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Article *in* Biological Conservation · September 2016

DOI: 10.1016/j.biocon.2016.09.010

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Biological Conservation xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Citizen scientists help unravel the nature of cattle impacts on native mammals and birds visiting fruiting trees in Brazil's southern Pantanal

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ARTICLE INFO

Article history:
Received 17 October 2015
Received in revised form 30 August 2016
Accepted 9 September 2016
Available online xxxx

Keywords:
Biodiversity loss
Camera-trap survey
Cattle impact
Forest frugivores
Pantanal
Tayassu pecari

ABSTRACT

We used 2 years of camera-trap surveys conducted by citizen scientists to compare native mammal and bird visits to dominant fruiting-tree species in low and high cattle-impact areas of rarely-flooded “cordilheira” forests in the Brazilian Pantanal. Monthly fruit censuses showed greater diversity of fruiting-tree species in low cattle-impact areas. Citizen scientists documented 29 native mammal and bird species among 5639 photo records obtained at fruiting trees. Analyses of 3 sets of camera-trap samples comprising: (1) only *Attalea phalerata* palms, (2) all ten dominant fruiting-tree species, and (3) all except a species with a highly-valued fruit and an unusual distribution, showed that faunal composition in low cattle-impact areas was significantly different and more diverse compared to that in high cattle-impact areas. Long-term cattle-related alterations of forest vegetation and short-term fruit depletion and interference by cattle explained faunal differences. While 5 frugivores and 1 carnivore were consistent indicators of low cattle-impact conditions, the value of 2 other frugivores (*Tayassu pecari* and *Crax fasciolata*) as indicators of cattle impact varied depending on fruit-species nutritive value, timing, and distribution. Improved cattle management is needed to prevent additional loss of forest biodiversity.

1. Introduction

Cattle rearing operations affect native fauna and flora, species interactions, and ecological communities across a wide range of climates, geographic regions, and environments (Bock and Bock, 1999; Chaikina and Ruckstuhl, 2006; Elliott and Barrett, 1985; Moser and Witmer, 2000; Shepherd and Ditgen, 2005). Negative impacts on native fauna can result from habitat and vegetation alterations, diet overlap with cattle, and alterations in behavior or habitat use associated with avoidance of cattle (Chaikina and Ruckstuhl, 2006; Elliott and Barrett, 1985; Moser and Witmer, 2000; Shepherd and Ditgen, 2005).

In the Brazilian tropics, cattle grazed in naturally-open rangelands or in areas that were deforested and converted to planted exotic, i.e., non-native, grass pastures (hereafter called planted pastures) also forage and seek shelter in nearby forests. Therefore, in addition to impacts on native grazers and browsers characteristic of open habitats, they potentially affect forest species, like ground-dwelling frugivores, which are the focus of this study. Frugivorous animals comprise a large part of vertebrate community biomass in tropical regions and are important seed dispersal agents, contributing to the dynamics and structure of forests (Jordano, 2000; Silman et al., 2003; Terborgh, 1983, 1986). Similar to cattle impacts on grazers and browsers, short-term indirect and direct effects on native frugivorous animals potentially include overlap in use of fruit resources and/or alterations of behavior and habitat use, e.g., if native fauna avoid areas where cattle congregate, or shift their spatial or temporal feeding patterns in the presence of cattle. Long-term indirect impacts of cattle on frugivores potentially include vegetation and habitat alterations caused by foraging and trampling of forest understory and shifts in seed dispersal and predation (Johnson et al., 1997; Nunes et al., 2008; Santos, 2011; Shepherd and Ditgen, 2005; Tomas et al., 2009).

The Pantanal of Bolivia, Paraguay, and the Mato Grosso region of central-western Brazil is an England + Wales-sized alluvial plain (150,500 km^2) that drains the upper Paraguay river basin and forms one of the largest seasonal tropical wetland systems in the world (Hamilton et al., 1996; Junk et al., 2006; Nunes da Cunha et al., 2014; Padovani, 2010). It supports a rich variety and abundance of wildlife, is recognized internationally as a region of conservation importance, and is an important production area that has supported extensive cattle ranching operations since the late 1800s (Junk et al., 2006; Mazza et al., 1994; Nunes da Cunha et al., 2014; Santos et al., 2002, 2008). The Pantanal is one of the few places in the American tropics where a wide variety of wildlife are easily observed. For this reason, ecotourism

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http://dx.doi.org/10.1016/j.biocon.2016.09.010

Please cite this article as: Eaton, D.P., et al., Citizen scientists help unravel the nature of cattle impacts on native mammals and birds visiting fruiting trees in Brazil's south..., Biological Conservation (2016), http://dx.doi.org/10.1016/j.biocon.2016.09.010

is popular in the Pantanal, and has been adopted by a number of property owners as an alternative economic activity to replace or supplement cattle ranching. North American and European tourists interested in citizen-scientist opportunities are drawn to the region, and as reported for other studies (e.g., McKinley et al., this issue) have been integral to the successful collection of field data described in this article.

Because >95% of the Brazilian Pantanal consists of privately-owned ranches called "fazendas", the region has been (and continues to be) vulnerable to development trends initiated in the 1960s that decrease the environmental sustainability of ranch properties. These trends have included the introduction of harmful ranching practices, most significantly deforestation, conversion of natural habitat to planted pasture, and subsequent intensification of cattle operations (Santos et al., 2008; Silva et al., 1999). So, in addition to impacts and probable species losses from deforestation and conversions, the remaining native fauna and flora have been exposed to increased levels of cattle activity associated with the expansion of planted pasture. By 2008 (the period of this study), approximately 13% of the natural vegetation cover had been altered in the Pantanal (15% by 2014; Instituto SOS Pantanal and WWF-Brasil, 2015). Forest formations called "cordilheiras", which were the focus of this study, have unfortunately been disproportionately targeted for deforestation and conversions in the Pantanal, because they occupy areas above typical peak flood levels and as a result are preferred locations for establishing the less flood-resistant exotic-grass monocultures (Silva et al., 1999).

Recent studies in the southern Pantanal, have shown that cattle-related impacts associated with both traditional and intensive (i.e., requiring deforestation and conversion to planted pasture) ranching practices may have negative consequences for forest flora and fauna, e.g., loss and simplification of forest understory vegetation (Nunes et al., 2008; Santos, 2011), alteration of forest structure and succession (Santos, 2011; Tomas et al., 2009), loss of insectivorous birds associated with forest litter (Nunes, 2009), loss of nesting cavity trees, *Sterculia apetala*, for threatened hyacinth macaws, *Anodorhynchus hyacinthinus* (Guedes et al., 2006), and altered range area and use by a wide-ranging prevalent frugivore, the white-lipped peccary, *Tayassu pecari* (Keuroghlian et al., 2015).

Our main objective was to determine whether native ground-dwelling mammalian and avian species visiting freshly-fallen fruits at trees in Pantanal forests were affected by cattle-related, or cattle-operation related, impacts. To that end, we relied on citizen scientists to conduct camera-trap surveys of forest fauna visiting fruiting trees in areas exposed to different levels of cattle activity. Using the data compiled from photo records by citizen scientists, we performed a range of analyses to evaluate impacts on faunal assemblages. Fruiting trees were ideal locations for monitoring the interactions between cattle and a wide range of native fauna, because they, like watering holes on dry savannas, are natural aggregation sites for fauna (Wemmer et al., 1996). A secondary objective of the study was to investigate the potential wider application of the procedures developed for citizen scientists as tools for evaluating and monitoring other types of environmental impacts in regional forests.

2. Materials and methods

2.1. Study area

We focused our investigation in the upper Rio Negro subregion of the southern Pantanal (Padovani, 2010), Município de Aquidauana, Mato Grosso do Sul, Brazil (Fig. 1). Native vegetation in the region, as is true for many parts of the Pantanal, is a complex mixture of aquatic, savanna, and forest formations that are strongly influenced by annual and multi-annual flood cycles, consequent moisture conditions, climatic and edaphic factors, and human alterations of the landscape (Nunes da Cunha et al., 2007; Pott and Pott, 2009). The woody vegetation in the study area, which combines species from bordering biomes, e.g., the Cerrado, Atlantic Forest, Amazon, and Chaco (Nunes da Cunha et al., 2007; Pott and Pott, 2009), includes periodically-flooded semi-open scrublands, a gradient of riparian forest types (200 to 1000 m in width) on seasonally-flooded levees associated with the Rio Negro, and rarely-flooded forested regions called "cordilheiras". The latter forest formations, which were the focus of the current study, are characteristic of long (tens of kilometers), narrow (50 to 500 m) paleo-levees that are 1 to 2 m above the average flood level and generally separate from present-day river levees (Nunes da Cunha et al., 2007; Salis et al., 2006; Santos, 2011). Bordering the "cordilheira" forests in the study area are flood-prone lower-lying grasslands and a range of aquatic environments that include seasonal and permanent wetlands and lakes and seasonal rainwater drainages called "vazantes" (Eaton, 2006). Based on GIS surveys of the "cordilheira" zone in the study area, 28% of the natural landscape was comprised of forest, while the remaining 72%, depending on season and extent of the annual flood, alternated between dry savanna and aquatic habitat. The climate is highly seasonal (Köppen-Geiger, tropical savanna, *Aw*) with annual rainfall in the study area from 1998 through 2009 averaging 1414 ± 196 mm (95% CI), and air temperatures during the hotter wet season (December to April) and cooler dry season (July through September) averaging 30 °C and 26 °C, respectively (D. P. Eaton and Fazenda Campo Lourdes, unpublished data).

The study area (S 19°29′–19°36′, W 55°32′–55°39′) encompassed three adjacent cattle ranches, i.e., 5700 ha Fazenda Campo Lourdes, 4400 ha Fazenda Santa Maria Pica Pau, and 2600 ha Fazenda Santa Emília. Largely related to management practices used on the ranches, the state of "cordilheira" forests (and other natural habitats) with respect to impacts from the cattle operations ranged from relatively undisturbed to highly disturbed, to absent. In the latter cases, "cordilheira" and riparian forests had been replaced recently (<10 years) with planted pastures. Within traditionally-managed sections of the ranches, where cattle were grazed on native pasture in large (typically >500 ha) enclosures for extended periods (3 months to year-round), uneven use of forage plants also caused a range of impacts by cattle herds in both pasture areas and adjacent forests and wetlands (Santos et al., 2004). In the "cordilheira" forests, cattle not only browsed and trampled understory vegetation, but also used particular sections for shade, latrines, and sleeping sites. The degree of these activities varied substantially among sections of "cordilheira" forest within the properties and within grazing enclosures, creating the array of low to high cattle-impact areas that were compared during this study.

2.2. Fruit census and choice of dominant fruiting species for camera-trap surveys

As part of a broader investigation of fruit availability for native frugivores, citizen scientists (from Global Ecotours and Earthwatch Institute) conducted monthly censuses of forest fruits from January 2006 to December 2008. They censused fruits along ten one-kilometer trails established to sample the range of forest types and conditions in the study region. Citizen scientists quantified fruit availability for ground-foraging animals by collecting fresh fruits from the forest floor within 20 randomly chosen 50 m^2 plots that were adjacent to census trails. All fruits from the plots were identified by project investigators and then counted and dried at 50 °C to a constant weight by citizen scientists. The census showed the monthly timing and abundance (dry mass, g m^{-2}) of forest-floor fruits.

For the camera-trap surveys of forest animals, we used fruit census results to choose dominant fruiting-tree species, which we defined for each sampling period as the one or two species with the most abundant fruit fall. Camera-trap sampling periods lasted two to six weeks and occurred at intervals of two to three months over the study period from January 2007 to December 2008. After identifying dominant fruiting species for a camera-trap sampling period, we led citizen scientists on systematic searches of "cordilheira" forests to locate individual trees with an abundance of freshly fallen fruits. The areas searched were

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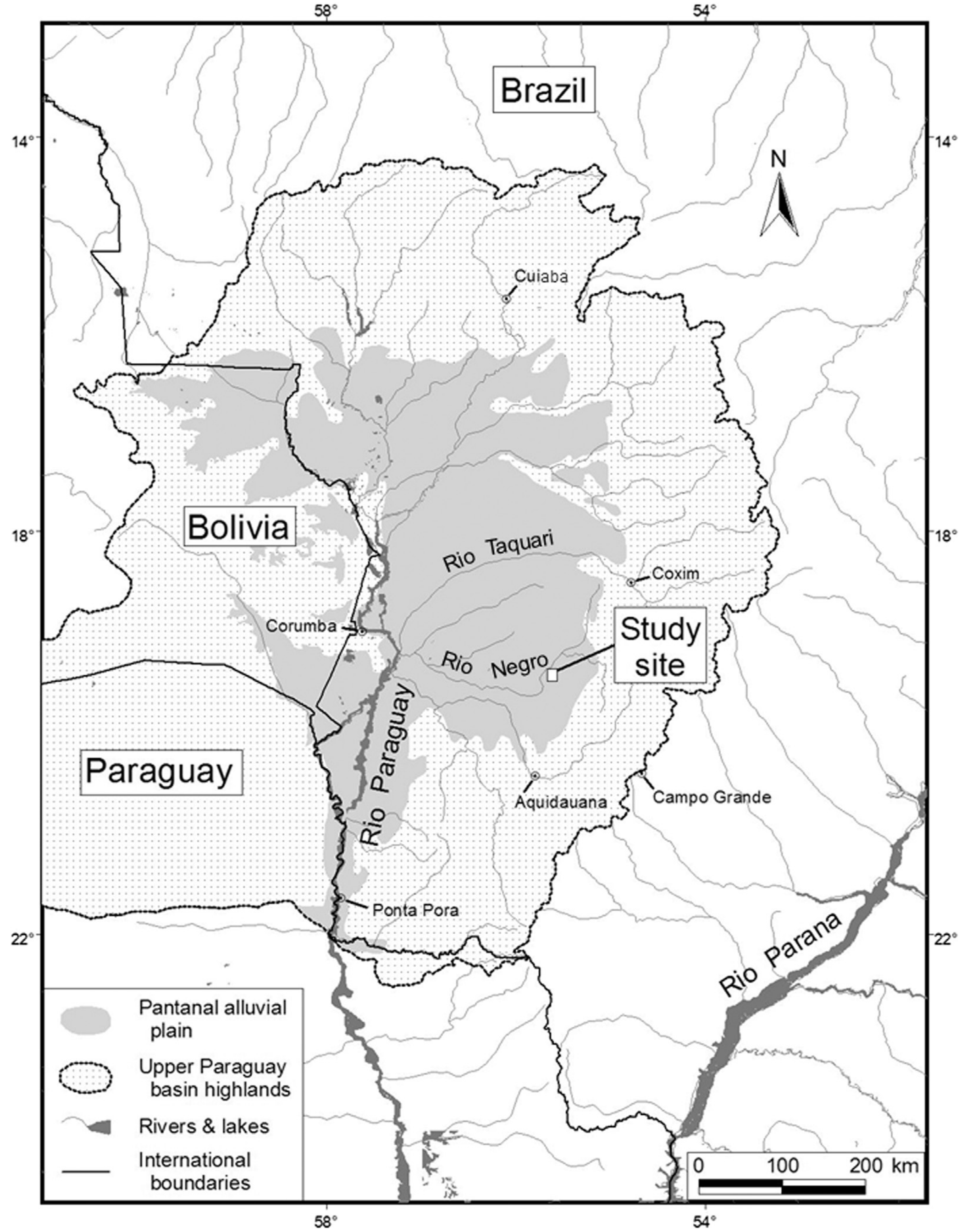

Fig. 1. Central-eastern South America showing the upper basin of the Paraguay River divided into highlands (stippled with dashed outline) and the alluvial plain of the Pantanal (light gray). The study site, which was comprised of 3 cattle ranches, was located in the upper Rio Negro subregion (Padovani, 2010) of the southern Pantanal, Município de Aquidauana, Mato Grosso do Sul, Brazil. International borders (black solid lines), selected rivers (dark gray lines and solid shapes), and principle cities (circular symbols) in the Pantanal and bordering highlands are also shown.

dispersed throughout the study region and included up to twenty cross-sectional transects (per sampling period) through “cordilheira” forest tracts. Depending on the abundance and distribution of dominant fruiting species, we chose from 2 to 5 focal trees for camera-trap surveys during each sampling period, and attempted to choose trees in both low and high cattle-impact areas.

2.3. Camera-trap surveys and quantification of animal visits to fruiting trees

Once focal trees of a fruiting species were chosen, citizen scientists placed digital camera traps (Cuddeback Capture IR 1132) one meter above the ground at a distance of approximately 3 to 4 m from the trees. Cameras were set to take pictures 24 h per day with a 1 min delay between consecutive photographs. We defined a camera-trap sample, i.e., the experimental unit for analyses, as all photo records of animals (frugivores and non-frugivores) from a single forest site with one focal fruiting tree. At each focal tree, only one camera-trap sample was collected.

To quantify animal visits to fruiting trees, citizen scientists recorded two variables from the photo records archived for each camera-trap sample: (1) the species of mammals and birds that visited the fruiting tree, and (2) the number of individuals of each animal species that visited the fruiting tree per unit time. For the second variable, citizen

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scientists counted the number of individuals of each animal species in each photo, summed the counts of all photos, and divided the totals by the number of camera-trap hours. The accuracy of species identifications by citizen scientists was facilitated by providing training with archived photos and regional fauna guides and encouraging questions and feedback. Project investigators evaluated accuracy of identifications and counts by verifying subsamples of the camera-trap sample photos. The second variable, number of photo records of an animal species per camera-trap hour, was well-suited to the objectives of the current study, because it gave more weight to species and individual animals (mainly frugivores) that appeared in multiple photos as they revisited or remained at a fruiting tree. This provided a measure of site (and possibly fruit) use, or foraging success, by the different animal species (Inouye, 1978).

2.4. Evaluation of cattle impact at camera-trap survey sites

We quantified the level of cattle impact at "cordilheira" forest sites where focal fruiting trees were surveyed based on: (1) current signs of cattle use, i.e., tracks, dung, and presence of grazed or browsed understory vegetation, (2) the number of months a site was occupied by cattle (period of use), and (3) the density of cattle within the grazing enclosure that included the forest site. We obtained period of use and cattle density information from ranch property records and interviews with landowners and workers, and cattle sign data from direct observations at forest sampling sites before camera traps were installed. We combined the direct observations, records and reports to give each forest site a cattle-impact score that ranged from 2 (occasional, low-intensity use by cattle, plus no direct signs of cattle use) to 6 (constant, high-intensity use by cattle, plus clear signs of cattle use). To test the efficacy of the scoring system for the forest sites, we regressed the number of cattle recorded in camera-trap samples on the assigned cattle-impact scores. For correlations with ordination axes (described below), we used the scoring system from 2 to 6. For all other analyses (described below and in Appendix A), we lumped scores from 2 to <4 and ≥4 to 6 into low and high cattle-impact categories, respectively.

2.5. Analyses of animal assemblages and comparisons between cattle-impact levels

To describe and compare the animal assemblages associated with dominant fruiting trees in low and high cattle-impact areas of "cordilheira" forests, we analyzed three sets of camera-trap samples. The 1st included the camera-trap samples of a single widespread palm species, *Attalea phalerata*, which was abundant in both low and high cattle-impact areas and had a lengthy (9 to 11 month) asynchronous fruiting period. In addition to a higher sample size obtained for the palm, the analysis had the advantage of partitioning out variability associated with multiple fruiting-tree species. The 2nd analysis included all camera-trap samples from all fruiting-tree species surveyed during the study. This analysis provided a more comprehensive test of cattle impact on fauna visiting fruiting trees by sampling the full range of dominant fruiting species in the study area. However, in addition to cattle-impact effects on faunal assemblages, the analysis included variability associated with natural features of the different fruiting-tree species, e.g., unique fruiting periods and biased distributions of the trees in relation to cattle impact. The 3rd analysis included all of the camera-trap samples and fruiting-tree species of the 2nd analysis, except those of *Bocageopsis mattogrossensis*, which had an unusual distribution and fruiting pattern. By excluding *B. mattogrossensis*, we were able to evaluate its influence on the results of the 2nd analysis and clarify more subtle patterns associated with the remaining fruiting-tree species of the 3rd analysis. Analyzing different subsets of samples from a dataset is a commonly-used procedure for interpreting ecological community patterns (McCune and Grace, 2002).

For the 3 sets of fruiting-tree species described above, we compared animal assemblages between sites in low and high cattle-impact areas with three aggregate community variables: (1) number of animal species per camera-trap sample, (2) Shannon diversity per camera-trap sample and (3) number of animals recorded (regardless of species) per camera-trap sample. The first 2 variables measured the richness and diversity of animal species assemblages visiting the fruiting-tree sites, while the third variable indicated the degree that fruiting-tree species and sites were used by the animal assemblages. Statistical methods for comparing the three aggregate animal-community variables between low and high cattle-impact areas are presented in Appendix A.

We explored patterns of mammalian and avian species composition among camera-trap sample sites using NMS, nonmetric multidimensional scaling (Mather, 1976; McCune and Mefford, 2006; PC-ORD, v. 5). Procedures for NMS ordinations are presented in Appendix A. For analyses of the 3 sets of fruiting-tree species described above, the variable, number of animals per camera-trap hour, was used in camera-trap sample by animal species matrices. These were associated with matrices of camera-trap samples by environmental variables that described conditions at fruiting-tree sites (e.g., tree species and cattle-impact level). The latter matrices allowed us to investigate correlations between animal assemblages and continuous environmental variables and compare groups of camera-trap samples defined by categorical variables. We used joint plots to show the trends (strength and direction in species space) among camera-trap sites of key variables in relation to ecological community patterns extracted by ordination axes (McCune and Mefford, 2006). The variables included cattle-impact score and aggregate community metrics. To facilitate interpretation and comparisons of ordinations between the 3 sets of fruiting-tree species analyzed, we performed rigid rotations of each solution aligning the trends for cattle-impact scores with the most closely associated ordination axes (McCune and Grace, 2002; McCune and Mefford, 2006).

To compare animal communities between fruiting-tree sites in low and high cattle-impact areas, we used MRPP (Multi-response Permutation Procedures) and the same distance matrices used for NMS ordinations (McCune and Mefford, 2006; Mielke, 1984). If animal communities were significantly different between low and high cattle-impact areas ($\alpha = 0.05$), we used Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) to quantify the value of particular animal species in differentiating the communities (McCune and Grace, 2002; ISA analysis is described in Appendix A).

3. Results

3.1. Dominant fruiting-tree species surveyed

From January 2007 through December 2008, citizen scientists conducted 35 camera-trap surveys to monitor animal visits to dominant fruiting-tree species in "cordilheira" forests. Table 1 shows the ten species of dominant fruiting trees surveyed, months when fruit fall occurred and surveys were conducted, sample sizes of camera-trap surveys in low and high cattle-impact areas, mean Sørensen dissimilarity of recorded animal assemblages relative to assemblages recorded at other fruiting-tree species (i.e., greater dissimilarity corresponded with relatively distinct assemblages), and mean number of animal photos per camera-trap hour. Additional information on the timing and abundance of fruits are presented in Appendix A.

During extensive searches with citizen scientists each sampling period, we observed only two dominant fruiting-tree species that occurred in both low and high cattle-impact areas, i.e., *A. phalerata* and *Agonandra brasiliensis* (Table 1). We observed the fruiting trees of seven other species exclusively in low-impact areas, and those of *B. mattogrossensis* solely in high cattle-impact areas (Table 1).

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Table 1
Dominant fruiting-tree species of "cordilheira" forests monitored during 2007 and 2008 camera-trap surveys of mammals and birds in low and high cattle-impact areas of the upper Rio Negro subregion of the Pantanal. For each fruiting-tree species, we present the period (in months) when camera-trap surveys were conducted, the number of fruiting trees surveyed in low and high cattle-impact areas, mean Sørensen dissimilarity of the recorded animal assemblage relative to animal assemblages recorded at other fruiting-tree species, and mean number of animal photos, with and without (in parentheses) cattle, per camera-trap hour.

Family	Species[a]	Local name	Camera-trap survey periods	No. of trees surveyed:		Sørensen dissimilarity of animal assemblage	No. animals/camera-trap hour, cattle: included (excluded)
				Low cattle-impact areas	High cattle-impact areas		
Annonaceae	*Bocageopsis mattogrossensis*		Feb.–Mar.[b]		4	0.843[c]	3.52 (2.80)
Arecaceae	*Acrocomia aculeate*	bocaiúva	Oct.	2		0.789[c]	0.35 (0.35)
	Attalea phalerata	acuri	Oct.–Jul.	7	6	0.790[c]	0.38 (0.30)
Burseraceae	*Protium heptaphyllum*	amescla	Oct.–Nov.	2		0.759	0.31 (0.30)
Leguminosae-Faboideae	*Dipteryx alata*	cumbaru	Jul.	1		0.768	0.07 (0.07)
Malvaceae	*Guazuma ulmifolia*	Chico-magro	Jun.–Nov.	6		0.807[c]	0.15 (0.15)
Opiliaceae	*Agonandra brasiliensis*	quina brava	Oct.–Dec.	1	1	0.717	0.25 (0.24)
Rubiaceae	*Genipa americana*	jenipapo	Aug.–Oct.	3		0.760[c]	0.22 (0.20)
Sapindaceae	*Dilodendron bipinnatum*	Maria-pobre	Oct.	1		0.792	0.17 (0.17)
Verbenaceae	*Vitex cymosa*	tarumã	Nov.	1		0.711	0.15 (0.14)

[a] Authorities for Latin names of plants are presented in Pott and Pott (1994).
[b] High abundance fruit crop occurred only in 2007.
[c] 5 species with the highest mean Sørensen dissimilarities of recorded animal assemblages in relation to those of other fruiting-tree species.

3.2. Evaluation of cattle-impact scoring at camera-trap survey sites

The regression of numbers of cattle recorded per camera-trap hour (logarithm, base 10) on assigned cattle-impact scores at the 35 survey sites showed a significant positive relationship between cattle records and cattle-impact scores ($F_{1,\,33} = 36.10$, $P \ll 0.0001$, $r^2 = 0.52$), indicating that the scoring system was well suited to evaluating the level of cattle activity at camera-trap survey sites.

3.3. Animal species and frugivory records at fruiting trees

Citizen scientists processed 835 days of camera trap data, recording a total of 5639 animal visits to fruiting trees during the 2007 and 2008 camera-trap surveys (Table A.1; Appendix A). The 35 camera-trap sample periods lasted an average of 19.7 days (SD = 10.6), and the average number of animals recorded per sample period was 161 (SD = 111) with cattle included, and 140 (SD = 98) with cattle excluded. Based on assessments conducted by project investigators of subsamples of camera-trap records processed by citizen scientists, we found that >99% of species identifications and counts were correct. Because of uncertainties in distinguishing the 2 brocket deer species, *Mazama americana* and *M. gouazoubira*, and the 2 armadillo species, *Dasypus novemcinctus* and *Euphractus sexcinctus*, in some of the photos, we lumped their records into 2 categories for all analyses presented below, i.e., *Mazama* spp. and armadillos.

The native non-volant mammals recorded during the camera-trap surveys included 6 ungulates, 2 rodents, 4 xenarthrans, and 6 carnivores (Table A.1). Cattle, largely of the zebu variety (*Bos primigenius indicus*), and feral pigs (*Sus scrofa*) were the only exotic animals recorded. Eleven native bird species from 8 families were also recorded in the camera-trap samples (Table A.1). Twenty-five of the 29 native animals (86%) from "cordilheira" forests were either photographed foraging on fruits during the surveys, or are known from the literature to include fruits in their diet (Eisenberg and Redford, 1999). The remaining 4 native species were either strict carnivores, *Leopardus pardalis* and *Puma concolor*, or insectivores, *Myrmecophaga tridactyla* and *Tamandua tetradactyla*. The percentages of camera-trap records at each fruiting-tree species for the ten most recorded animal species, plus the Shannon diversity and evenness of their visits, are presented in Fig. A.1 (Appendix A).

3.4. Comparisons of animal communities recorded at dominant fruiting trees between low and high cattle-impact areas of "cordilheira" forests

For the three sets of camera-trap samples analyzed, i.e., camera-trap samples from: (1) *A. phalerata* only, (2) all 10 fruiting-tree species, and (3) all fruiting tree-species, except *B. mattogrossensis*, Table 2 compares three aggregate variables describing animal communities (cattle records excluded) at fruiting-tree sites between low and high cattle-impact areas. The mean number of animal species per camera-trap sample and Shannon diversity per camera-trap sample were significantly greater at low cattle-impact sites in comparison to high cattle-impact sites for all three sets of camera-trap samples analyzed (Table 2). The total number of animal records per camera-trap sample was significantly greater at low-cattle impact sites in comparison to high cattle-impact sites for the first (*A. phalerata*-only) and third (all fruiting tree-species, except *B. mattogrossensis*) analysis sets, but for the analysis including all 10 fruiting-tree species, there was no significant difference between cattle-impact categories (Table 2). The lack of significant difference in total number of animals between low and high cattle-impact areas for the analysis including all 10 fruiting-tree species was due to the inclusion of *B. mattogrossensis* camera-trap samples, which included 67% of all animal records from high cattle-impact areas (Tables 1, 2 and A.1; Fig. A.1).

Results, settings and matrix dimensions for the best NMS ordination solutions describing and summarizing animal-species compositional trends among camera-trap sample sites in relation to cattle impact, fruiting-tree species, and aggregate community variables are presented in Table A.2 (Appendix A) for the three sets of camera-trap samples analyzed. The number of readily-interpretable ordination axes was 2 for the *A. phalerata*-only camera-trap sample dataset, and 3 for both the dataset of camera-trap samples from all 10 fruiting-tree species, and the dataset of all fruiting tree-species, except *B. mattogrossensis* (Table A.2). The final stress values were similar and <14 for all three NMS ordination solutions, indicating significant structure or differentiation among animal communities of camera-trap samples in the datasets, and all three ordinations represented substantial proportions (>0.7) of the variance in the original datasets (Table A.2). Overall, the results indicated that the ordination solutions obtained were useful for interpreting trends among camera-trap samples of animal communities at fruiting-tree sites.

Biplots of the best NMS ordinations of animal communities from the three sets of camera-trap samples analyzed are shown in Fig. 2a–c. Camera-trap samples (points) are coded by cattle impact category (i.e., low vs. high), and joint plots (dashed arrows) show the strength and direction in relation to camera-trap samples of trends in cattle impact scores (Impact) and two aggregate community variables, i.e., no. of animal species recorded in camera-trap samples (No. spp.) and total number of animals recorded per camera-trap sample (No. anim.; Fig. 2a–c).

For all three sets of camera-trap samples analyzed, ordinations clearly discriminated the animal assemblages of low cattle-impact sites with

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Table 2

Comparisons of aggregate variables describing animal assemblages at fruiting trees (cattle records excluded) between low and high cattle-impact areas of "cordilheira" forests in the upper Rio Negro subregion of the Pantanal. The variables are: number of animal species recorded per camera-trap sample (mean ± 95% CI), Shannon diversity of animal species per camera-trap sample (mean ± 95% CI), and total number of animals recorded (regardless of species) per camera-trap sample (mean ± 95% CI). Values are shown for each of the three analysis categories described in the text: 1. the data set of surveys from *Attalea phalerata*, 2. the full data set of surveys from 10 dominant fruiting species, and 3. the data set excluding surveys of *Bocageopsis mattogrossensis*. For the three variables, we present probabilities (*P*-values) from Monte-Carlo permutation tests (500 runs, $\alpha = 0.05$) showing whether differences observed between means of low and high cattle-impact areas (i.e., d_{obs}) were greater than differences calculated from an equal number of randomly-chosen camera-trap samples (low and high cattle-impact samples pooled). Sample sizes for the means of randomly-chosen camera-trap samples were equal to the number of samples in high cattle-impact areas, i.e., for analysis levels 1, 2, and 3, $n = 6$, 11 and 7, respectively.

	No. species/camera-trap sample		Shannon diversity/camera-trap sample		No. animals/camera-trap sample	
Analysis Category:	Low cattle-impact areas	High cattle-impact areas	Low cattle-impact areas	High cattle-impact areas	Low cattle-impact areas	High cattle-impact areas
1. Surveys of *A. phalerata*	9.4 (± 1.8)	2.7 (± 2.5) $d_{obs} = 6.76$[a] $P \ll 0.004$[b,c]	1.27 (± 0.30)	0.48 (± 0.59) $d_{obs} = 0.80$ $P \ll 0.004$[c]	148 (± 52.3)	35 (± 32.7) $d_{obs} = 113.3$ $P = 0.005$[c]
2. Full data set, surveys of 10 fruiting-tree species	9.3 (± 1.2)	4.2 (± 2.2) $d_{obs} = 5.10$ $P \ll 0.004$[c]	1.32 (± 0.20)	0.54 (± 0.36) $d_{obs} = 0.79$ $P \ll 0.004$[c]	143 (± 29.9)	133 (± 83.2) $d_{obs} = 9.1$ $P = 0.616$
3. *B. mattogrossensis* surveys excluded from full data set	9.3 (± 1.2)	3.6 (± 3.0) $d_{obs} = 5.68$ $P \ll 0.004$[c]	1.32 (± 0.20)	0.60 (± 0.56) $d_{obs} = 0.72$ $P \ll 0.004$[c]	143 (± 29.9)	48 (± 37.4) $d_{obs} = 95.0$ $P < 0.004$[c]

[a] d_{obs}, observed difference between low and high cattle-impact areas.

[b] Probability of obtaining observed difference between low and high cattle-impact areas relative to differences obtained from an equal number of randomly chosen camera-trap samples (500 permutations).

[c] Significant difference between cattle-impact categories ($\alpha = 0.05$).

relatively high numbers of animal species from those of high cattle-impact sites with relatively low numbers of animal species (Fig. 2a–c). These differences were most strongly associated with ordination axis 1 and are demonstrated by joint plots of the variables, cattle-impact score (Impact) and number of animal species (No. spp.), which show strong, but opposite trends (Fig. 2a–c). For the three sets of camera-trap samples, *A. phalerata* only, all 10 fruiting-tree species, and all fruiting tree-species, except *B. mattogrossensis*, cattle-impact score was negatively correlated with axis 1, i.e., $r = -0.842$, $r = -0.809$, and $r = -0.829$, respectively, while number of animal species was positively correlated with axis 1, i.e., $r = 0.700$, $r = 0.540$, and $r = 0.541$, respectively. These strong cattle-impact related trends captured by the ordination are illustrated in Fig. 3a and b with regressions of cow records per camera-trap hour (as a measure of cattle impact), and animal species richness, on scores of ordination axis 1. The regression of cow records on axis-1 scores, which decrease with increasing cattle impact, showed a significant negative relationship ($F_{1,\,33} = 64.01$, $P \ll 0.0001$, $r^2 = 0.66$; Fig. 3a), while the regression of no. of animal species on axis-1 scores showed a significant positive relationship ($F_{1,\,33} = 18.23$, $P = 0.0002$, $r^2 = 0.36$; Fig. 3b).

Ordination axis-2 was strongly correlated with overall number of animal records at camera-trap survey sites (No. anim.) for all three sets of camera-trap samples analyzed, i.e., $r = 0.756$, $r = 0.638$ and $r = 0.776$, respectively, for *A. phalerata* only, all 10 fruiting-tree species, and all fruiting tree-species, except *B. mattogrossensis* (Fig. 2a–c). However, the animal species records and fruiting trees most strongly associated with these abundance trends were different for the full dataset of all 10 fruiting-tree species in comparison to the analysis excluding *B. mattogrossensis*. For the full dataset, large numbers of *T. pecari* and cow records at *B. mattogrossensis* trees in high cattle-impact areas were strongly correlated with the abundance trend of axis 2 (Fig. 2b), while in the dataset excluding *B. mattogrossensis*, records from a variety of animal species were associated with the abundance trend and a range of fruiting-tree species, mostly in low cattle-impact areas, including *A. phalerata*, *G. ulmifolia*, *P. heptaphyllum*, *A. brasiliensis*, and *A. aculeate* (Fig. 2c). For the full dataset, the joint plot of total number of animal records (No. anim.) and polygons outlining high cattle-impact sites of *A. phalerata* and *B. mattogrossensis*, show how ordination axis 2 differentiated high cattle-impact sites of the two fruiting-tree species; both cows and *T. pecari* being more strongly associated with the *B. mattogrossensis* sites (Fig. 2b). In contrast, the joint plot of total number of animal records (No. anim.) for the dataset excluding *B. mattogrossensis* shows that greater abundance is more strongly associated with low cattle-impact sites (Fig. 2c). This is even more apparent based on the joint plot of total number of animal records (No. anim.) in the *A. phalerata*-only dataset (Fig. 2a). For *A. phalerata*, the largest differences in the number of animal records occurred among low cattle-impact sites with a variety of animal species contributing to the observed abundance trends, i.e., *T. pecari* ($r = 0.716$), the armadillos, *D. novemcinctus* and *E. sexcinctus* ($r = 0.552$), *C. fasciolata* ($r = 0.542$), *S. scrofa* ($r = 0.473$), and *Mazama* spp. ($r = 0.435$).

Confirming the patterns observed in the three ordinations described above, MRPP comparisons using Sørensen dissimilarity showed that the animal assemblages of camera-trap samples in low and high cattle-impact categories were significantly different, i.e., for the *A. phalerata* only dataset, $T = -3.742$, $A = 0.211$, $P = 0.0030$; for the dataset of all 10 fruiting-tree species, $T = -6.9176$, $A = 0.1209$, $P < 0.0001$, and for the dataset of all fruiting tree-species, except *B. mattogrossensis*, $T = -6.23$, $A = 0.134$, $P < 0.0001$.

3.5. Indicator species of low cattle-impact conditions in "cordilheira" forests

Based on ordinations trends and significant differences shown by MRPP comparisons of animal communities, we conducted Indicator Species Analyses (ISA) for the three sets of camera-trap samples analyzed to identify animal species that were characteristic (or good indicators) of low, or high, cattle-impact sites. Table 3 presents indicator values and Monte Carlo test probabilities for species that were significant ($\alpha = 0.05$) or nearly significant ($\alpha = 0.07$) indicators of impact categories for at least one of the 3 datasets analyzed.

The frugivorous brocket deer species (*M. americana* and *M. gouazoubira*) and the insectivorous/omnivorous yellow and nine-banded armadillos (*D. novemcinctus* and *E. sexcinctus*) were significant, or nearly-significant, indicators of low cattle-impact conditions for all three of the fruiting-tree species datasets (Table 3). The frugivorous collared peccary (*P. tajacu*) was a significant indicator of low cattle-impact conditions for the ISAs that included multiple fruiting-tree species, but because it was a relatively infrequent visitor to fruiting *A. phalerata* palms in both low (4.0% of *P. tajacu* records) and high (0.1% of records) cattle-impact areas (Fig. A.1), it was not a significant indicator of *A.*

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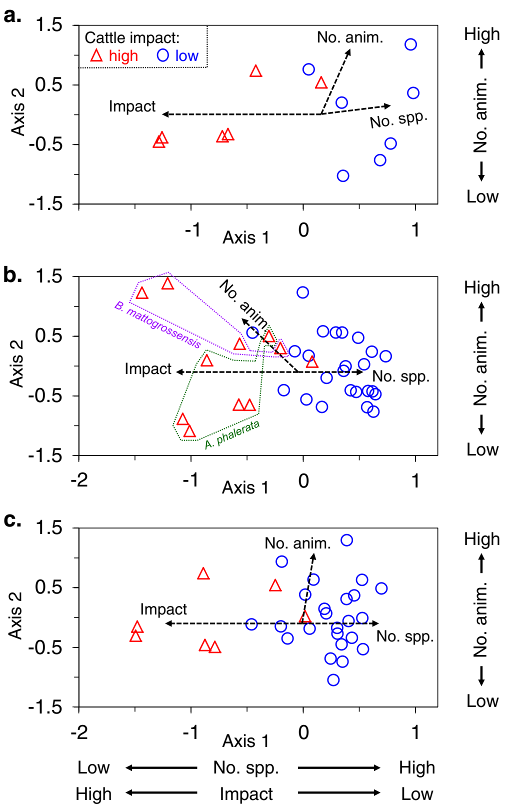

Fig. 2. NMS ordinations of camera-trap animal records at fruiting-tree sites in "cordilheira" forests of the upper Rio Negro subregion of the southern Pantanal, Município de Aquidauana, Mato Grosso do Sul, Brazil (2007–2008). Figures show biplot views of the 2-dimensional solution for: **a.** the data set of surveys from *A. phalerata*, and the 3-dimensional ordination solutions for: **b.** the full data set of animal records from 10 dominant fruiting-tree species, and **c.** the full data set with *B. mattogrossensis* records excluded. Sites are coded by cattle-impact category (i.e., low or high), and joint plots (dashed arrows) show strength and direction of environmental variables (**Impact** = cattle impact) and aggregate animal community variables (**No. spp.** = number of animal species in camera-trap samples, **No. anim.** = total number of animal records in camera-trap samples). In **b.**, polygons outline high cattle-impact sites of *A. phalerata* and *B. mattogrossensis*. For the three plots, axis notes show principal environmental and community trends.

phalerata sites with either low or high cattle-impact conditions (Table 3). The carnivorous ocelot (*L. pardalis*), which was recorded 24 out of 26 total times at low cattle-impact sites (Table A.1), was a nearly-significant indicator of low cattle-impact conditions for the *A. phalerata*-only and full 10 fruiting-tree species datasets (Table 3). With the obvious exception of cows, none of the mammal or bird species recorded during camera-trap surveys, including exotic feral pigs (*S. scrofa*), were significant indicators of high cattle-impact conditions.

The roles of highly-frugivorous white-lipped peccaries (*T. pecari*) and bare-faced curassows (*C. fasciolata*) as indicators of cattle impact were strongly affected by the inclusion or removal of *B. mattogrossensis* records in camera-trap sample datasets (Table 3). For the full dataset that included *B. mattogrossensis*, neither species was a significant indicator of either low or high cattle-impact conditions. However, because of the high number of visits by *T. pecari* to *B. mattogrossensis* trees, the ISA placed *T. pecari* in the high cattle-impact category (Table 3). For the multiple fruiting-tree species dataset that excluded *B. mattogrossensis* records, the categorical placement of *T. pecari* switched from the high to low cattle-impact group, indicating that in the absence of *B. mattogrossensis* samples, *T. pecari* occurred more frequently and in greater abundance in low cattle-impact areas. Additionally, the Monte Carlo probability values (for obtaining the observed indicator values) of both *T. pecari* and *C. fasciolata* decreased, suggesting increased value of these species as indicators of low cattle-impact conditions (Table 3). In marked contrast to results

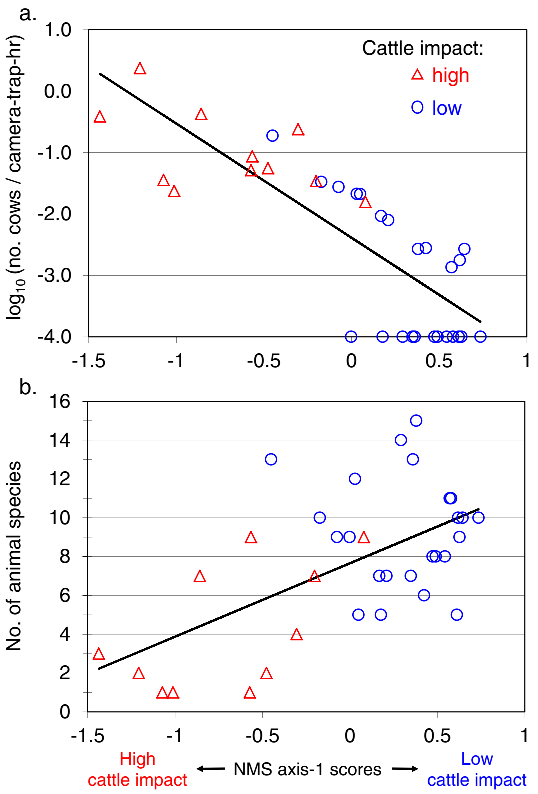

Fig. 3. Opposing trends of: **a.** camera-trap records of cattle and **b.** animal species richness, associated with a cattle-impact gradient (NMS axis-1) extracted by ordination of the full data set of camera-trap animal records at 10 fruiting-tree species in "cordilheira" forests of the upper Rio Negro subregion of the southern Pantanal, Município de Aquidauana, Mato Grosso do Sul, Brazil (2007–2008). Fruiting-tree sites (plot points) are coded by cattle-impact category (i.e., low or high).

from the full data set, the ISA of cattle-impact categories for the *A. phalerata*-only dataset identified both *T. pecari* and *C. fasciolata* as highly-significant indicators of sites with low cattle-impact conditions (Table 3).

4. Discussion

4.1. Cattle impacts on dominant fruiting-tree species of "cordilheira" forests

Our systematic searches of "cordilheira" forests with citizen scientists suggested that a majority of dominant fruiting-tree species had uneven distributions, and/or fruiting patterns, in relation to the degree of cattle-impact, and that overall fruiting-tree diversity was lower in areas of high cattle-impact. For example, we only found fruiting *B. mattogrossensis* trees in areas of high cattle-impact, and fruiting *P. heptaphyllum* trees in areas of low cattle-impact. These results were consistent with tree-density estimates of Santos (2011), who conducted a parallel survey in our study area comparing woody (>10 cm dbh) and understory vegetation between "cordilheira" forest plots in areas of low and high cattle use. Also similar to our results, Santos (2011) showed that the diversity of all woody plant species in low cattle-impact forest plots was greater than it was in high cattle-impact forest plots.

Long-term cattle-related vegetation and habitat alterations are the most plausible explanations for: (1) the uneven distribution of fruiting-tree species between "cordilheira" forest areas with differing levels of cattle impact and (2) the greater diversity of fruits available in forested areas with low levels of cattle activity. Johnson et al. (1997) and Santos Júnior (2010) showed that recruitment of the tree *Sterculia apetala*, has been reduced in Pantanal forests accessible to cattle, and that losses of adult trees, as well as seedlings, have been due to a

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Table 3
Indicator Species Analysis (Dufrêne and Legendre, 1997) of mammalian and avian fauna recorded during camera-trap surveys of dominant fruiting-tree species in low and high cattle-impact areas of "cordilheira" forests in the upper Rio Negro subregion of the Pantanal. Indicator values (%) and probabilities (*P*-values) of Monte Carlo tests are shown for species that were significant ($\alpha = 0.05$), or nearly significant ($\alpha = 0.07$), indicators of impact categories in at least one analysis category: 1. the data set of surveys from *Attalea phalerata*, 2. the full data set of surveys from 10 dominant fruiting species, and 3. the full data set excluding surveys of *Bocageopsis mattogrossensis*. *P*-values represent the proportions of Monte-Carlo runs with indicator values equal to, or greater than, observed indicator values (McCune and Mefford, 2006).

	Analysis categories for camera-trap surveys of animal assemblages at fruiting-tree species:					
	1. Surveys of *A. phalerata*		2. Full data set, surveys of ten fruiting-tree species		3. *B. mattogrossensis* surveys excluded from full data set	
Cattle impact category: *Indicator species*	Indicator value (%)	Monte Carlo *P*-value	Indicator value (%)	Monte Carlo *P*-value	Indicator value (%)	Monte Carlo *P*-value
Low cattle-impact:						
Mazama spp.[a]	57.1	0.0682[b]	66.7	0.0066[c]	66.7	0.0200[c]
Pecari tajacu	54.3	0.1136[d]	65.2	0.0312[c]	72.0	0.0256[c]
Dasypus novemcinctus[e] *Euphractus sexcinctus*[e]	78.8	0.0196[c]	51.7	0.0406[c]	53.7	0.0778[d]
Leopardus pardalis	57.1	0.0668[b]	41.7	0.0666[b]	45.3	0.1114[d]
Crax fasciolata	95.2	0.0140[c]	61.8	0.3923[d]	76.3	0.1340[d]
Tayassu pecari	86.9	0.0250[c]	–	–	62.3	0.1954[d]
High cattle-impact:						
Bos primigenius indicus	81.6	0.0450[c]	96.2	0.0002[c]	90.2	0.0010[c]
Tayassu pecari	–	–	67.1	0.4803[d]	–	–

[a] Records of *Mazama* spp. were lumped.
[b] Nearly significant indicator of low or high cattle-impact sites ($\alpha = 0.07$) within analysis category.
[c] Significant indicator of low or high cattle-impact sites ($\alpha = 0.05$) within analysis category.
[d] Not a significant indicator of impact within analysis category.
[e] Records of armadillo species (*D. novemcinctus* and *E. sexcinctus*) were lumped.

range of other factors related to cattle operations, e.g., deforestation, increased wind damage in remaining forest fragments, and uncontrolled pasture fires. Nunes et al. (2008) demonstrated that as the area of naturally-occurring forest patches, like "cordilheiras", is reduced, there is a decline in the biomass of understory vegetation and litter in response to increasing intensities of cattle use. Similarly, Santos (2011) showed that the densities of tree seedlings and shrubs comprising "cordilheira" forest understory were significantly greater in low cattle-impact plots, while the densities of herbaceous understory plants were greater in high cattle-impact plots. A shift to herbaceous vegetation in cattle-impacted areas would be expected to affect long-term forest successional patterns (Tomas et al., 2009), reducing the availability of fruiting-tree species as observed in the current study.

4.2. Cattle impacts on animal assemblages visiting fruiting trees

Citizen-scientist camera-trap monitoring has provided the first definitive evidence that cattle have a strong impact on the animal assemblages visiting fruiting trees in "cordilheira" forests of the southern Pantanal. Whether we analyzed camera-trap records of fauna from only *A. phalerata* palms, all 10 dominant fruiting-tree species, or all fruiting-tree species, except *B. mattogrossensis*, the composition of animal assemblages was always significantly different between low and high cattle-impact areas, and the number of animal species and Shannon diversity per camera-trap sample were always greater at low cattle-impact sites. From a spatial perspective that includes whole "cordilheira" forest patches and multiple fruiting-tree species, a greater diversity of animals visiting areas with less cattle impact makes sense if, as described above, a greater diversity of fruit resources were available, and if, as observed from the camera-trap surveys, the fauna characteristically visited a wide range of fruiting-tree species (Fig. A.1). Preferential use of areas with a wider range of fruit resources by most fauna would also explain the species compositional differences between the impact categories. At this multiple fruiting-tree species scale of analysis, the data suggested that reduced faunal diversity and species compositional differences in areas with high levels of cattle impact were primarily due to long-term cattle-mediated alterations of "cordilheira" forest vegetation, which as outlined above, reduced the diversity of woody plants and fruit availability (Santos, 2011).

In addition to long-term vegetation alterations, our analysis of fauna visiting a single fruiting-tree species, i.e., *A. phalerata*, suggested that cattle impacts occurring during the study period may also have affected faunal diversity and composition by interfering with native fauna use of *A. phalerata* fruits and/or by depleting *A. phalerata* fruit resources. In support of this idea, Desbiez et al. (2011) showed that *A. phalerata* fruits were an important component of dry season cattle diets when their grazing enclosures included "cordilheira" forests. In addition, of the 443 camera-trap records of cattle obtained at *A. phalerata* sites, none showed other animal species, including feral pigs, simultaneously foraging for the fruits, suggesting that the larger and more numerous cows either displaced other fruit consumers (interference competition), or consumed so many of the fruits that other frugivores were less drawn to the sites (exploitation competition).While it is common in open grasslands of the Pantanal to observe cattle grazing in the vicinity of native species, like capybaras (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) (Desbiez et al., 2011), in the confines of the forest at a concentrated patch of fruits, limited space and food may promote episodes of interspecific competition (see also Shepherd and Ditgen, 2005).

The lower diversity (and total number) of animals visiting high cattle-impact sites may also be related to altered movements and routes of some frugivorous animals in response to a reduction in the diversity of fruit resources and/or fragmentation and disturbance of the naturally-patchy "cordilheria" forests (Keuroghlian et al., 2015; Nunes et al., 2008). For example, it may be energetically more efficient for highly-mobile white-lipped peccaries, which in the Pantanal form subherds of 30 to 80 individuals and characteristically seek out abundant fruit resources, to abandon routes through fruit-poor, high cattle-impact areas in favor of fruit-rich, low cattle-impact areas (Altrichter et al., 2001; Beck, 2006; Keuroghlian and Eaton, 2008; Keuroghlian et al., 2015). In addition, in areas where deforestation has occurred, *T. pecari* routes that characteristically wind through and along the edges of the long and narrow "cordilheira" forest formations may be disrupted, reducing visits to isolated "cordilheira" forest patches as herds are forced to find alternate routes around matrices of exotic-grass monocultures (Keuroghlian et al., 2015). Visits by native frugivores to fruiting trees isolated in "cordilheira" forest fragments will be further reduced as the intensity of cattle activity in the surrounding matrix of exotic grasses and in the forest patches increases (Nunes et al., 2008).

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4.3. Cattle impacts on animal species visiting fruiting trees

From ordination trends of animal species records, and results from Indicator Species Analyses, we distinguished 3 groups of animal species based on their responses to increasing levels of cattle impact: (1) species that were relatively intolerant of cattle impact, (2) species that appeared unaffected by cattle impact, and (3) species with different responses to cattle impact depending on the fruit resource. The brocket deer, *Mazama* spp., and collared peccary, *P. tajacu*, which mix frugivory with varying degrees of browsing and grazing, the armadillos, *D. novemcinctus* and *E. sexcinctus*, which mix frugivory with insectivory and omnivory, and the carnivorous ocelot, *L. pardalis*, were consistently associated with fruiting-tree sites where cattle activity was low. In other words, these species were negatively affected by cattle impacts. In addition to long-term vegetation alterations described previously, both displacement of native fauna and depletion of fruit patches by cattle were plausible explanations for the relative absence of the above frugivorous species from high cattle-impacts sites. Among common medium–large sized mammals in the Pantanal, brocket deer and collared peccaries are prone to flee when disturbed and are more frequently encountered in forested, rather than open habitats (Desbiez et al., 2009, 2010; Keuroghlian et al., 2009a). So, displacement of these species by a herd of cattle foraging in "cordilheira" forest is one possible scenario. The small-sized armadillos, in addition to being vulnerable to cattle trampling and fruit depletion, may also avoid areas where cattle herds have cleared forest litter and the associated insects, e.g., as Nunes (2009) documented for 3 understory insectivorous birds of "cordilheira" forests. Based on our results, it is clear that cattle impacts were significant, and that these frugivorous indicator species, which are regionally abundant and important in structuring forest communities via seed dispersal and predation (Desbiez et al., 2009, 2010; Keuroghlian et al., 2009b), would benefit from the range of available, but rarely adopted, ranch management practices that reduce cattle activities in "cordilheira" forests and other non-pasture environments (e.g., Eaton et al., 2011; Santos et al., 2004, 2008).

This study provides some of the first evidence showing that cattle have a negative impact on a native carnivore in the Pantanal, namely the ocelot (*L. pardalis*). Clearly, if potential prey aggregate at fruiting trees in "cordilheira" forests, and are more diverse and abundant at low cattle-impact sites, it makes sense that ocelots search for prey more frequently at fruiting trees in low cattle-impact areas.

Agoutis (*Dasyprocta azarae*), coatis (*Nasua nasua*), Brazilian tapirs (*Tapirus terrestris*), and feral pigs (*S. scrofa*) were not significant indicators of low or high cattle-impact conditions, and appeared relatively unaffected by cattle activity. *T. terrestris*, in addition to fruits, includes a large proportion of herbaceous plants in its diet (Bodmer, 1990), *N. nasua* is highly omnivorous (Schaller, 1983) and *S. scrofa*, in addition to fruits, includes a variety of herbaceous vegetation and sources of animal protein in its diet (Campos, 1993; Desbiez et al., 2009). This flexibility potentially allows these species to consume alternative foods in areas and during periods of cattle-mediated fruit depletion.

D. azarae, however, is highly frugivorous and territorial with a small home range (approximately 2 to 4 ha) (Eisenberg and Redford, 1999; Jorge and Peres, 2005; Schaller, 1983), so would be expected to have fewer dietary or ranging options for adjusting to the presence of foraging cattle. Its abundance and role as a principal consumer of *A. phalerata* in the Pantanal (Desbiez, 2007; Desbiez et al., 2010), and our results showing substantial *D. azurae* activity in high cattle-impact areas, suggested that the species had an effective means of coexisting with cattle. Possibilities include staggering their foraging periods so as not to overlap with cattle herds, and consuming scatter-hoarded fruits when cattle activity was high around fruiting trees and palms.

The unique and varied response of highly-frugivorous bare-faced curassows, *C. fasciolata*, and white-lipped peccaries, *T. pecari*, to increasing cattle impact at fruiting-tree sites appeared to depend on the spatial and temporal availability, as well as the appeal and nutritional value, of the available fruits. Both species used the full range of dominant fruit sources in the region (Fig. A.1) and based on studies of *T. peccary* ranging behavior, were continually on the move in response to temporal and spatial fruit availability patterns (Keuroghlian et al., 2009b; Keuroghlian et al., 2015). When the dominant fruit available during a sampling period was distributed relatively evenly among areas differentially affected by cattle, e.g., as is the case for *A. phalerata*, both *C. fasciolata* and *T. pecari* preferentially used fruiting-tree sites in low cattle-impact areas. Explanations (discussed previously) included greater energetic efficiency of traveling through undisturbed natural habitat and greater availability and diversity of other fruit sources. However, if a highly-valued fruit, like *B. mattogrossensis*, was available only in high cattle-impact areas, *T. pecari* and *C. fasciolata* actively sought out the fruits, making frequent visits to highly-impacted sites. As a measure of the overall use, or appeal, of *B. mattogrossensis* fruits, the average number of animal records per camera-trap hour was 9 times greater than that of the second-ranked fruiting-tree species, *A. phalerata* (Table 1). Based on our observations, the fruits of *B. mattogrossensis* contained a considerable amount of edible pulp, and if they are similar to others in the family Annonaceae, are highly nutritious (Joly, 1987). The appeal of the fruit was so great for *T. pecari* that on several occasions, they were recorded foraging simultaneously with cattle.

4.4. Conservation implications of cattle-related impacts in the Pantanal

Not surprisingly, results from our camera-trap surveys concurred with related studies from the Pantanal (Johnson et al., 1997; Nunes, 2009; Tomas et al., 2009) and studies from many other environments and regions, demonstrating that cattle, and cattle industry-related activities, have strong and often negative impacts on native fauna and flora (Chaikina and Ruckstuhl, 2006; Elliott and Barrett, 1985; Moser and Witmer, 2000). Overall, our results, and those of Santos (2011), showed that in areas of "cordilheira" forest used heavily by cattle, the flora was impoverished, fruit diversity was less, and animal assemblages were reduced to a small subset of native forest fauna, namely, those that were tolerant of cattle-related disturbance. This simplification, or homogenization, of the forest community appeared to be a consequence of cascading cattle-mediated impacts that potentially threaten the long-term persistence of Pantanal forests, especially in regions where native habitat conversion and fragmentation are increasing (Tomas et al., 2009).

For example, as shown by this study, the loss of key fruiting-tree species in high cattle-impact areas, e.g., *G. ulmifolia*, which potentially sustain native frugivores during dry-season fruit-scarcity periods, reduced the abundance of common frugivorous species like brocket deer and collared peccaries. As a consequence, frugivore services, such as seed dispersal and forest regeneration, were undoubtedly degraded in high cattle-impact areas, leading in turn to additional homogenization of forest vegetation. Extensive foraging and trampling by cattle in forests and consequent removal of understory vegetation and litter may have other cascading impacts that disrupt soil nutrient cycles and forest regeneration (Johnson et al., 1997; Santos, 2011; Shepherd and Ditgen, 2005; Tomas et al., 2009). Related cattle-mediated removal of understory and litter-associated invertebrates, which are responsible for processing and decomposing organic matter, also has negative impacts on a range of insectivorous forest animals, including understory birds (Nunes, 2009; Tizianel, 2008) and as suggested by this study, armadillos. A key solution for conserving "cordilheira" forest flora and fauna will be to test and develop land-use practices, e.g., rotational grazing of native pasturelands, that limit the use of forests by cattle and reduce economic incentives for deforestation and conversions to planted exotic pasture (Eaton et al., 2011).

4.5. Camera-trap surveys of fruiting trees as an environmental monitoring tool

The procedures we developed with citizen scientists to compare groups of forest sites exposed to differing levels of an environmental

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impact using records of animal visits to fruiting trees showed great potential as an environmental monitoring tool that could be managed by dedicated volunteers. As natural congregation points for tropical forest fauna, fruiting trees are excellent sites for general surveys of fauna (Wemmer et al., 1996), e.g., to generate a species list for a region, or as in this study, to evaluate environmental impacts. Compared to a list of medium–large sized mammals from an extensive general survey conducted in the study area by Trolle (2003), our surveys, which focused only on fruiting trees, captured 83% of all documented species. In addition, the time and effort spent setting up and taking down camera traps was minimal in comparison to other methods, e.g., conducting line-transect censuses (Wemmer et al., 1996). So, citizen-scientist-run camera-trap surveys of fauna associated with fruiting trees appeared to be a time- and cost-effective way of monitoring or evaluating the status of most ground-dwelling mammals and large birds of Pantanal forests. It is a procedure that can potentially be applied and scaled-up to include a variety of tropical forest formations and environmental impacts.

Acknowledgements

This project was funded by Wildlife Conservation Society-Brazil, Blue Moon Fund, Wallace Global Fund, Fundação Manoel de Barros, and The Waterloo Foundation. We thank "Global Ecotours" teachers: J. Wilford, E. Kinzly, M. Simonds, and C. Caprio, and their students for their enthusiasm, support, and friendship. We are also grateful for the hard work of our Brazilian colleagues that helped gather and organize the data: Perola Lopes A. Sanabria, Celso Vicente da Silva, Divino Aparecido Elias, and Wilson Carlos de Silva Leite. Special thanks to the landowners and cowboys of Fazendas Campo Lourdes, Santa Maria, and Santa Emília for their collaboration and hospitality, and we thank Arnildo and Vali Pott for identifying *B. mattogrossensis*. Comments from two anonymous reviewers and editors, Dr. Libby Ellwood, Dr. Theresa Crimmins, and Dr. Abe Miller-Rushing, greatly improved an earlier version of the manuscript.

Appendix A. Supplementary data

It includes additional methods and results for NMS ordination procedures, permutation procedures for comparing aggregate animal community variables and Indicator Species Analyses. It also includes additional information on the abundance and timing of fruit fall, the distribution of dominant fruiting-tree species and the records of all faunal species visiting fruiting trees. For the ten most recorded animal species from all camera-trap samples, the diversity and evenness of their visits to dominant fruiting-tree species is also presented and discussed. Supplementary material associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.biocon.2016.09.010.

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