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

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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. Mecocarnivores 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 & 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 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 to 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, McManus and Santos, 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 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 119537) 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 second 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 in order 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 to July 2014.

Data Analysis

All species captured on the cameras were recorded, however, all consecutive records of a species which occurred within 30 minutes 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, Kinnaird and Wibisono, 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 five 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 Δ=0.76 for jaguars and pumas, Δ=0.73 for jaguars and ocelots, and Δ=0.70 for jaguars and crab-eating foxes. Pumas on average overlapped with ocelots by Δ=0.71, and crab-eating foxes by Δ=0.78. Ocelots and crab-eating foxes also had a high average degree of overlap of Δ=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 - 06.00), however, jaguars also showed a small spike in activity during late afternoon hours (between 12.00 - 18.00, Fig. 2). Crab-eating foxes were 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 - 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 - 22.00 hours (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 - 01.00 hours and tayras between 06.00 - 12.00 hours. 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 - 22.00 hours. 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 meso carnivores), 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. 2016). 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 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 (De Oliveira et al. 2010; De Oliveira and Pereira, 2014; Sunquist and Sunquist, 2017). Specifically, De 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, Roman and Sunquist, 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, Swenson, and Andersen, 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).

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Conflicts of interest

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

Literature Cited

Asensio N, and 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. Journal of Arid Environments 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 B M, Barnett A A, Souto A, and Jones G (2009) Predation by the tayra on the common marmoset and the pale-throated three-toed sloth. Journal of Ethology 27: 91.

Broekhuis F, Grünewälder S, McNutt JW, Macdonald DW (2014) Optimal hunting conditions drive circalunar behavior of a diurnal carnivore. Behavioral Ecology 25: 1268-1275.

Caro T M, and Stoner C J (2003) The potential for interspecific competition among African carnivores. Biological Conservation 110: 67-75.

Cavalcanti S M, Azevedo F D, Tomás W M, Boulhosa R L, Crawshaw Jr P G (2012) The status of the jaguar in the Pantanal. Cat News Special Issue 7: 29-34.

Dalerum F, Cameron E Z, Kunkel K, and Somers M J (2009) Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biology letters 5: 35-38.

De Abreu U G P, McManus C, and Santos S A (2010) Cattle ranching, conservation and transhumance in the Brazilian Pantanal. Pastoralism, 1: 99-114.

De Oliveira T G, and Pereira J A (2014) Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. Journal of Mammalian Evolution, 21: 427-436.

De Oliveira T G, Tortato M A, Silveira L, Kasper C B, Mazim F D, Lucherini M, Jácomo A T, Soares J B G, Marques R V, and Sunquist M (2010) Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. Biology and conservation of wild felids 559-580.

Dröge E, Creel S, Becker M S, M'soka J (2017) Spatial and temporal avoidance of risk within a large carnivore guild. Ecology and Evolution 7: 189-199.

Donadio E, and Buskirk S W (2006). Diet, morphology, and interspecific killing in Carnivora. The American Naturalist 167: 524-536.

Durant S M (1998) Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal ecology 67: 370-386.

Emmons L H (1987) Comparative feeding ecology of felids in a neotropical rainforest. Behavioral ecology and sociobiology 20: 271-283.

Farrell L E, Roman J, and Sunquist M E (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. Molecular Ecology 9:1583-1590.

Foster V C, Sarmento P, Sollmann R, Tôrres N, Jácomo A T, Negrões N, Fonseca C, and Silveira L (2013) Jaguar and puma activity patterns and predator‐ prey interactions in four Brazilian biomes. Biotropica 45: 373-379.

Gantchoff M G, and Belant J L (2016) Patterns of coexistence between two mesocarnivores in northern Patagonia in the presence of invasive hares and anthropogenic disturbance. Austral Ecology 41: 97-105.

Harmsen B J, Foster R J, Silver S C, Ostro L E, and Doncaster C P (2011) Jaguar and puma activity patterns in relation to their main prey. Mammalian Biology 76: 320-324.

Hayward M W, and Slotow R (2009) Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. African Journal of Wildlife Research 39: 109-125.

Holland A E, Byrne M E, Bryan A L, DeVault TL, Rhodes O E, Beasley J C (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 R D, Polis G A (1997) A theoretical framework for intraguild predation. The American Naturalist 149: 745-764.

Karanth K U (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biological conservation 71: 333-338.

Karanth K U, and Sunquist M E (1995) Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology 439-450.

Karanth K U, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, and Kumar N S (2017) Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B: Biological Sciences 284: 20161860.

Lacher T E, Gonçalves H C (1988) Environmental degradation in the Pantanal ecosystem. Bioscience 38: 164-171.

Lashley M A, Cove M V, Chitwood M C, Penido G, Gardner B, DePerno C S, and Moorman C E (2018) Estimating wildlife activity curves: comparison of methods and sample size. Scientific reports 8: 1-11.

Linnell J D, and Strand O (2000) Interference interactions, co‐ existence and conservation of mammalian carnivores. Diversity and Distributions 6: 169-176.

Linnell J D, Swenson J E, and Andersen R (2000) Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones?. Biodiversity and Conservation 9: 857-868.

Lucherini M, Reppucci J I, Walker R S, Villalba M L, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. Journal of Mammalogy 90: 1404-1409.

Macdonald D, and Loveridge A (2010) The biology and conservation of wild felids (Vol. 2). Oxford University Press, Oxford.

Meredith M, and Ridout M (2014) Overview of the overlap package. R, Project 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. Journal of Animal Ecology 87: 1709-1726.

Mourão G, and Medri Í M (2007) Activity of a specialized insectivorous mammal (Myrmecophaga tridactyla) in the Pantanal of Brazil. Journal of zoology 271:187-192.

O'Brien T G, Kinnaird M F, and Wibisono H T (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6: 131-139.

Osorio C, Muñoz A, Guarda N, Bonacic C, and 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.

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. Journal of Zoology 303: 90-98.

Ridout M S, and Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14: 322-337.

Romero-Munoz A, Maffei L, Cuéllar E, and Noss A J (2010) Temporal separation between jaguar and puma in the dry forests of southern Bolivia. Journal of Tropical Ecology 303-311.

Rovero F, and Zimmermann F (2016) Camera trapping for wildlife research. Pelagic, Exeter.

Rowcliffe, J M., Field J, Turvey S T, and Carbone C (2008). Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45: 1228-1236.

Rowcliffe J M, Kays R, Kranstauber B, Carbone C, and Jansen P A (2014) Quantifying levels of animal activity using camera trap data. Methods in Ecology and Evolution 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 T W (1974) Resource partitioning in ecological communities. Science 185: 27-39.

Scognamillo D, Maxit I E, Sunquist M, and Polisar J (2003) Coexistence of jaguar (Panthera onca) and puma (Puma concolor) in a mosaic landscape in the Venezuelan llanos. Journal of Zoology 259: 269-279.

Sévêque A, Gentle L K, López- Bao J V, Yarnell R W, and Uzal A (2020) Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biological Reviews.

Silver S C, Ostro L E, Marsh L K, Maffei L, Noss A J, Kelly M J, Wallace R B, Gomez H, and 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 M J, Parakkasi K, and Hutajulu M B (2015) Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. Journal of Zoology 296: 104-115.

Sunquist M, and Sunquist F (2017) Wild cats of the world. University of chicago press, Chicago.

Swanepoel L H, Lindsey P, Somers M J, Van Hoven W, and Dalerum F (2013) Extent and fragmentation of suitable leopard habitat in South Africa. Animal Conservation 16: 41-50.

Tobler M W, Carrillo- Percastegui S E, Pitman R L, Mares R, and Powell G (2008) An evaluation of camera traps for inventorying large- and medium- sized terrestrial rainforest mammals. Animal Conservation 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 ethologica 19: 123-132.

Wang E, Donatti C I, Ferreira V L, Raizer J, and Himmelstein J (2011) Food habits and notes on the biology of Chelonoidis carbonaria (Spix 1824)(Testudinidae, Chelonia) in the southern Pantanal, Brazil. south american Journal of herpetology 6: 11-19.

Wolf C, and Ripple W J (2016) Prey depletion as a threat to the world's large carnivores. Royal Society Open Science 3: 160252.

Zhao G, Yang H, Xie B, Gong Y, Ge J, and Feng L (2020) Spatio-temporal coexistence of sympatric mesocarnivores with a single apex carnivore in a fine-scale landscape. Global Ecology and Conservation 21: e00897.

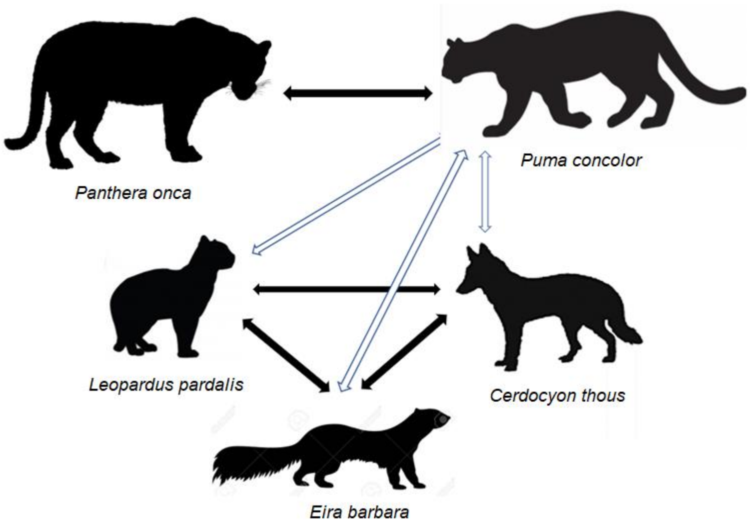

Fig. 1 Carnivore guild in the study area, showing the expected pair interactions among species from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013-2015. Solid black arrows related to Hypothesis 1 (niche segregation among species of similar size), white arrows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

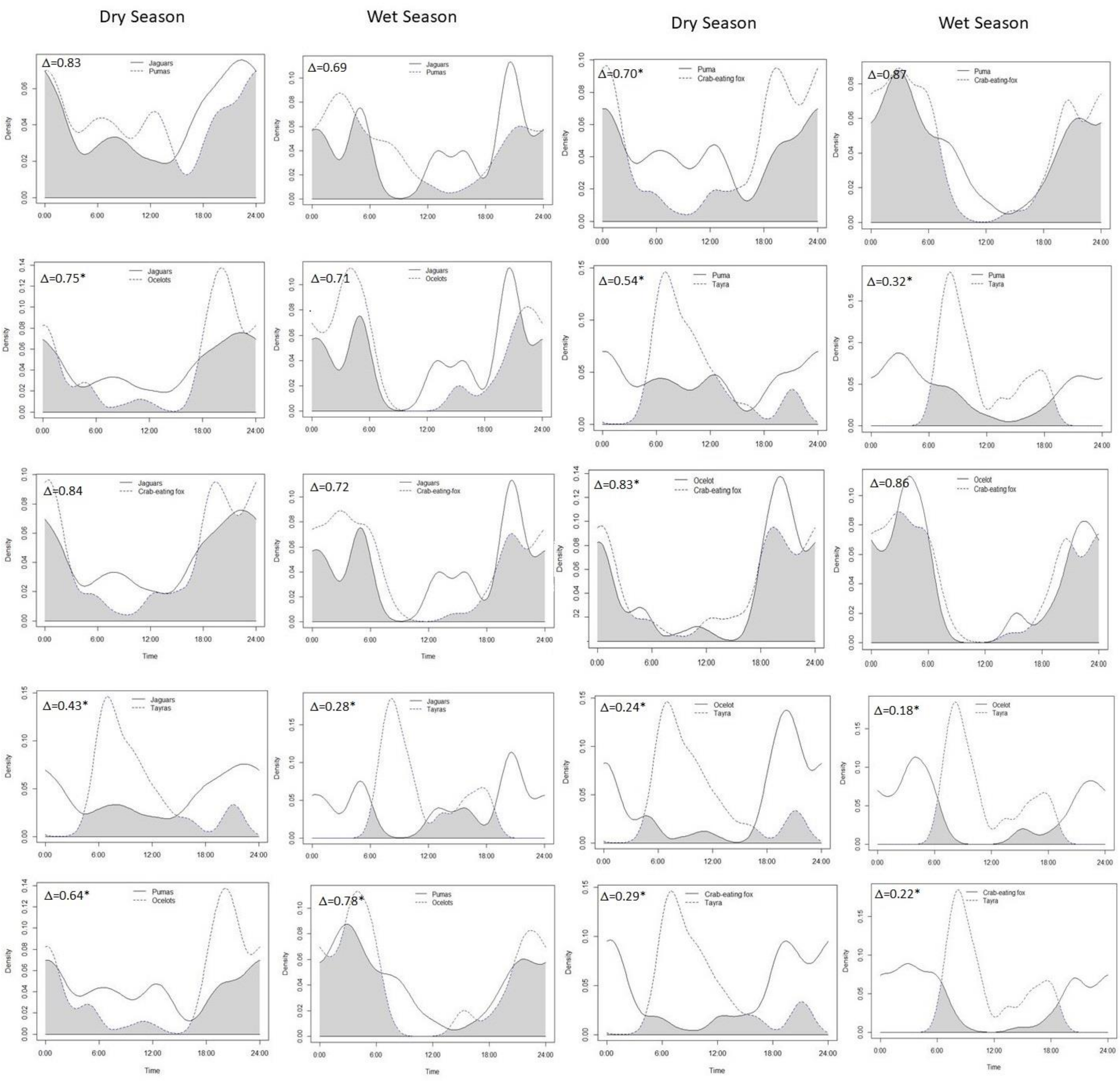

Fig. 2 Density estimates of daily activity patterns between five species of sympatric carnivores in the dry and wet season from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013-2015. Time along the x-axis is in a 24 hour format with noon in the center. The coefficient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

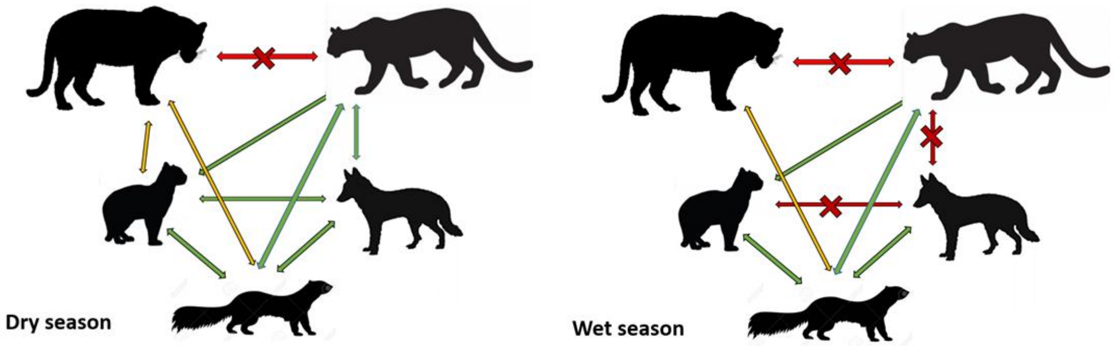

Fig. 3 Documented temporal segregation in both dry and wet seasons within a carnivore guild from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013-2015 (clockwise from top left the species are: jaguar, puma, crab-eating fox, tayra, ocelot). Green indicates a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

Appendix

Table S1: Results from Wald statistic significance tests on ten pairwise species comparisons of activity patterns and Δ coefficient overlaps (SE = standard error) from a camera trapping study across 134 stations in the southern Brazilian Pantanal between 2013-2015.

Species	**Dry season p-value**	**Sample size**	**SE**	**Overlap**	**Wet season p-value**	**Sample size**	**SE**	**Overlap**
jaguar – puma	0.221	104	0.04	0.83	0.340	111	0.08	0.69
jaguar – ocelot	0.007**	116	0.04	0.75	0.291	66	0.08	0.71
jaguar – crab-eating fox	0.060	367	0.03	0.84	0.324	350	0.07	0.72
jaguar – tayra	<0.001***	58	0.06	0.43	<0.001***	24	0.10	0.28
puma – ocelot	<0.001***	144	0.04	0.64	0.031*	159	0.03	0.78
puma - crab-eating fox	<0.001***	395	0.03	0.70	0.060	443	0.02	0.87
puma – tayra	<0.001***	86	0.06	0.54	<0.001***	117	0.06	0.32
ocelot - crab-eating fox	0.037*	407	0.02	0.83	0.247	398	0.03	0.86
ocelot – tayra	<0.001***	98	0.06	0.24	<0.001***	72	0.07	0.18
crab-eating fox - tayra	<0.001***	349	0.05	0.29	<0.001***	356	0.06	0.22