Mammalian Biology (2021) 101:631–638
https://doi.org/10.1007/s42991-021-00110-9

ORIGINAL ARTICLE

"When the felid's away, the mesocarnivores play": seasonal temporal segregation in a neotropical carnivore guild

Shannon P. Finnegan[1,3] · Mariela G. Gantchoff[1] · Jacob E. Hill[2] · Leandro Silveira[3] · Natalia M. Tôrres[3,4] · Anah T. Jácomo[3] · Antonio Uzal[5]

Received: 25 October 2020 / Accepted: 10 February 2021 / Published online: 8 March 2021

Abstract

Interspecific competition within a carnivore guild can result in segregation along dietary, spatial, and temporal scales. Species interactions and resulting avoidance behavior can change seasonally as landscape features and resource abundance may fluctuate. In this study, we examined a carnivore guild in the Pantanal wetland of Brazil to determine whether temporal niche partitioning was a mechanism for coexistence, and if this differed between the wet and dry season. We used camera trapping data to fit kernel density functions of time observations for five species of carnivores to determine activity patterns. We calculated the coefficient of overlap between all species-pair's activity patterns. Our results found support for temporal segregation among this carnivore guild, with stronger segregation evident during the dry season. Jaguars and pumas showed large overlap in activity in both seasons, while all three mesocarnivores (ocelot, tayra, and crab-eating fox) showed temporal avoidance toward pumas. Mesocarnivores displayed segregating temporal patterns between pairs in both seasons. Temporal segregation is a mechanism for coexistence within this carnivore guild, suggesting increased competition between species especially during the dry season. To maintain carnivore populations, a broader knowledge of interspecific interactions and how this may affect species, utilization or avoidance of habitats is needed. Given the complexities of interspecific interactions among carnivores, conservation efforts should address the needs of the entire guild rather than focus on a single species.

Keywords Activity patterns · Carnivores · Camera trapping · South America · Temporal partitioning

Introduction

Carnivores face many ecological constraints while seeking to maximize fitness, including producing offspring while locating and hunting prey of variable size, abundance and spatial distribution (Caro and Stoner 2003; Swanepoel et al. 2013; Wolf and Ripple 2016). Species that inhabit the same distributional range often partition resources, which can occur through a combination of mechanisms grouped around different niche dimensions, such as diet, space, or time (Schoener 1974). Divergence in prey selection and avoidance of areas used by a competitor may reduce exploitative competition and minimize the likelihood of interspecific encounters (e.g. Dröge et al. 2017; Durant 1998; Karanth and Sunquist 1995; Ramesh et al. 2012). Morphological adaptations of a subordinate species may allow them to employ both of these strategies through increases in home range size, providing access to additional resources while simultaneously avoiding a competitor (Holland et al. 2017). Finally, animals may also exhibit temporal segregation, decreasing chances of

Handling Editor: Luca Corlatti.

Shannon Patricia Finnegan
shannonfinnegan8@yahoo.com

1 Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY, USA

2 Savannah River Ecology Laboratory, University of Georgia, PO Drawer E, Aiken, SC, USA

3 Jaguar Conservation Fund/Instituto Onça-Pintada, Mineiros, GO, Brazil

4 Federal University of Uberlândia, Uberlândia, Brazil

5 School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Brackenhurst, Southwell, NG, UK

interaction with a competitor by minimizing activity when a dominant competitor is more active (e.g. Hayward and Slotow 2009; Lucherini et al. 2009).

Carnivores are more likely to interact with species within their own family than with other groups, and frequently exhibit high levels of niche partitioning due to competing for resources while sometimes also engaging in interspecific killing (Holt and Polis 1997; Donadio and Buskirk 2006; Lucherini et al. 2009). Relative body size among carnivores appears to be the principal determinant of interspecific killing probability (Donadio and Buskirk 2006; Lucherini et al. 2009); at small and large differences, attacks are less likely to occur; at intermediate differences, intraguild killings are more frequent (Donadio and Buskirk 2006). Thus, there is a combination of competition and predation within the guild, which could be expected to promote marked partitioning of resources and complex patterns of segregation. In some areas, for example, lions (*Panthera leo*) outcompete both cheetahs (*Acinonyx jubatus*) and African wild dogs (*Lycaon pictus*), but wild dogs spatially avoid lions while cheetahs do not (Dröge et al. 2017). Similarly, felids in the Andes temporally avoid some potential competitors but not others (Lucherini et al. 2009), while culpeo foxes (*Lycalopex culpaeus*) do not temporally or spatially segregate from pumas (*Puma concolor)* (Osorio et al. 2020). Additionally, there may be seasonal patterns in avoidance related to factors such as food availability (Torretta et al. 2016). Consequently, region-specific analyses are often warranted to understand the factors facilitating coexistence of a particular carnivore guild.

The Brazilian Pantanal is the world's largest wetland, consisting of a 140,000 km^2 floodplain located in the center of South America (Lacher and Gonçalves 1988). Large swaths of intact habitat combined with a large prey base have made the Pantanal an important area for jaguar (*Panthera onca*) conservation and estimates suggest that the population may be increasing (Cavalcanti et al. 2012). In addition to jaguars, there are many other carnivores inhabiting the region, including pumas, ocelots (*Leopardus pardalis*), tayras (*Eira barbara*), and crab-eating foxes (*Cerdocyon thous*). However, interactions among carnivores in the Pantanal have not been thoroughly examined. The Pantanal is characterized by seasonal inundation of vast portions of land during the rainy season (November–April) (Lacher and Gonçalves 1988). This may result in seasonal shifts in species' diet and space use, creating the potential for dynamic changes in carnivore interactions. The carnivore guild in the Pantanal thus presents a unique opportunity to investigate niche partitioning among a diverse carnivore guild across a landscape impacted by dynamic seasonal fluctuations in rainfall.

Our objective was to evaluate if the carnivore guild in the Pantanal exhibits temporal niche partitioning as a potential mechanism for coexistence. Given both the potential competitive and killing interactions that could occur among the five species in this guild (Fig. 1), we predicted that we would find three main patterns of temporal segregation: (1) similar-sized carnivore species will segregate to minimize exploitative competition due to niche overlap (i.e. puma-jaguar, fox-ocelot-tayra), (2) species of intermediate size difference will segregate due to the smaller species avoiding the larger one in an attempt to minimize the risk of intraguild killing (fox-puma, ocelot-puma, tayra-puma), and (3) temporal segregation will occur more during the dry season, when the more limited resources could intensify competitive interactions.

Methods

Study site

The Pantanal has a tropical semi-humid climate. The dry season spans May to October with average temperatures ranging around 21 °C (Wang et al. 2011). The wet season runs November to April, with water levels in the Pantanal basin rising between two and five meters, inundating up to 80% of the floodplains (De Abreu et al. 2010). Vegetation in the area consists of a matrix of savannah, gallery forest segments, scrub savannah and seasonally flooded grasslands, intermixed with temporary and permanent water bodies (Mourão and Medri 2007).

We carried out this study across 23,000 ha encompassing several private farms in the Nhecolândia region of the southern Pantanal. The study was centered on Fazenda Barranco Alto ranch (19º 33′35 ″S 56º 09′22″ W) in the State

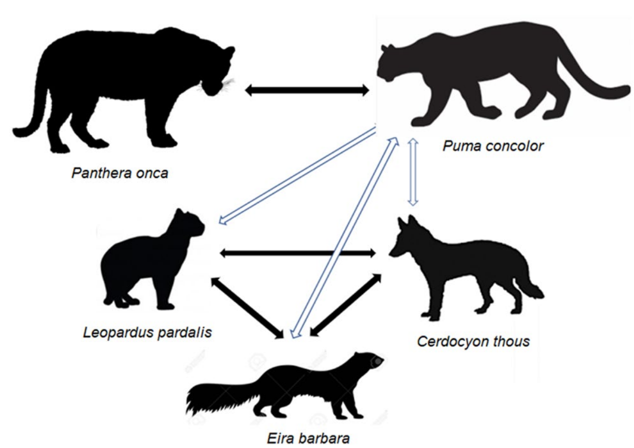

Fig. 1 Carnivore guild in the study area, showing the expected pair interactions among species from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013 and 2015. Solid black arrows related to Hypothesis 1 (niche segregation among species of similar size), white arrows to Hypothesis 2 (intraguild killing for species of intermediate size difference)

of Mato Grosso do Sul, along the banks of the Rio Negro river, but also included portions of the neighboring Diacuí, Vera Lúcia, and Embiara farms. The primary activity in these ranches is Nelore cattle production with an emphasis on eco-tourism. The ranches in this study contain preserved habitat composed of largely natural vegetation structure and a mosaic of natural water bodies.

Field methods

We placed 120 individual wildlife cameras (120 in the dry season, 101 in the wet season) (Bushnell HD trophy cam, model 119,537) spaced 1.5–2 km apart across 230 km^2 between September 2013 and May 2015 (One camera per location). We placed cameras in a grid formation, with additional deployment along the main river and trails where carnivores were more likely to be captured (Karanth 1995). Cameras were placed 45 cm above the ground on wooden fence posts or trees, a height ideal for capturing medium-to-large mammals (Tobler et al. 2008). Cameras were triggered via motion and recorded a 60 s video upon trigger for older model cameras, and photo and video simultaneously with a one second delay between subsequent captures on newer models. All camera traps in the study were checked every 4 weeks to replace batteries and change memory cards. All species captured on cameras were recorded along with location, date, time, group size, and sex where possible. We defined the wet season as the period between December 2013 to March 2014, and the dry season between April–July 2014.

Data analysis

All species captured on the cameras were recorded, however, all consecutive records of a species which occurred within 30 min at the same site were omitted from the data set. This interval between images is commonly used to separate single passing animals from repeated captures of the same animals in one event (O'Brien et al. 2003). Only cameras which worked for a length of > 10 days in a given season were included in data analysis (Rowcliffe et al. 2008). Any cameras which malfunctioned and did not record time and date correctly were also removed from the study sample. After considering this, 96 and 72 cameras were included for the dry and wet season, respectively.

We fit kernel density functions to times of observations of animals and to calculate the coefficient of overlap (Δ), through a quantitative measure extending from 0 (no overlap) to 1 (complete overlap), whilst confidence intervals are calculated via bootstrapping, following Ridout and Linkie (2009). This measure of temporal overlap is obtained by taking the minimum of the density functions of two cycles being compared at each time point (Rovero and Zimmermann 2016). The overlapping coefficient (Δ), is the area which underlies both lines on the fitted density curve. Choosing best fitting estimators is important for activity pattern analysis and is generally dependent on sample sizes. Following Ridout and Linkie (2009), two circular nonparametric estimators were applied in this study, Δ^1 and Δ^4. Δ^1 was used for small sample sizes (< 50), and Δ^4 for larger sample sizes (> 50) (Meredith and Ridout 2014).

We used a smoothed bootstrap, with 10,000 samples, and applied it by fitting a kernel density to the radian time of day data and drawing simulated observations randomly from the entire kernel distribution (Ridout and Linkie 2009). We calculated 95% confidence intervals for Δ as percentile intervals similar to Foster et al. (2013). To test for significant differences in activity between species at an alpha of 0.05, we compared the bootstrapped activity patterns of each species with a Wald statistic on a chi-square distribution with one degree of freedom (Rovero and Zimmermann, 2016; Santos et al. 2019). However, the coefficient of overlap is descriptive, without a clear indication of a threshold value below which two activity curves are significantly different (Lashely et al. 2018). All statistical analysis were carried out with the software R, version 3.3.2 (R core team 2016), using the package 'overlap' with scripts adapted from Meredith and Ridout (2014).

Results

We obtained a total of 524 records of 5 species from 4895 trapping nights during the wet season (jaguars $n=9$, pumas $n=102$, ocelots $n=57$, crab-eating foxes $n=341$, tayras $n=15$), and 531 records from 4669 trapping nights during the dry season (jaguars $n=38$, pumas $n=66$, ocelots $n=78$, crab-eating foxes $n=329$, tayras $n=20$). We observed a low degree of temporal overlap between tayras and all other carnivores (range Δ 0.18–Δ 0.54) (Fig. 2). We observed an overlap average of $\Delta=0.76$ for jaguars and pumas, $\Delta=0.73$ for jaguars and ocelots, and $\Delta=0.70$ for jaguars and crab-eating foxes. Pumas on average overlapped with ocelots by $\Delta=0.71$, and crab-eating foxes by $\Delta=0.78$. Ocelots and crab-eating foxes also had a high average degree of overlap of $\Delta=0.85$. We tested whether any individual species changed their activity patterns between the wet and dry season and found no evidence of significant changes in temporal activity.

During the wet season, jaguars had a high degree of overlap in activity with all species apart from tayras, which exhibited significantly different activity patterns (Table S1). Jaguars, ocelots, and pumas exhibited primarily nocturnal behavior (between 18.00 and 06.00), however, jaguars also showed a small spike in activity during late afternoon hours (between 12.00 and 18.00, Fig. 2). Crab-eating foxes were

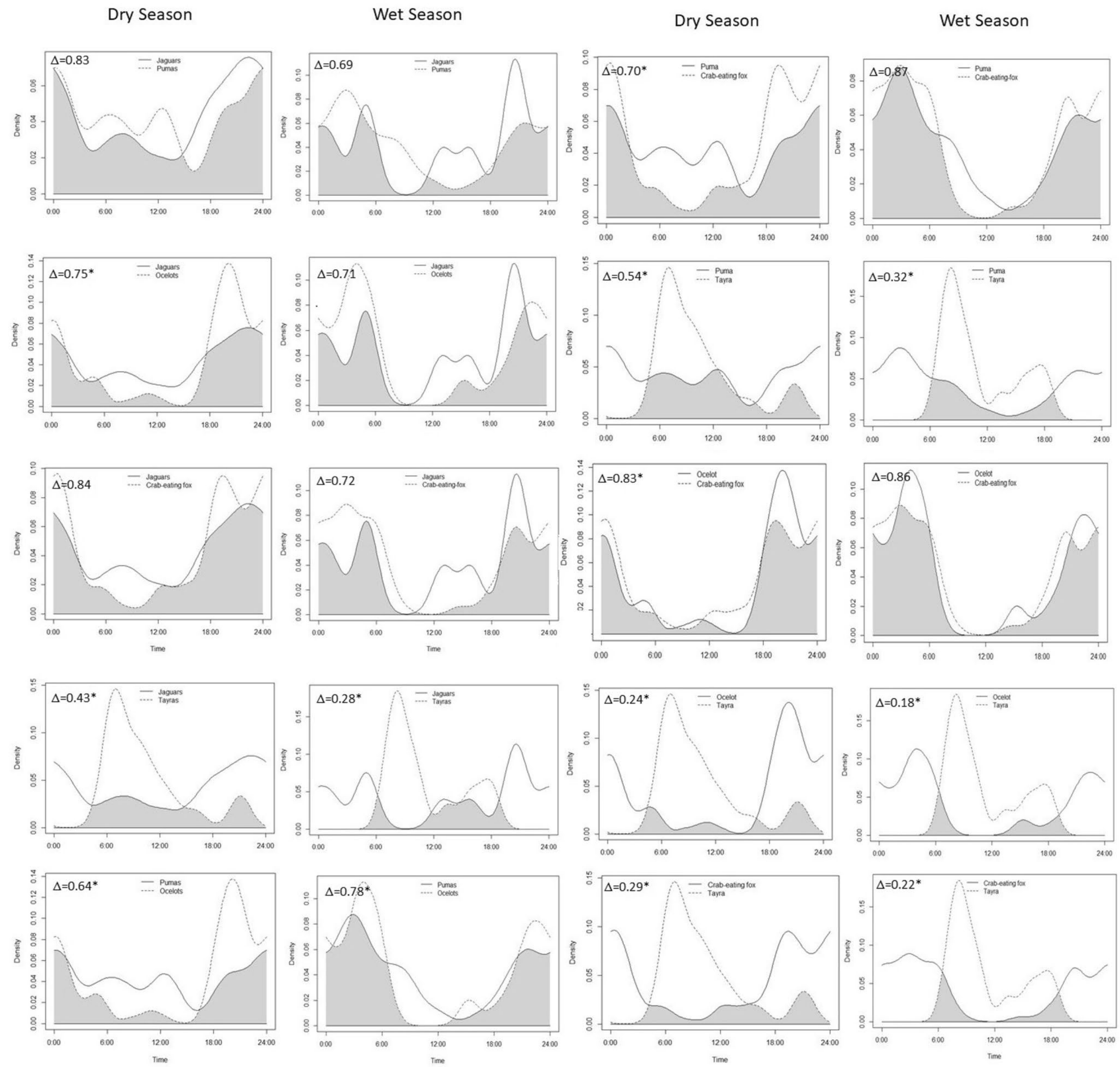

Fig. 2 Density estimates of daily activity patterns between five species of sympatric carnivores in the dry and wet season from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013 and 2015. Time along the x-axis is in a 24 h format with noon in the center. The coefficient overlap is shown on each graph, and represented as the shaded area in each plot. (*) Indicates significant differences

also largely active at night with some tendency toward crepuscular activity. Pumas and ocelots differed in their activity patterns, with ocelots showing a spike in activity between 03.00 and 06.00. Pumas, ocelots, and crab-eating foxes all had significantly different activity patterns compared to tayras (Table S1), which exhibited only diurnal activity.

During the dry season, jaguars again exhibited significantly different activity patterns to that of tayras which were primarily diurnal (Table S1). In this season, jaguars also displayed significantly different activity patterns than ocelots. Although both species were most active at night, ocelots showed a higher spike in activity between 18.00 and 22.00 h (Fig. 2). Pumas had significantly different activity patterns than all other mesocarnivores in the dry season. Pumas were most active between the hours of 18.00–05.00, while crab-eating foxes showed activity peaks between 19.00 and 01.00 h and tayras between 06.00 and 12.00 h. Although ocelots and crab-eating foxes overlapped to a large degree in their activity, there was a significant difference between both species in the dry season (Table S1), with ocelots peaking between 18.00 and 22.00 h. Both ocelots and crab-eating foxes displayed significantly different activity patterns to tayras.

We found partial support for our first prediction (segregation among similar sized species); there was segregation among smaller species with each other but not among the two large species (Fig. 3). We found considerable support for our second hypothesis (competition among large and mesocarnivores), indicated by consistent segregation between pumas and the smaller species (Fig. 3). Finally, we supported our third prediction of stronger segregation in the dry vs wet season: eight of the ten pairs showed significant differences in the dry season, but only five of ten showed significant differences during the wet season (Fig. 3).

Discussion

We found support for temporal segregation as a mechanism likely facilitating coexistence in a neotropical carnivore guild, located in the Brazilian Pantanal. Results supported our prediction that the dry season would result in stronger temporal segregation. We found that 80% of the pair interactions showed significant segregation in the dry season, but only 50% showed significant differences during the wet season. Six of the seven predicted pair interactions were confirmed by the results in at least one season, the only exception being jaguars and pumas, which displayed large overlap in their activity patterns, suggesting that temporal partitioning is not a major factor contributing to their coexistence in this area. All three mesocarnivores (crab-eating foxes, ocelots, tayras) showed temporal segregation with pumas, suggesting that pumas have a stronger intraguild effect on mesocarnivores compared to jaguars. Among the mesocarnivore guild (crab-eating foxes, ocelots, tayras), almost all pairs showed segregating temporal patterns in both seasons.

Increased temporal segregation within the carnivore guild in the dry season may likely be attributed to decreased concentration of food resources and, therefore, increased competition during this period. Throughout the wet season, prey species are often more spatially and temporally clumped in the remaining areas of dry land, decreasing competitive interactions within the guild (Karanth et al. 2017). Similarly, Torretta et al. (2016) reported that during winter, in periods of low food abundance, competitive interactions between two European carnivore species likely increased and explained shifts in temporal activity to reduce encounters. It is possible that during the wet season (higher resource abundance) spatial segregation becomes a more important mechanism for carnivore coexistence, while temporal segregation plays a larger role in the dry season, when resources might be scarce and carnivores are forced into the same areas to find prey (Torretta et al. 2016; Zhao et al. 2020).

Jaguars and pumas displayed large overlap in their activity patterns, suggesting that temporal partitioning is not a major factor contributing to their coexistence in this area. Other studies have also found substantial temporal overlap between these species (Foster et al. 2013; Porfirio et al. 2017); however, there is reported evidence for temporal segregation (Harmsen et al. 2011; Romero-Munoz et al. 2010), and an analysis of jaguar–puma partitioning across Neotropical forests documented significant differences in activity at some study sites but not at others (Santos et al. 2019). In the Pantanal, temporal activity patterns of both species overlaps with that of their major prey (Porfirio et al. 2017). The increase in foraging opportunities may offset the negative impacts from potential competition. Similarly, activity patterns of cheetahs were driven by optimal hunting conditions, as capturing prey outweighed the risk of encountering lions, their main mortality risk (Broekhuis et al. 2014). In another study site in Brazil, very high temperatures

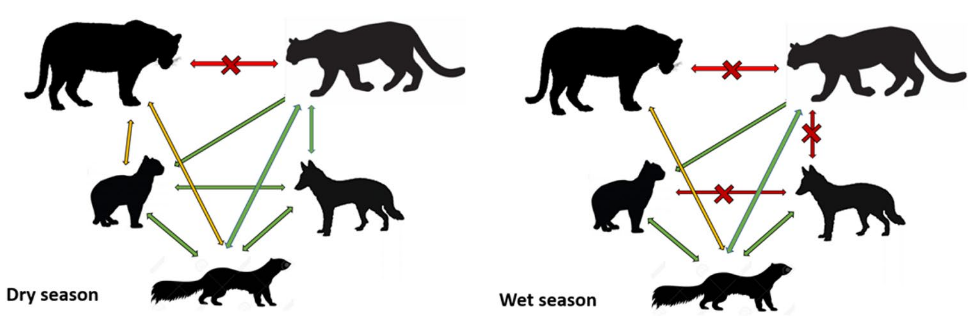

Fig. 3 Documented temporal segregation in both dry and wet seasons within a carnivore guild from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013 and 2015 (clockwise from top left the species are: jaguar, puma, crab-eating fox, tayra, ocelot). Green indicates a supported prediction (see Fig. 1), red with an X an unsupported prediction, and yellow not predicted but documented temporal segregation

decreased diurnal activity of both jaguars and pumas, and these thermoregulatory constraints led to similar activity patterns (Astete et al. 2017). Overall, competition is but one factor shaping an animal's behavior, and other mechanisms such as habitat preferences, prey availability and selection, or physiological considerations may play a stronger role in determining how jaguars and pumas coexist in different areas (Scognamillo et al. 2003).

All three mesopredators (crab-eating foxes, ocelots, tayras) showed temporal segregation with pumas in the wet season, while ocelots and tayras also exhibited temporal segregation with pumas in the dry season, suggesting that pumas have a stronger intraguild effect on mesocarnivores compared to jaguars. Overlap in diet (Emmons 1987), along with similarities in body size, may be the key factor causing increased avoidance between pumas and mesopredators, compared to the jaguar (Donadio and Buskirk 2006), which often preys on larger bodied prey (Scognamillo et al. 2003). However, all three mesocarnivores in our study could potentially, or have previously been, predated on by both apex predators (De Oliveira and Pereira 2014). Therefore, the stronger effect of pumas on mesopredators could simply be attributed to the higher observed records of pumas in our study area, compared to lower records of jaguars.

Within the mesocarnivore guild (crab-eating foxes, ocelots, tayras), all pairs showed segregating temporal patterns in both seasons, except for ocelots and crab-eating foxes in the wet season. Specifically, we found evidence that crab-eating foxes and tayras may show temporal avoidance toward ocelots, particularly in the dry season. Previous results suggest ocelots exert a somewhat suppressive force on other mesocarnivores through interference competition (Oliveira et al. 2010; De Oliveira and Pereira 2014; Sunquist and Sunquist 2017). Specifically, Oliveira et al. (2010) described what they called the "ocelot effect", where increasing densities of this species negatively impacted smaller carnivores in many parts of their range, and in some cases impose a larger threat than that of large carnivores (De Oliveira and Pereira 2014). These dominant mesocarnivores are believed to compete both directly and indirectly with smaller felids and canids across South America, especially in the absence of larger predators (Macdonald and Loveridge 2010). However, it is important to note that trophic partitioning among these species could be a more important coexistence mechanism. The crab-eating fox is a generalist species, relying on a combination of fruit and small vertebrates, while ocelots are obligate carnivores that rely largely on small-to-medium sized vertebrates and reptiles (Farrell et al. 2000). Coexistence by diverging diet instead of spatial and temporal overlap was also observed for a mesocarnivore canid-felid pair in northern Patagonia (Gantchoff and Belant 2016). Similarly, Osorio et al (2020) found dietary divergence the most likely mechanism facilitating coexistence between a canid-felid pair in central Chile. Tayras are generally reported to be more arboreal, and are described as opportunistic omnivores that have been recorded to prey on primates (Asensio and Gómez-Marín 2002; Bezerra et al. 2009); therefore, the strong segregation we observed with other mesopredators is likely strongly influenced by their natural history, behavior, and prey activity, rather than solely intraguild interactions.

Examining carnivore assemblages from other parts of the world suggests that patterns of temporal partitioning are influenced by a number of site-specific attributes. In Asia, leopards may increase their diurnal activity in response to the presence of tigers, the top predator in the system (Azlan and Sharma 2006). African carnivores exhibited decreased temporal partitioning in densely vegetated habitats, because vegetative cover offered protection from predators despite similar activity patterns (Rich et al. 2017). Patterns of temporal partitioning between lions and leopards in Africa change as a function of prey availability (Miller et al. 2018). These divergent patterns are possible, because carnivores tend to have high degrees of behavioral plasticity. Natural selection has likely favored this fluidity, because it allows carnivores to shift temporal patterns of activity in response to changing environmental conditions. As a consequence, carnivores are likely able to adopt the behavioral strategies that optimize fitness under a given set of ecological circumstances. Human disturbance influences the three dimensions of niche partitioning in carnivore guilds (Seveque et al. 2020). However, the effects of humans on the intensity of intraguild competition is context dependent and, therefore, contrasting effects on the same guild might be reported in different study areas.

Like most field studies, our conclusions are subject to some logistic limitations that should be considered when interpreting results. For example, camera malfunctions together with flooding of some areas during the rainy season may have led to differences in the rate of detection of some species. Camera stations were established both in random and select locations along trails and rivers to increase the likelihood of large carnivore captures (Silver et al. 2004). It is possible that traps occurring on highly active carnivore trails may lead to an activity estimation based on trail use, rather than a true estimation throughout utilized habitat (Rowcliffe et al. 2014). Number of detections for some of the pairs was limited (i.e. jaguar-tayra) and this might have affected the estimation of temporal overlap. Despite these limitations, given the large area surveyed and time span of the surveys, we believe these results are a valuable contribution to our knowledge of temporal partitioning as a potential mechanism for coexistence in this neotropical carnivore guild.

The maintenance of carnivore diversity and subsequent conservation of species and their habitats relies on a broader knowledge of interspecific interactions, and how this might affect other species, utilization or avoidance of certain areas (Sunarto et al. 2015). Competitive interactions between carnivores can result in suppression of subordinate species, which may have strong implications for species endangered by regional or local extinction (Linnell and Strand 2000). Given these constraints, focusing on larger species for conservation benefits may not necessarily impose an umbrella effect for all species, expecting that all co-occurring carnivores will benefit (Linnell et al. 2000). It may be necessary to design carnivore conservation programs that address the needs of the entire guild rather than placing emphasis on one species (Dalerum et al. 2009). Overall, it is apparent that interspecific relationships within carnivore guilds are highly complex and flexible in nature, and can have measurable impacts on the occurrence and persistence of certain species. A better understanding of interspecific relationships within carnivore guilds and how rising anthropogenic pressure on carnivore habitats influence such relationships are research areas that are in need of further development for future carnivore conservation planning (Seveque et al. 2020; Linnell and Strand 2000).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42991-021-00110-9.

Acknowledgements The authors extend thanks to Lucas Leuzinger, his family, and all the staff of Fazenda Barranco Alto in the Pantanal for assistance and logistical support for this project. We are also grateful to members of the Jaguar Conservation Fund who participated in data collection and data processing. Partial Funding was provided by Nottingham Trent University.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Asensio N, Gómez-Marín F (2002) Interspecific interaction and predator avoidance behavior in response to tayra (*Eira barbara*) by mantled howler monkeys (*Alouatta palliata*). Primates 43:339–341
Astete S, Marinho-Filho J, Kajin M, Penido G, Zimbres B, Sollmann R, Jácomo A, Tôrres N, Silveira L (2017) Forced neighbours: Coexistence between jaguars and pumas in a harsh environment. J Arid Environ 146:27–34
Azlan JM, Sharma DS (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40:36–41
Bezerra BM, Barnett AA, Souto A, Jones G (2009) Predation by the tayra on the common marmoset and the pale-throated three-toed sloth. J Ethol 27:91
Broekhuis F, Grünewälder S, McNutt JW, Macdonald DW (2014) Optimal hunting conditions drive circalunar behavior of a diurnal carnivore. Behav Ecol 25:1268–1275
Caro TM, Stoner CJ (2003) The potential for interspecific competition among African carnivores. Biol Conserv 110:67–75
Cavalcanti SM, Azevedo FD, Tomás WM, Boulhosa RL, Crawshaw PG Jr (2012) The status of the jaguar in the Pantanal. Cat News Spec Issue 7:29–34
Dalerum F, Cameron EZ, Kunkel K, Somers MJ (2009) Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biol Lett 5:35–38
De Oliveira TG, Pereira JA (2014) Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. J Mamm Evol 21:427–436
De Abreu UGP, McManus C, Santos SA (2010) Cattle ranching, conservation and transhumance in the Brazilian Pantanal. Pastoralism 1:99–114
Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in Carnivora. Am Nat 167:524–536
Dröge E, Creel S, Becker MS, M'soka J (2017) Spatial and temporal avoidance of risk within a large carnivore guild. Ecol Evol 7:189–199
Durant SM (1998) Competition refuges and coexistence: an example from Serengeti carnivores. J Anim Ecol 67:370–386
Emmons LH (1987) Comparative feeding ecology of felids in a neotropical rainforest. Behav Ecol Sociobiol 20:271–283
Farrell LE, Roman J, Sunquist ME (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. Mol Ecol 9:1583–1590
Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácomo AT, Negrões N, Fonseca C, Silveira L (2013) Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. Biotropica 45:373–379
Gantchoff MG, Belant JL (2016) Patterns of coexistence between two mesocarnivores in northern Patagonia in the presence of invasive hares and anthropogenic disturbance. Austral Ecol 41:97–105
Harmsen BJ, Foster RJ, Silver SC, Ostro LE, Doncaster CP (2011) Jaguar and puma activity patterns in relation to their main prey. Mamm Biol 76:320–324
Hayward MW, Slotow R (2009) Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. Afr J Wildl Res 39:109–125
Holland AE, Byrne ME, Bryan AL, DeVault TL, Rhodes OE, Beasley JC (2017) Fine-scale assessment of home ranges and activity patterns for resident black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*). PLoS ONE 12:e0179819
Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. Am Nat 149:745–764
Karanth KU (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture: recapture models. Biol Conserv 71:333–338
Karanth KU, Sunquist ME (1995) Prey selection by tiger, leopard and dhole in tropical forests. J Anim Ecol 64:439–450
Karanth KU, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, Kumar NS (2017) Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proc R Soc B 284:20161860
Lacher TE, Gonçalves HC (1988) Environmental degradation in the Pantanal ecosystem. Bioscience 38:164–171
Lashley MA, Cove MV, Chitwood MC, Penido G, Gardner B, DePerno CS, Moorman CE (2018) Estimating wildlife activity curves: comparison of methods and sample size. Sci Rep 8:1–11
Linnell JD, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. Divers Distrib 6:169–176
Linnell JD, Swenson JE, Andersen R (2000) Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? Biodivers Conserv 9:857–868
Lucherini M, Reppucci JI, Walker RS, Villalba ML, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity

pattern segregation of carnivores in the high Andes. J Mammal 90:1404–1409
Macdonald D, Loveridge A (2010) The biology and conservation of wild felids (Vol. 2). Oxford University Press, Oxford
Meredith M, Ridout M (2014) Overview of the overlap package. R, Project, pp 1–9
Miller JR, Pitman RT, Mann GK, Fuller AK, Balme GA (2018) Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. J Anim Ecol 87:1709–1726
Mourão G, Medri ÍM (2007) Activity of a specialized insectivorous mammal (*Myrmecophaga tridactyla*) in the Pantanal of Brazil. J Zool 271:187–192
O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139
Oliveira TG, Tortato MA, Silveira L, Kasper CB, Mazim FD (2010) Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. In: MacDonald DW, Loveridge AJ (eds) Biology and conservation of wild felids. Oxford University Press, New York, pp 559–580
Osorio C, Muñoz A, Guarda N, Bonacic C, Kelly M (2020) Exotic prey facilitate coexistence between Pumas and Culpeo Foxes in the Andes of central Chile. Diversity 12:317
Porfirio G, Sarmento P, Foster V, Fonseca C (2017) Activity patterns of jaguars and pumas and their relationship to those of their potential prey in the Brazilian Pantanal. Mammalia 81:401–404
R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Ramesh T, Kalle R, Sankar K, Qureshi Q (2012) Dietary partitioning in sympatric large carnivores in a tropical forest of Western Ghats, India. Mammal Study 37:313–321
Rich L, Miller D, Robinson H, McNutt J, Kelly M (2017) Carnivore distributions in Botswana are shaped by resource availability and intraguild species. J Zool 303:90–98
Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat 14:322–337
Romero-Munoz A, Maffei L, Cuéllar E, Noss AJ (2010) Temporal separation between jaguar and puma in the dry forests of southern Bolivia. J Trop Ecol 26:303–311
Rovero F, Zimmermann F (2016) Camera trapping for wildlife research. Pelagic, Exeter
Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. J Appl Ecol 45:1228–1236
Rowcliffe JM, Kays R, Kranstauber B, Carbone C, Jansen PA (2014) Quantifying levels of animal activity using camera trap data. Methods Ecol Evol 5:1170–1179
Santos F, Carbone C, Wearn OR, Rowcliffe JM, Espinosa S, Lima MGM, Ahumada JA, Gonçalves ALS, Trevelin LC, Alvarez-Loayza P (2019) Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PLoS ONE 14:e0213671
Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39
Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. J Zool 259:269–279
Sévêque A, Gentle LK, López-Bao JV, Yarnell RW, Uzal A (2020) Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biol Rev 95:1689–1705
Silver SC, Ostro LE, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gomez H, Ayala G (2004) The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38:148–154
Sunarto S, Kelly MJ, Parakkasi K, Hutajulu MB (2015) Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J Zool 296:104–115
Sunquist M, Sunquist F (2017) Wild cats of the world. University of Chicago Press, Chicago
Swanepoel LH, Lindsey P, Somers MJ, Van Hoven W, Dalerum F (2013) Extent and fragmentation of suitable leopard habitat in South Africa. Anim Conserv 16:41–50
Tobler MW, Carrillo-Percastegui SE, Pitman RL, Mares R, Powell G (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim Conserv 11:169–178
Torretta E, Serafini M, Puopolo F, Schenone L (2016) Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (NW Italy). Acta Ethol 19:123–132
Wang E, Donatti CI, Ferreira VL, Raizer J, Himmelstein J (2011) Food habits and notes on the biology of Chelonoidis carbonaria (Spix 1824)(Testudinidae, Chelonia) in the southern Pantanal. Braz S Am J Herpetol 6:11–19
Wolf C, Ripple WJ (2016) Prey depletion as a threat to the world's large carnivores. R Soc Open Sci 3:160252
Zhao G, Yang H, Xie B, Gong Y, Ge J, Feng L (2020) Spatio-temporal coexistence of sympatric mesocarnivores with a single apex carnivore in a fine-scale landscape. Glob Ecol Conserv 21:e00897