Protected Area (APP, in Portuguese). The river and its APP are thought to function as a large-scale ecological corridor between the South-western portion of the state of Goiás and the state of Tocantins, where the Cantão State Park is located (CAN). Our results suggest that this may actually be the case, as indicated by the high occupancy probability observed for most species. We suggest that, due to the fact that this site is immersed in a highly fragmented landscape, the region must be currently functioning as a refuge for wild fauna, thus presenting a typical "crowding effect" (Lovejoy et al. 1986).

Overall our study highlights the importance of assessing other strategies with which sensitive species may deal with the impacts of fragmentation, other than changes in abundance and occupancy patterns. This is more likely to be the case in areas with a recent history of degradation, as a species can be present and striving for a period of time after the fragmentation has occurred (Tilman et al. 1994; Metzger et al. 2009). Thus, the comparison of biological patterns between sites that have been degraded in different time frames would prove valuable for the understanding of the complex ways in which biodiversity responds to fragmentation.

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