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COMMUNICATION

Temporal overlap between two sympatric carnivores in northwestern Peru and southwestern Ecuador

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Abstract: The coexistence of sympatric species is determined by differences in their ecological niche. Thus, for taxonomically and ecologically similar species to coexist, they must segregate in at least one of the three most important dimensions of the ecological niche: space, time or diet. The Pampas Cat *Leopardus colocola* and the Sechuran Fox *Lycalopex sechurae* are sympatric species; and they are the most common medium-sized carnivores in the Sechura Desert and in the lowland seasonally dry tropical forest of Peru and Ecuador. We evaluated the activity pattern of both mesocarnivores using camera trapping and temporal overlap analysis in both arid ecosystems. We found a high degree of activity overlap and no statistically significant difference in the activity pattern of both species (Δ = 0.85 with 95% CI = 0.81 – 0.94; W = 0.531, SD = 2, P = 0.767), both being cathemeral. There is, however, a contrasting pattern in the daytime activity of these species in the dry forest. These results suggest that the different diet composition may be the main dimension that is facilitating the coexistence of both mesocarnivores in the arid ecosystems of northern Peru and southern Ecuador.

Keywords: Activity pattern, dry forest, mesocarnivores, Pampas Cat, Sechura Desert, Sechuran Fox.

Resumen: La coexistencia de especies simpátricas es determinada por las diferencias en su nicho ecológico. Por la tanto, para que especies taxonómica y ecológicamente similares coexistan, deben de segregarse en por lo menos una de las tres principales dimensiones del nicho ecológico: espacio, tiempo o dieta. El Gato del Pajonal Leopardus colocola y el Zorro de Sechura Lycalopex sechurae son especies taxonómica y ecológicamente similares que viven en simpatría, siendo los carnívoros de mediano tamaño más comunes del Desierto de Sechura y de las partes bajas del Bosque Tropical Estacionalmente Seco de Perú y Ecuador. Debido a esto, evaluamos los patrones de actividad de ambos mesocarnívoros usando cámaras trampas y análisis de actividad temporal en ambos ecosistemas áridos. Encontramos un alto nivel de superposición de actividad temporal y ninguna diferencia significativa en los patrones de actividad de ambas especies (Δ = 0.85 con 95% CI = 0.81–0.94; W = 0.531, DE = 2, p = 0.7668), siendo las dos especies catemerales. Sin embargo, hay un patrón contrastante en la actividad diurna de estas especies en el bosque seco. Estos resultados sugieren que la diferente dieta de ambas especies puede ser el principal factor que está facilitando la coexistencia de ambos mesocarnívoros en los ecosistemas áridos del norte de Perú y sur de Ecuador.

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For **Author details, Author Contribution,** and **Acknowledgements** see end of this article.

INTRODUCTION

The coexistence of sympatric species is determined by their ecological niche. To facilitate coexistence in the same space, taxonomically similar species need to distinguish themselves by having different diets, habitat use or temporal patterns (Schoener 1974). The temporal pattern is determined by behavioural responses of the species to abiotic pressures and biotic interactions (Beltran & Delibes 1994; Weller & Bennett 2001). Abiotic pressures such as intense temperatures and moonlight, can influence the diel activity of a species. Similarly, activity patterns can be determined by biotic interactions such as predator species synchronizing their activity with their most profitable prey (Monterroso et al. 2013; Marinho et al. 2017), or competing species having a different activity pattern to avoid direct encounters with dominant species (Di Bitetti et al. 2009).

Generally, sympatric mesocarnivores (i.e., mammalian carnivore species situated at an intermediary trophic level that could weigh up to 15kg) are considered competing species. This is because of their similar morphology, body size, and ecosystem function as controllers of prey species (Davies et al. 2007; Prugh et al. 2009). We studied two sympatric mesocarnivores that inhabit the arid ecosystems of Peru and Ecuador, the Pampas Cat *Leopardus colocola* and the Sechuran Fox *Lycalopex sechurae.*

The Pampas Cat is a small wild felid (2–5kg), widely distributed from northern Ecuador to southern Argentina. It occurs at elevations from sea level to 5,704m in a great variety of habitats, such as desert, dry forest, wetlands, savannas, cerrado, and Andean ecosystems like paramo and puna (Silveira 1992; Bagno et al. 2004; Cossíos et al. 2007; García-Olaechea & Hurtado 2018). It is an obligate carnivore, mainly feeding on rodents and birds (Napolitano et al. 2008; Fajardo et al. 2014). In the Cerrado, it is mainly a diurnal species, while in the Andes it is mainly nocturnal and cathemeral (Silveira et al. 2005; Lucherini et al. 2009; Huaranca et al. 2019). The Sechuran Fox is a medium-sized canid (2.5–5kg), distributed only from southern Ecuador to central Peru. It occurs from sea level to 1,800m in the Sechura Desert and the seasonally dry tropical forest of the Tumbesian Region and Marañon Valley (Cossíos 2007; Figueroa et al. 2013). It is an omnivorous species, feeding on different small vertebrates, arthropods, and fruits; and is considered mainly nocturnal (Cossíos 2007).

Given the wide distribution of the Pampas Cat and its variation in temporal activity across different ecosystems, our main objective was to quantify the temporal overlap of the Pampas Cat and a potential competing species, the Sechuran Fox, in the Sechura Desert and seasonally dry tropical forest of northwestern Peru and southwestern Ecuador. These two species are the only carnivores of similar size in the Sechura Desert, and the two most common carnivores in the lowland dry forest (Chávez-Villavicencio et al. 2015; García-Olaechea & Hurtado 2018).

STUDY AREAS

This project was conducted along the southern Ecuadorian and northern Peruvian coastline ecosystems: the Sechura Desert (SD; limited to Peru) and the seasonally dry tropical forest (SDTF; Brack-Egg 1986). Both arid ecosystems are among the Global 200 priority ecoregions for global conservation; the SD is categorized as Vulnerable while the SDTF is considered Critically Endangered (Olson & Dinerstein 2002). We surveyed three SD localities: (a) San Pedro de Vice Mangrove (5.524^{0}S, 80.886^{0}W), (b) Ñapique Lake (5.503^{0}S, 80.704^{0}W), (c) Illescas Reserve Zone (6.079^{0}S, 81.055^{0}W); and three SDTF localities: (d) El Virrey (5.511^{0}S, 79.951^{0}W), (e) Cerros de Amotape National Park (3.963^{0}S, 80.517^{0}W), and (f) La Ceiba Natural Reserve (4.167^{0}S, 80.261^{0}W) (Figure 1). The SD extends from the coast 20–100 km inland to the adjacent dry forest. It is an arid ecoregion almost devoid of vegetation, except for certain riverine areas (Brack-Egg 1986). The annual average temperature varies between 16°C and 24°C, and the average precipitation is lower than 100mm per year (Richer & Ise 2005).

The SDTF stretches over 100–150 km on the western slopes of the Andes and meets the coast of the Pacific Ocean in northern Peru. The climate is hot and dry with an annual average temperature of approximately 24°C, with highs of 40°C during the summer, receiving <200mm of rain per year (Brack-Egg 1986). It has some patches of forest that grows green during the rainy season and is adapted to arid conditions in the dry season (Linares-Palomino et al. 2010).

MATERIALS AND METHODS

Data collection

Between April 2015 and February 2016, we surveyed each locality with 32 camera traps (12 Illuminator Covert DLC and 20 Bushnell Trophy Cam) separated by at least 300m. Each camera trap was positioned on a mammal

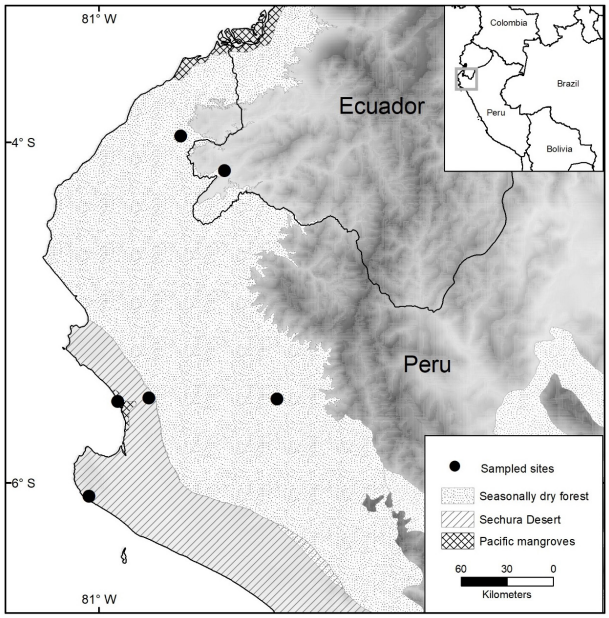

Figure 1. Studied localities in northwestern Peru and southwestern Ecuador, highlighting the Sechura Desert and the seasonally dry tropical forest.

trail or near a water source approximately 30cm above the ground, and set to take three photos per second after each detection. To increase the capture rate, we placed shiny CDs in front of the cameras as a visual attractant (Cove et al. 2014). The sampling effort at each locality varied from 50 to 340 camera trap days.

Data analyses

We consider an independent event when the same species was recorded by the same camera trap within one hour (Marinho et al. 2017). The independent events were classified into three categories: diurnal events recorded between 1h after sunrise and 1h before sunset, nocturnal events between 1h after sunset and 1h before sunrise, and crepuscular events from 1h before to 1h after sunrise and sunset (Lucherini et al. 2009; Foster et al. 2013). We determined the time of sunset and sunrise using the software Moonrise 3.5 (Sidell 2002). We followed Gómez et al. (2005) in classifying both species into five possible categories: diurnal with <10% of independent events at night, nocturnal with >90% of independent events at night, mostly diurnal with 10–30 % of independent events at night, mostly nocturnal with 70–90 % of independent event at night, and cathemeral with 30–70 % of activity during day or night.

To statistically compare the activity patterns of the Pampas Cat and the Sechuran Fox in each ecosystem, we used the non-parametric Mardia-Watson-Wheeler test (Batschelet 1981). Additionally, we used the same test and found no significant differences in the activity patterns of each species in both ecosystems, i.e., the activity pattern of Pampas Cat was the same in the SD and the SDTF (Appendix 1). Thus, we pooled the data from both ecosystems, for an overall activity pattern comparison between the two species.

To estimate the temporal overlap between the Pampas Cat and the Sechuran Fox, we estimated the diel activity pattern using the kernel density analysis with a smoothing parameter of 1.00 (Ridout & Linkie 2009). First, we calculated the overlap estimator of the pooled data, followed by the overlap in each ecosystem. The overlap coefficient (Δ) ranges from 0 (no overlap) to 1 (complete overlap) and uses four estimators, from which two estimators, Δ1 and Δ4, are recommended (Ridout & Linkie 2009). The first one is recommended for small samples sizes of <50 events, while the second one is best for large sample sizes of >50 events (Meredith & Ridout 2017). We used the Δ1 for the overlap in each ecosystem, and the Δ4 for the pooled overlap for both ecosystems. The precision of the estimators was obtained through 95% confidence intervals from 10,000 bootstrap samples. We followed Monterroso et al. (2014) in defining a low overlap when the Δ was <0.5, moderate when the Δ was between 0.5 and 0.75, and high overlap when the Δ was >0.75. The analyses were done with the Overlap (Meredith & Ridout 2017) and Circular packages (Agostinelli & Lund 2017) in the R software (R Core Team 2015).

RESULTS

We obtained 58 independent events of Pampas Cat (58.6% in the SD and 41.4% in the SDTF) and 373 of Sechuran Fox (78.8% in the SD and 21.2% in the SDTF) in 1,783 camera trap days (Image 1). We also registered seven events of Ocelot *Leopardus pardalis* and two events of Margay *Leopardus wiedii* in Cerros de Amotape National Park of the SDTF. These last two taxonomically and ecologically similar species, however, were not included in the analyses because of the low number of records.

The activity pattern of the Pampas Cat and the Sechuran Fox were both categorized as cathemeral, but with more activity at night than during the day and the crepuscule. Although not significant, the Pampas Cat showed less diurnal activity in the SD than in the SDTF (17.6% vs 41.8%), while for the Sechuran Fox the diurnal activity was similar across both ecosystems (21.4% vs 21.5%) (Figure 2).

Image 1. A Pampas Cat *Leopardus colocola* and a Sechuran Fox *Lycalopex sechurae* in the Sechura Desert. © Peruvian Desert Cat Project.

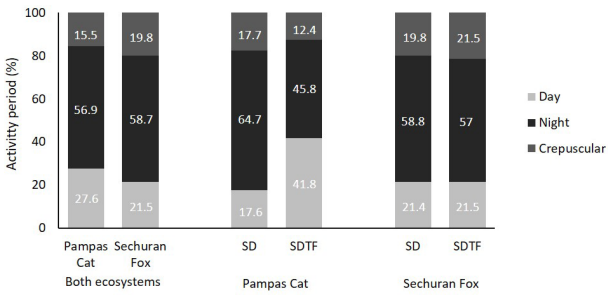

Figure 2. Activity patterns of Pampas Cat and Sechuran Fox in both arid ecosystem of northwestern Peru and southwestern Ecuador: the Sechura Desert (SD) and the seasonally dry tropical forest (SDTF).

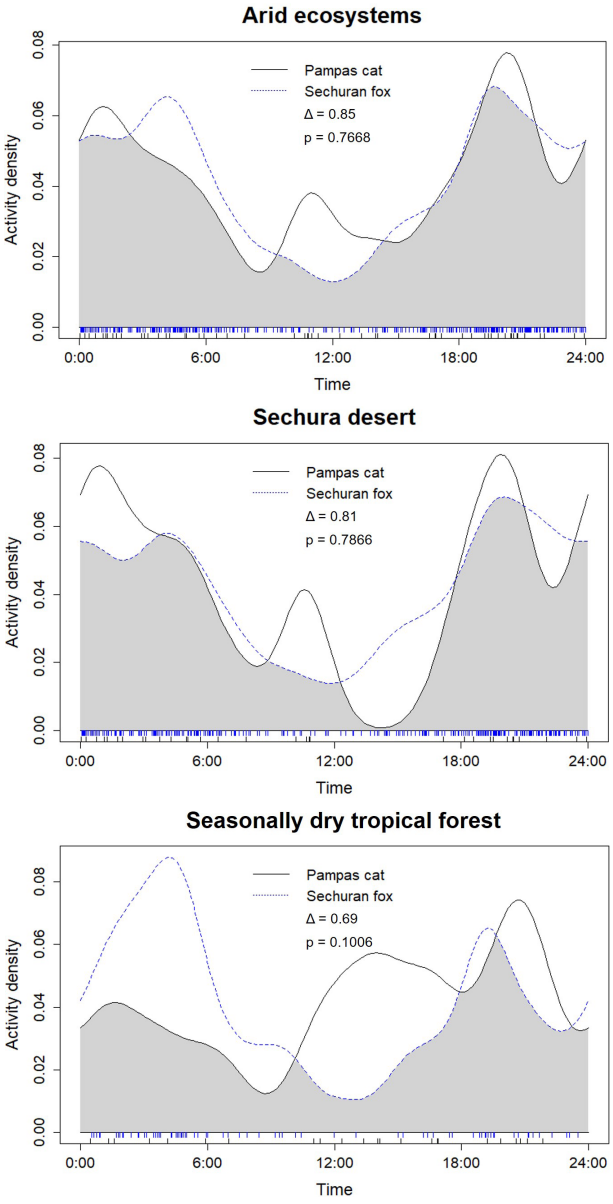

Figure 3. Overlap of diel activity patterns of Pampas Cat *Leopardus colocola* (solid black lines) and Sechuran Fox *Lycalopex sechurae* (dashed blue lines) in a) both arid ecosytems, b) in the Sechura Desert, and c) in the seasonally dry tropical forest. Gray area represents the estimate overlap of both activity patterns (Δ), and p values show the significance.

The temporal overlap between the activity pattern of the Pampas Cat and the Sechuran Fox in both arid ecosystems was high (Δ = 0.85 with 95% CI = 0.81–0.94) and not statistically different (W = 0.531, SD = 2, P = 0.767). Similarly, the overlap in the Sechura Desert was also high (Δ = 0.81 with 95% CI = 0.76–0.92) and not statistically different (W = 0.481, SD = 2, P = 0.787). Finally, the temporal overlap between both species in the dry forest was moderate (Δ = 0.69 with 95% CI = 0.53–0.75), but not statistically different (W = 4.592, SD = 2, P = 0.101) (Figure 3).

DISCUSSION

Our results are partially consistent with the available literature for both carnivores in other regions of South America. The Pampas Cat in the Brazilian Cerrado is mainly a diurnal species, with some crepuscular and occasional nocturnal activity (Silveira et al. 2005). In three countries in the Andes, however, it is mainly nocturnal (Lucherini et al. 2009), while a recent study in the Bolivian Andes determined that it is cathemeral (Huaranca et al. 2019). Latter study results are consistent with our results, which also found most of the events at night (50%). This overall flexibility of the Pampas Cat's activity pattern can be explained by the different environmental conditions of the studied ecosystems, and because of the different carnivore communities that exerted different coexistence adaptations.

Information about the Sechuran Fox is scarce, as it is an endemic and under-studied species. Asa & Wallace (1990) suggested that in the Sechura Desert it is mostly nocturnal. We found, however, that it is cathemeral in both ecosystems. This discrepancy could be due to different methodologies used. While Asa & Wallace (1990) radio-tracked four individuals (three of them were possibly a family) for five weeks in just one locality (Bayovar, close to Illescas Reserve Zone), we used camera traps for 14 weeks in six different localities. These differences in survey period, area, and equipment allowed us to cover a larger area and record more individuals, thus obtaining a larger data set for a more representative estimate of the population's activity. Additionally, the Sechuran Fox family that showed a more nocturnal activity may have used a different foraging strategy when accompanied by juveniles, or where the density of intraguild conspecifics like the Pampas Cat was low.

The activity overlap of the Pampas Cat and the Sechuran Fox in both arid ecosystems was high, which represents a lack of temporal segregation between these sympatric species. If we focus on the SDTF populations, however, we see a trend of temporal avoidance, and potentially with other carnivores as well. This trend was observed mainly during daytime when the Pampas Cat is more active than the Sechuran Fox. The Pampas Cat's higher activity during the day in the SDTF compared to the SD, may be a consequence of the higher vegetation cover and thus lower temperatures in the SDTF compared to the SD. The greater continuous forest cover facilitates movement to capture prey and hide from predators while avoiding exposure to the intense heat of the desert. Another potential reason for this discrepancy in the activity pattern in the SDTF compared to the SD may be to avoid direct encounters with other potential nocturnal competitor species, e.g., Ocelot and Margay also occur in one of the survey localities of the SDTF (Hurtado & Pacheco 2015).

As the theory of the niche partitioning proposes, a high degree of overlap in one dimension should be associated with a low degree of overlap in at least one other dimension (Macarthur & Levins 1967). We assume that the coexistence of Pampas Cat and Sechuran Fox is facilitated to a higher degree by their different diet compositions than by temporal segregation. While the Pampas Cat is an obligate carnivore, feeding on small vertebrates such as rodents and birds (Napolitano et al. 2008; Fajardo et al. 2014), the Sechuran Fox is an omnivorous species, feeding on fruits like *Prosopis pallida*, *Cordia lutea*, *Ficus*, and *Cocoloba ruiziana,* and on rodents, ground birds, and lizards (Cossíos 2007; Escribano-Avila 2019). Furthermore, the Sechuran Fox prefers feeding on plants over vertebrate sources (Asa & Wallace 1990; Cossíos 2005). This pattern of coexistence was also found between other feline and canine species in South America, the Geoffroy's Cat *Leopardus geoffroyi* and the Culpeo Fox *Lycalopex culpaeus* (Gantchoff & Belant 2016). Latter authors concluded that the different diet compositions have stronger evidence of segregation than activity patterns and occupancy.

Most of the available information on Pampas Cat is from the Andes, where its interaction with the Andean Cat *Leopardus jacobita* and other high-altitude carnivores has been studied (Walker et al. 2007; Napolitano et al. 2008; Lucherini et al. 2009; Reppucci et al. 2011; Villalba et al. 2012; Huaranca et al. 2019). This is the first time that Pampas Cat ecology has been studied in different arid ecosystems, bringing insights about its coexistence with the endemic Sechuran Fox. Activity patterns of Pampas Cats have neither been studied before in the SD nor in the SDTF, and there is only one publication about the activity patterns of radio-tracked Sechuran Foxes in the SD (Asa & Wallace 1990). Studies of the biology of the carnivore community in the Sechura Desert and in the seasonally dry tropical forests will help understand the needs of these species and serve to develop species-specific conservation plans.

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Appendix 1. Mardia-Watson-Wheeler tests between the Sechura Desert and the seasonally dry tropical forests for both species. W is the static of the test, and large W values indicate greater differences between species distributions. d.f are the degrees of freedom, and the statistically difference for P< 0.05.

Species	W	d.f	P
Pampas Cat	2.8953	2	0.2351
Sechuran Fox	4.1528	2	0.1254

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