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Original investigation

Activity patterns of ocelots and their potential prey in the Brazilian Pantanal

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ABSTRACT

Camera trapping has been widely used to study different aspects of animal ecology, increasing scientific knowledge and helping in conservation initiatives. Recently, some studies demonstrated the use of this technique to study temporal predator-prey interactions, most of which focused on large felids. In this study, we investigate the activity patterns of the ocelot (*Leopardus pardalis*)—a medium-sized neotropical cat—and its known potential prey in the Brazilian Pantanal using photographs taken by camera traps. We tested for seasonal differences in activity patterns, and assessed the patterns of temporal overlap between this felid and three known potential prey: the Brazilian rabbit (*Sylvilagus brasiliensis*), Azara's agouti (*Dasyprocta azarae*), and Paraguayan punaré (*Thrichomys pachyurus*). We estimated activity patterns using kernel density and measured the overlap between estimated paired distributions using a coefficient of overlap, hypothesizing that activity patterns would change between the rainy and dry season, and that overlap would be higher with rodents since they comprise the bulk of the ocelot's diet in the Pantanal and elsewhere. Azara's agouti and the Paraguayan punaré were the only species that presented significant changes in their activity patterns between seasons. Contrary to our hypothesis, there was low coincidence of activity patterns between ocelots and Azara's agouti for both seasons, but temporal overlap between ocelots and Paraguayan punarés was high with no significant difference, at least in the dry season. Overall, temporal overlap between ocelots and Brazilian rabbits was high, with no significant differences. In general, our results suggest that ocelots may tailor their activity to that of some of their potential prey to increase the probability of encounters. The results provide the first insight into temporal interactions involving ocelots and their potential prey in the Brazilian Pantanal.

Introduction

The ocelot is the largest of the world's small spotted cats (Kolowski and Alonso, 2010), with a geographic distribution ranging from the southern United States to North Argentina (Murray and Gardner, 1997). Ocelots prefer dense habitats to open areas (Haines et al., 2006; Haverson et al., 2004), are almost strictly nocturnal (Di Bitetti et al., 2006; Kolowski and Alonso, 2010; Maffei et al., 2002), and are opportunistic predators (Emmons, 1987), preying on a wide spectrum of prey such as small mammals, birds, lizards and snakes (Bianchi et al., 2013; Emmons, 1987), although they occasionally prey on larger animals (Bianchi et al., 2013; Villa Meza et al., 2002). Despite being listed as Vulnerable in Brazil and Least Concern globally (IUCN, 2016), the ocelot is considered abundant in the Brazilian Pantanal (Bianchi, 2009; Porfirio et al., 2014).

According to Optimal Foraging Theory, predators tend to minimize energy costs involved in seeking and manipulating prey, which should not be greater than the energy benefits obtained from those activities (MacArthur and Pianka, 1966). In terms of daily activity, ocelots must divide their time between several behaviors which include, amongst others, resting, hunting, and patrolling their territories, while avoiding potential dangerous encounters with jaguars and pumas (Di Bitetti et al., 2006; Emmons et al., 1989). Thus, an understanding of their daily activity patterns provides a behavioral and ecological metric that can be used as an indicator of energetic expenditure, foraging effort (Weckel et al., 2006) and predation risk (Rowcliffe et al., 2014).

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Recently, camera trapping has been used to study temporal predator-prey interactions using photographic capture data to quantify the activity patterns of predators and their potential prey (*e.g.* Foster et al., 2013; Hernández-Saintmartín et al., 2013; Linkie and Ridout, 2011; Monterroso et al., 2013, 2014; Romero-Muñoz et al., 2010). These studies are based on the assumption that predators may tailor their activity to that of their potential prey to increase the probability of encounters, thereby reducing the energy expended in capturing prey (Emmons, 1987; Foster et al., 2013; Harmsen et al., 2011). In response, it has also been reported that prey may alter their foraging times to avoid predators (Harmsen et al., 2011; Ross et al., 2013). Most such studies have focused on the interactions of larger felids (*e.g. Panthera onca*, *Puma concolor* and *Panthera tigris sumatrae*) with their potential prey (Foster et al., 2013; Hernández-Saintmartín et al., 2013; Linkie and Ridout, 2011; Romero-Muñoz et al., 2010), although there is also some information available for mesocarnivores (Monterroso et al., 2014). Nevertheless, information is still scarce concerning small-to medium-sized neotropical felids, such as the ocelot.

As for many other felids, ocelots are difficult to study in wild habitats due to their secretive habits, natural low densities and large territories (Trolle and Kéry, 2003). Thus, camera trapping has helped to substantially increase knowledge about this species which, over some of its distribution, is threatened mainly by fragmentation and habitat loss (IUCN, 2016). Here, using camera trapping, we study the effect of seasonality on the activity patterns and overlap in daily activity of ocelots and three of its known potential prey in the Brazilian Pantanal: the Brazilian rabbit (*Sylvilagus brasiliensis*) and the two rodents, Azara's agouti (*Dasyprocta azarae*) and the Paraguayan punaré (*Thrichomys pachyurus*) (Bianchi et al., 2013; Rocha-Mendes et al., 2010).

The Pantanal biome belongs to the category of temporary wetland (Junk et al., 2006), playing an important role in biodiversity due to its diversity of natural habitats, which offer several opportunities for feeding and reproductive niches (Alho, 2008). The annual wet and dry periods have a strong impact on distribution, community structure and population size of several animal species (Junk et al., 2006; Mamede and Alho, 2006). Thus, we designed our research to answer the following questions: (1) Do the activity patterns of ocelots and their potential prey differs between the rainy and dry seasons?; and (2) What are the patterns of overlap between the daily activities patterns of ocelots and potential prey? We hypothesized that activity patterns would change in response to seasonality and, since rodents comprise the bulk of ocelot prey in the Pantanal (Bianchi et al., 2013), we hypothesized that the overlap in activity would be higher with these prey compared to other non-rodent prey species.

Material and methods

Study area

The study was carried out at two adjacent sites at Amolar Mountain Ridge: Santa Tereza Ranch (18°18′38″ S, 57°30′10″ W) and Engenheiro Eliezer Batista Private Protected Area (18°05′25″ S, 57°28′24″ W) (Fig. 1). Both study sites are nearly 830 km^2 in area. Amolar Mountain Ridge is located in the Upper Paraguay River Basin in the western Brazilian Pantanal, close to the border with Bolivia. It is a Precambrian massif that establishes an abrupt ecotone with the seasonally flooded plains of the Brazilian Pantanal (Junk et al., 2006), functioning as a geological control of the water drainage and a refuge for several species of mammals. The climate of the Upper Paraguay Basin is seasonal and, according to the Köppen classification is tropical savannah (AW) with hot and humid weather in the summer and dry and cold weather during the winter (Cadavid-Garcia, 1984). The rainy season is October–April, while the dry season is May–September (Junk et al., 2006). The main vegetation types at both sites includes dry and humid savannahs (50%), which can be submerged during the flood periods, gallery and riparian forest (5%), seasonal deciduous forest (10%), seasonal semi-deciduous forest (14%), rocky fields (1%), as well as permanent rivers and lakes that comprise approximately 20% of both areas.

Camera trapping

We conducted six camera-trapping surveys separated temporally between August 2011 and September 2013 (Table 1). A total of 119 cameras were spaced in an arrangement with a distance that varied between 500 and 2000 m, and total cameras used in each survey ranged from nine to 41 units. All surveys did not have the same duration (1–5 months) (Table 1). Each station had one camera placed 40–50 cm above the ground along dirt roads, river margins and in the forest. We used Bushnell Trophy Cam (Bushnell®, Kansas, USA) and Panthera V3 (Panthera, New York, USA) digital cameras. Cameras operated 24 h/day, with 30 s intervals between pictures. The camera triggering time was set at five seconds. We checked stations at 15–30 day intervals to change batteries and/or to download pictures. Malfunctioning cameras were replaced and 8 GB memory cards were used to ensure sufficient memory for all records.

Statistical analysis

We categorized photos by rainy (October–April) or dry season (May–September) following Junk et al. (2006). To avoid autocorrelation, we only used photos taken at least one hour apart for each species, unless it was possible to distinguish individuals, in which case each photo was considered independent (Foster et al., 2013; Linkie and Ridout, 2011; Romero-Muñoz et al., 2010). To reduce bias caused by repeated records of the same animal due to the proximity of some cameras (cameras placed 500 m apart), we only used the first record per hour per camera site as a detection event for each 24 h period, and the remaining records were eliminated from the analysis (Ross et al., 2013). We classified observations as diurnal (if activity was predominantly between 1 h after sunrise and 1 h before sunset), nocturnal (if activity was predominantly between 1 h after sunset and 1 h before sunrise), and crepuscular (if activity occurred up to 1 h before and after sunrise and sunset). We obtained times of sunrise and sunset from Moonrise 3.5 (Sidell, 2002), and converted the time of each photo to solar time following Foster et al. (2013). Moonrise 3.5 considers dates and geographic positions, thus correcting for changes during winter and summer times, in order to make data comparable since it accounts for solar time that compensates for local time and daylight savings. Following Gómez et al. (2005) and Romero-Muñoz et al. (2010), we classified species as diurnal (<15% of the observations were at night), nocturnal (>85% of the observations at night), mostly diurnal (15–35% of the observations at night), mostly nocturnal (65–85% of the observations at night), crepuscular (50% of the observations during the crepuscular period), and cathemeral (species that were active both day and night).

We used the approach developed by Ridout and Linkie (2009) to estimate the activity patterns of each species in each season using kernel density and, next, to measure the overlap between the two estimated distributions using a coefficient of overlapping (Δ), which varies from 0 (no overlap), to 1 (complete overlap) (Ridout and Linkie 2009; Linkie and Ridout 2011) using R package *Overlap* (Meredith and Ridout, 2014). Kernel density treats pictures as random samples from an underlying continuous distribution instead of grouping them into discrete time categories (Foster et al., 2013). Of the several methods described by these authors for calculating this coefficient, we used the estimator Δ_1, which is recommended for

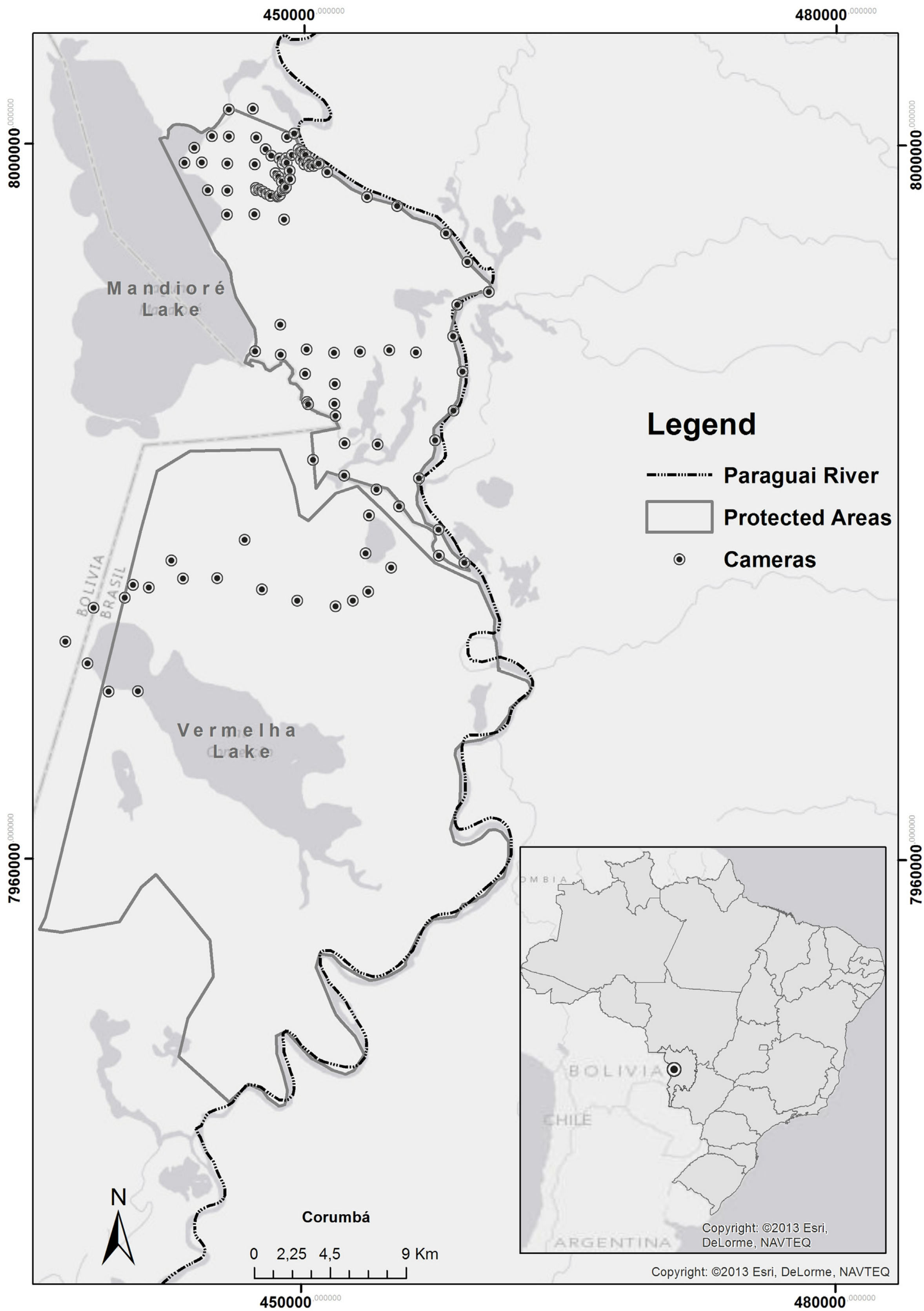

Fig. 1. Map of the study sites located at Engenheiro Eliezer Batista Protected Area and Santa Tereza Ranch, and camera trap locations in the Brazilian Pantanal of Amolar Mountain Ridge.

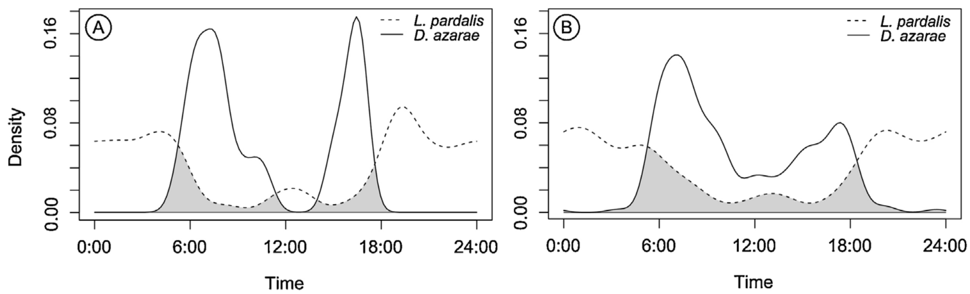

Fig. 2. Activity patterns and extension of overlap between ocelots (dashed line) and Azara's agoutis (bold line) in the dry (A) and rainy (B) seasons at Amolar Mountain Ridge (Brazilian Pantanal, August 2011–September 2013). Overlap is represented by the shaded grey area.

Table 1
Data from camera-trapping campaigns carried out in Engenheiro Eliezer Batista Protected Area and Santa Tereza Ranch, both located at Amolar Mountain Ridge (western Brazilian Pantanal), from August 2011 to September 2013.

Survey ID	Survey period	No. of camera traps	Average distance between cameras (m)	Survey days	Sampling effort (camera-days)
I	August–September 2011	23	500	62	1426
II	November 2011–January 2012	12	1500	58	696
III	February–May 2012	20	1500	95	1900
IV	August–September 2012	14	500	30	420
V	November 2012–May 2013	41	2000	169	6929
VI	April–September 2013	9	500	148	1332
Total	–	119	–	562	12,703

small sample sizes (Linkie and Ridout, 2011). A confidence interval was calculated for Δ_1 as a percentile of intervals from 500 bootstrap samples (Foster et al., 2013; Linkie and Ridout, 2011). Then, we used Watson's two-sample test of homogeneity used for circular data (Jammalamadaka and Sengupta, 2001), with solar time converted to radians (varying from 0 to 2π) to test for seasonal differences in the activity patterns for each species. This test gives a result based on a critical value. If U^2 is greater than the critical value, then the null hypothesis is rejected and the two samples are deemed to differ significantly. When the test statistic U^2 is less than the critical value, the null hypothesis cannot be dismissed. Scripts are available at http://artax.karlin.mff.cuni.cz/rhelp/library/CircStats/html/watson.two.html. Then, we followed the same procedures to test activity overlap between predator and prey according to season. All statistical analyses were performed in R software (R Development Core Team 2013).

Potential prey species

Few attempts have been made to describe the diet of ocelots in the Brazilian Pantanal. We used data available from studies by Bianchi (2009) and Bianchi et al. (2013) (both of which were carried out in the Brazilian Pantanal), and by Rocha-Mendes et al. (2010) (Atlantic Forest of Brazil), which demonstrate the importance of rodents and the lagomorph, the Brazilian rabbit, in the diet of ocelots to inform our approach at Amolar Mountain Ridge. In their study in the Central Pantanal, Bianchi et al. (2013) found 18 different *taxa* in the diet of ocelots, with rodents comprising 56.5% of their diet (three species and one family; notably *T. pachyurus*: 17.4% of occurrence and *D. azarae*: 15.2% of occurrence). In the Atlantic Forest, Rocha-Mendes et al. (2010) found ten food items in ocelots' diets, with only seven identified to species level. The percentages of occurrence were very similar among food items found in that study, with *S. brasiliensis* comprising 5.6% of ocelots' diets. The same percentages were observed for other species such as *Didelphis auritus*, *Monodelphis* sp. (Didelphimorphia), *Akodon* sp., *Holochilus brasiliensis* (Rodentia), and *Picumnus cirratus* (Aves: Picidae).

Results

With a total effort of 12,703 camera-days, we obtained 176 independent photos of ocelots ($n = 105$ in the rainy season; $n = 71$ in the dry season), 366 photos of Azara's agouti ($n = 216$ and $n = 150$ in the rainy and dry seasons, respectively), 67 photos of Paraguayan punaré ($n = 43$ and $n = 24$ in the rainy and dry seasons, respectively) and 27 photos of Brazilian rabbit ($n = 24$ and $n = 3$ in the rainy and dry seasons, respectively), as well as photos of another 24 species of ground-dwelling mammals (see Supplementary material S1). Two species presented statistically significant differences in their activity patterns between the rainy and dry seasons; Azara's agouti was diurnal during the rainy season and diurnal with crepuscular peaks during the dry season [$\Delta_1 = 0.76$ (0.67–0.80), $U^2 = 0.2841$, $p < 0.01$], and the Paraguayan punaré was nocturnal in the rainy season, and mostly nocturnal in the dry season [$\Delta_1 = 0.66$ (0.46–0.73), $U^2 = 0.1752$, $p < 0.01$]. We did not find significant differences in activity patterns between the rainy and dry season for ocelots, which were mostly nocturnal in both seasons [$\Delta_1 = 0.88$ (0.76–0.91), $U^2 = 0.0426$, $p > 0.01$]. It was not possible to carry out analyses to disentangle the effect of seasonality on the Brazilian rabbit due to the low number of records ($n = 24$ in the rainy season; $n = 3$ in the dry season), but this species was nocturnal in both seasons.

Considering the overlap between ocelots and their potential prey, it was observed that this felid had little coincidence of activity times with Azara's agoutis both during rainy and dry seasons, with patterns of activity differing significantly [$\Delta_1 = 0.35$ (0.26–0.40), $U^2 = 3.3517$, $p < 0.01$–rainy season; $\Delta_1 = 0.23$ (0.16–0.30), $U^2 = 2.7801$, $p < 0.01$–dry season] (Fig. 2). Although exhibiting a high degree of overlap, ocelots and Paraguayan punarés showed significant differences in activity patterns during the rainy season [$\Delta_1 = 0.75$ (0.62-0.81), $U^2 = 0.3283$, $p < 0.01$], but activity in the dry season overlapped extensively with no significant differences [$\Delta_1 = 0.79$ (0.59–0.84), $U^2 = 0.0541$, $p > 0.01$] (Fig. 3). Overall, the activity of ocelots coincided extensively with that of Brazilian rabbits [$\Delta_1 = 0.76$ (SE = 0.66-0.95), $U^2 = 0.2307$, $p > 0.01$], with no significant differences (Fig. 4).

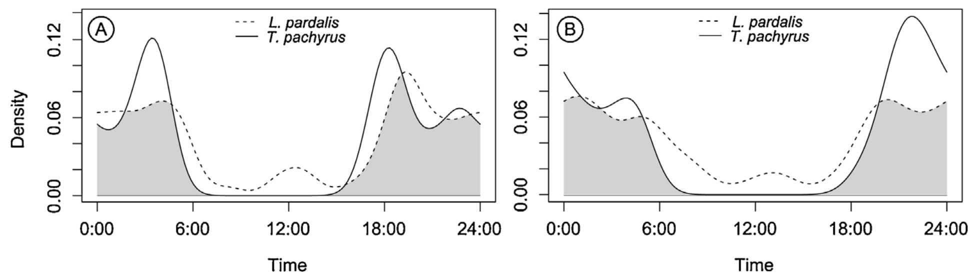

Fig. 3. Activity patterns and extension of overlap between ocelots (dashed line) and Paraguayan punarés (bold line) in the dry (A) and rainy (B) seasons at Amolar Mountain Ridge (Brazilian Pantanal, August 2011–September 2013). Overlap is represented by the shaded grey area.

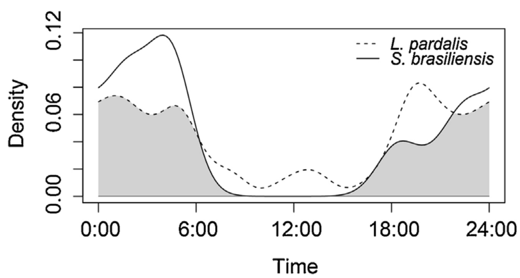

Fig. 4. Activity patterns and extension of overlap between ocelots (dashed line) and Brazilian rabbits (bold line) with data combined between the dry and rainy seasons at Amolar Mountain Ridge (Brazilian Pantanal, August 2011–September 2013). Overlap is represented by the shaded grey area.

Discussion

This is the first study that has attempted to disentangle the effect of seasonality on activity patterns and incidence of overlap between ocelots and some of their potential prey in the Brazilian Pantanal, where the species is relatively abundant (Bianchi, 2009; Porfirio et al., 2014). Furthermore, this study was carried out in one of the most pristine areas within the Brazilian Pantanal, where the influence of cattle ranching and its impact is low, thus presenting a good opportunity to study the relationships between predators and their potential prey in a more natural setting.

In a temporary wetland like the Pantanal, changes in spatial and temporal patterns are usually related to resource availability (food, reproductive niche and space) (Junk et al., 2006; Mamede and Alho, 2006), and as expected, at least for some species, activity patterns changed somewhat between the rainy and dry seasons. This change was observed for the Azara's agouti that was diurnal in the rainy season and diurnal with crepuscular peaks in the dry season, although both habits are in accordance to what has previously been described for the species (Kaiser et al., 2011; Oliveira-Santos et al., 2013). There was no previous systematic data on activity patterns of free-ranging populations of Paraguayan punarés. We found that their activity patterns also changed between the rainy and dry season. Although it was not possible to test the effect of seasonality on Brazilian rabbits, their nocturnal habits have also been found in other localities such as the Amazon Forest (Gómez et al., 2005) and in Bolivia (Maffei et al., 2002; Romero-Muñoz et al., 2010). Contrary to our predictions, the activity patterns of ocelots did not change, and they were mostly nocturnal in both seasons. This pattern has been reported elsewhere for ocelots, such as in the Bosque Chiquitano of Bolivia (Maffei et al., 2002), the Bolivian Amazon (Gómez et al., 2005), the Atlantic Forest of Argentina (Di Bitetti et al., 2006), and the Peruvian Amazon (Kolowski and Alonso, 2010). Thus, at least for this species, seasonality does not seem to affect activity patterns.

Overall, ocelots are reported to consume mainly small mammals that tend to be nocturnal (Emmons, 1987), but can also prey on larger animals such as agoutis and armadillos, as well as birds, reptiles and invertebrates (Emmons, 1987; Silva-Pereira et al., 2011; Wang, 2002). In their study of ocelot diet in the Nhecolândia subregion of Pantanal, Bianchi et al. (2013) found that ocelots may consume a wide variety of items, but that amongst them Paraguayan punarés and Azara's agouti appeared to comprise a high percentage of the diet (Bianchi et al., 2013). The Brazilian rabbit seems to do not occur at Nhecolândia (Alho et al., 1987; Desbiez et al., 2010), but since its occurrence is known at Amolar Mountain Ridge and since the species is reported as a prey item of ocelots in another area of Brazil (Rocha-Mendes et al., 2010), we also included this species in our study. In fact, the selection of target prey for our analyses was challenging due to the fact that most ocelot prey is comprised of small mammals (Emmons, 1987), and camera trap sensors tend to be biased in favor of medium-to large-sized terrestrial mammals (Harmsen et al., 2010; Porfirio et al., 2014), thus not favoring records of small mammals. A previous study carried out at Amolar Mountain Ridge using camera traps to inventory mammals recorded 33 species, of which only five were considered small mammals (Porfirio et al., 2014). As a result, here, we could only consider three of these five species of prey; although the other two (*Philander opossum* and *Urosciurus spadiceus*) are also considered prey of ocelots but at lower frequencies (Emmons, 1987; Rocha-Mendes et al., 2010), and due to the low number of records we could not carry out more extensive analyses.

We hypothesized that ocelots would overlap their activity to a higher degree with the two rodent species studied, since they are important items of ocelots' diet in the Pantanal (Bianchi et al., 2013), followed by the Brazilian rabbit. Our hypothesis was partially confirmed, since the highest incidence of activity overlap was found for Paraguayan punarés, especially in the dry season. However, the second highest incidence of overlap was not with Azara's agouti as expected, but with Brazilian rabbits.

Although Azara's agouti seem to be the most abundant mammal species in our study site (Porfirio et al., 2014), which would be a factor influencing its consumption due to the opportunistic behavior of ocelots (Bianchi et al., 2013), our results suggest that this prey species may not be amongst the most consumed since its activity cycles do not favor encounters with ocelots. During the night, Azara's agouti usually sleeps inside warrens that are relatively inaccessible to predators (Kaiser et al., 2011). In addition, some of our digital videos occasionally recorded vigilance behavior on the part of agoutis during their diurnal activity (unpublished results). This behavior, together with their diurnal activity, may be a strategy adopted by Azara's agouti to reduce the risk of predation (Harmsen et al., 2011). Nevertheless, since ocelots present some activity during crepuscular and diurnal periods (around 10 percent of ocelot records in the dry season and 13 percent in the rainy season), we cannot discount the possibility that ocelots may allocate some hunting effort to this diurnal species, given that its occurrence in the diet has already been reported in another area of the Pantanal (Bianchi et al., 2013). Moreover, ocelots may also allocate hunting effort to other small mammal species in our study sites, but the method we employed was not capable of detecting them. Considering the other prey species, besides having activity cycles that favor ocelots (being either nocturnal or mostly nocturnal), Paraguayan punarés and Brazilian rabbits may offer substantial energy to the felids due to their relatively large size compared to other smaller mammals.

The mostly nocturnal activity patterns observed for ocelots showed high coincidence with some of their potential small prey, and so it does not seem to be related to a strategy to avoid larger felids (jaguars and pumas), since both these latter predators are cathemeral at Amolar Mountain Ridge (unpublished results) and can therefore be active at any time of the day or night.

In conclusion, camera trapping can be considered an efficient tool to provide initial insights into the temporal interactions of ocelots and their potential small to medium-sized prey in the Brazilian Pantanal. Our hypotheses were partially supported, since some of the target species showed changes in their activity patterns between the rainy and dry season and since ocelots presented high incidences of overlap with the rodent, the Paraguayan punaré during both seasons (as well as with the lagomorph, the Brazilian rabbit), suggesting that these felids, as also demonstrated for others (*e.g.* jaguars, pumas and European mesocarnivores), can coincide their activity patterns with those of their potential prey, possibly in an attempt to increase encounter probabilities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.06.006.

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