Temporal overlap in the activity of *Lynx rufus* and *Canis latrans* and their potential prey in the Pico de Orizaba National Park, Mexico

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Abstract

Temporal overlap in the activity of Lynx rufus *and* Canis latrans *and their potential prey in the Pico de Orizaba National Park, Mexico.* Species of the same trophic guild are thought to coexist through their differential use of resources, including food, space and time. Time understood as the pattern of activity is highly dynamic. Fourteen camera–traps were set up in the Pico de Orizaba National Park and active for 12 months. Frequency histograms were used to analyze their activity patterns (AP) and a coefficient of overlap (Δ) was used to determine the temporal overlap between two predators, *Lynx rufus and Canis latrans,* and the predators and their potential prey. A sampling effort of 5,110 traps/night obtained 217 independent records of *L. rufus* (45), *C. latrans* (27) and eight potential prey species (145). The predators were cathemeral and four potential prey mainly lagomorphs and rodents were nocturnal. The temporal overlap between the predators $\hat{\Delta}$ = 0.80, and the highest overlap between predators and prey were for *C. latrans* and rodents ($\hat{\Delta}$ = 0.80), and *L. rufus* and lagomorphs ($\hat{\Delta}$ = 0.58), with differences between the degree of overlap in dry and rainy seasons. The cathemeral habits of the predators likely increase their likelihood of hunting success, particularly for prey with variable activity patterns. The APs support information on dietary breadth and the differential use of resources and temporal differences as strategies for coexisting predators, continually adapting to a highly dynamic and changing environment.

Key words: Coefficient of overlap, Co–predators, Coyote, Bobcat, Lagomorphs, Rodents

Resumen

Superposición temporal de la actividad de Lynx rufus *y* Canis latrans *y sus presas potenciales en el Parque Nacional Pico de Orizaba, en México*. Se cree que el uso diferencial de los recursos, en especial del espacio, la comida y el tiempo, permite la coexistencia de especies del mismo gremio trófico. El tiempo entendido como el patrón de actividad es altamente dinámico. En el Parque Nacional Pico de Orizaba se instalaron 14 cámaras-trampa que estuvieron activas durante 12 meses. Se analizaron los patrones de actividad (PA) de las especies mediante histogramas de frecuencia y se calculó el índice de solapamiento (Δ) para determinar la superposición temporal entre dos depredadores, *Lynx rufus* y *Canis latrans* y entre los depredadores y sus presas potenciales. Con un esfuerzo de muestreo de 5.110 noches/trampa se obtuvieron 217 registros independientes de *L. rufus* (45), *C. latrans* (27) y de ocho especies de presas potenciales (145). Los depredadores fueron catamerales y cuatro presas, nocturnas, principalmente lagomorfos y roedores. La superposición temporal entre ambos depredadores fue $\hat{\Delta}$ = 0,80 y entre estos y sus presas, los valores más altos se encontraron entre *C. latrans* y los roedores ($\hat{\Delta}$ = 0,80) y entre *L. rufus* y los lagomorfos ($\hat{\Delta}$ = 0,58), con variaciones entre la estación seca y la de lluvias. Al ser de hábitos catamerales, los depredadores tienen más posibilidades de cazar más presas, en especial las que tienen patrones de actividad variables. Los PA validan la información sobre la variedad de la alimentación y la utilización diferencial de los recursos y las diferencias temporales como estrategias de coexistencia de los depredadores, que se adaptan constantemente a un entorno muy dinámico y cambiante.

Palabras clave: Índice de solapamiento, Codepredadores, Coyote, Gato montés, Lagomorfos, Roedores

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Introduction

Several mechanisms are used to explain the coexistence of species with similar trophic niches, including their ability to segregate shared resources in space and time (Schoener, 1974; Gordon, 2000; Di Bitetti et al., 2010). However, the impact of the time of day on community dynamics, particularly the interactions between species that share food resources, has been neglected and is probably underestimated (Morgan, 2004). The activity pattern (AP) of an animal varies according to many factors, including its feeding habits (Karanth and Sunquist, 2000; Scognamillo et al., 2003; Carrillo et al., 2009), prey availability and diversity (Sunquist and Sunquist, 2002), the presence of predators and competitors (Scognamillo et al., 2003; Delibes–Mateos et al., 2014), temperature (Hernández–SaintMartin et al., 2013) and the level of natural and human disturbances (Van Dyke et al., 1986; Paviolo et al., 2009). Therefore, studying the APs of species with overlapping distributions can help explain how they partition their shared resources (Kronfeld–Schor and Dayan, 2003), including the temporal relationships between coexisting predatory species and their potential prey, which have resulted from evolutionary changes driven by competition for food (Abrams and Cortez, 2015).

Camera traps are increasingly being used to monitor and assess the biodiversity of Protected Areas (Mandujano, 2017). They are also used to study the APs of wildlife (Di Bitetti et al., 2010; Hernández–SaintMartin et al., 2013; Rowcliffe et al., 2014; Ávila–Nájera et al., 2016) and to gather data on community interactions, such astemporal niche partitioning (Steenweg et al., 2017), community dynamics and species' responses to global climate change (Frey et al., 2017).

The Pico de Orizaba National Park (PONP) contains several nationally important ecosystems that are at risk of habitat fragmentation and anthropogenic disturbance despite having a protected status (SEMARNAT and CONABIO, 2015). The PONB is also thought to have a nationally important population of bobcat (*Lynx rufus*), and coyote (*Canis latrans*), but records from PONP are few (SEMARNAT and CONABIO, 2015) and information on coexistence strategies between both predators in Mexico (Hidalgo–Mihart et al., 2009; Elizalde–Arellano et al., 2014) is lacking. The aim of this study was to assess the APs of *L. rufus* and *C. latrans,* and their main prey species in the PONP, including the temporal overlap between these co–predators and potential prey. This will provide baseline data about the level of competition between them, including any evidence of temporal segregation and shared prey. These data could be used to monitor changes in this dynamic environment, which is at high risk of anthropogenic pressure.

Material and methods

The study took place around the PONP, Mexico. This park consists of 19,756 ha in the Tlachichuca, Chalchicomula de Sesma and Atzitzintla municipalities in Puebla State, and the Chalcahualco and La Perla municipalities in Veracruz State. PONP is located between 18º 56' 30" and 19º 09' 3" N and 97º 12' 30" and 97º 2' 30" W and has an altitudinal range of 2,700 to 5,760 m a.s.l. It has three main vegetation types: pine forest (up to 3,000 m a.s.l.), subalpine vegetation (3,000 to 4,000 m a.s.l.), and mountain scrub (4,000 to 4,200 m a.s.l.), with bare volcanic rock at higher altitudes. Despite its protected status, PONP is at risk of overgrazing by livestock, forest fires, and deforestation due to illegal logging (Martínez–Vázquez et al., 2010). Its fauna include 47 mammal, 48 amphibian and reptile, and 67 bird species, many of which are endangered in Mexico (Fa and Morales, 1991).

Camera trapping

Fourteen passive infrared sensor cameras (Cuddeback 1231 and Black Flash E3®) were sited in areas where mammals had been seen in a pilot study, with six on the western slope and eight on the eastern slope of the Pico de Orizaba Volcano. The positions of the camera stations were taken with a GPS–Garmin (fig. 1), with a distance between 1–3 km one from another. The cameras operated 24 h/day for 12 months (January–December 2017). They were placed 40 cm above ground level on tree trunks, and at an angle that avoided direct sunlight on the lens.

The camera traps were examined monthly for battery replacement and SD memory cards. Videos were downloaded and reviewed, and records of predators and/or prey were sorted into different taxa for analysis (Mandujano, 2017).

Activity patterns

The following rules were applied to ensure that only independent records of individual animals were used when calculating AP: (i) individuals of the same species recorded in consecutive videos could identified by a distinguishing feature; (ii) when not possible to distinguish between individuals of the same species, at least 3 h had elapsed between the photos; (iii) more than one individual of the same species was visible in a single photo (Ávila–Nájera et al., 2016).

The SUN TIMES V7.1 program (Kay and Du Croz, 2008) was used to determine the time of sunrise and sunset. All records of activity were classified according to the time on the video as: nocturnal (20:00–06:00 h), diurnal (08:00–18:00 h), or crepuscular (06:00–08:00 and 18:00–20:00 h). Species records were grouped into different APs: diurnal (< 15 % of observations at night), mainly diurnal (15 to 35 % of observations at night), nocturnal (> 85 % of observations at night), mainly nocturnal (65 to 85 % of the observations at night), cathemeral (intermittently active both at night and day) and crepuscular (active in the early hours of sunrise and sunset) (Gómez et al., 2005).

Overlap in activity patterns

The species were identified with their scientific name; in case of doubts with the family name only. As we were unable to identify small rodents they were all included as order Rodentia.

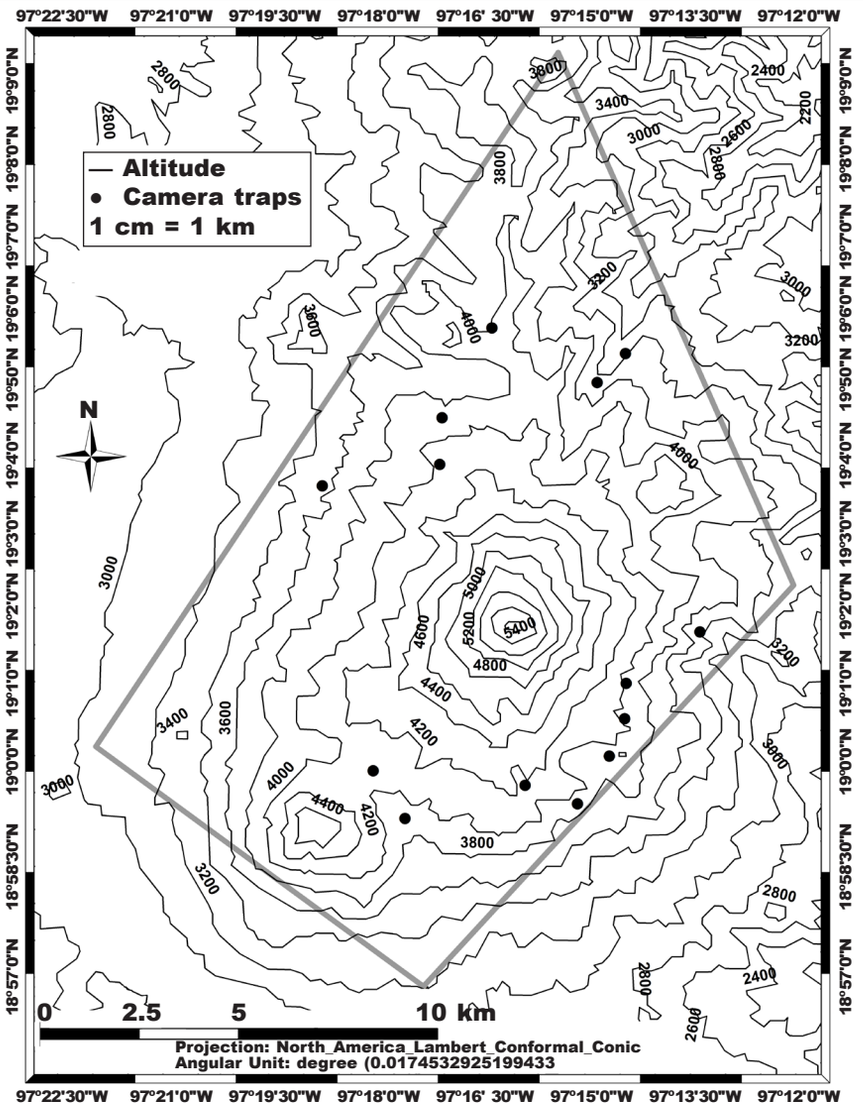

Fig. 1. Position of the camera traps (black dots) used to monitor wildlife in the Pico de Orizaba National Park, Veracruz, Mexico, with the park boundary shown as a thick grey line, and contour lines in black (altitude, m a.s.l.).

Fig. 1. Posición de las cámaras–trampa (puntos negros) utilizadas para monitorear la fauna silvestre en el Parque Nacional Pico de Orizaba, Veracruz, en México: La línea gris gruesa señala el límite del Parque y líneas negras, la altimetría (altitud, m s.n.m.).

The overlap in the APs between predators and their prey was calculated using the total records for the whole year, and then for the dry (December–May) and the rainy seasons (June–November). As AP data have a circular distribution (Zar, 2010), we used a coefficient (Δ) to estimate the temporal overlap in the AP between predators and prey, where Δ is between 0 (no overlap) and 1 (complete overlap) (Ridout and Linkie, 2009) using the equation:

$$\Delta \quad \min \{f(t), g(t)\} / dt$$

where are the values of two APs, and 95% confidence intervals of Δ were estimated using 1,000 bootstrap repetitions at 2.5 and 97.5 percentiles. Statistical analyses were performed using the overlap library of R (version 3.1.0).

Results

A total sampling effort of 5,110 traps/night yielded 217 independent photographs of predators and potential

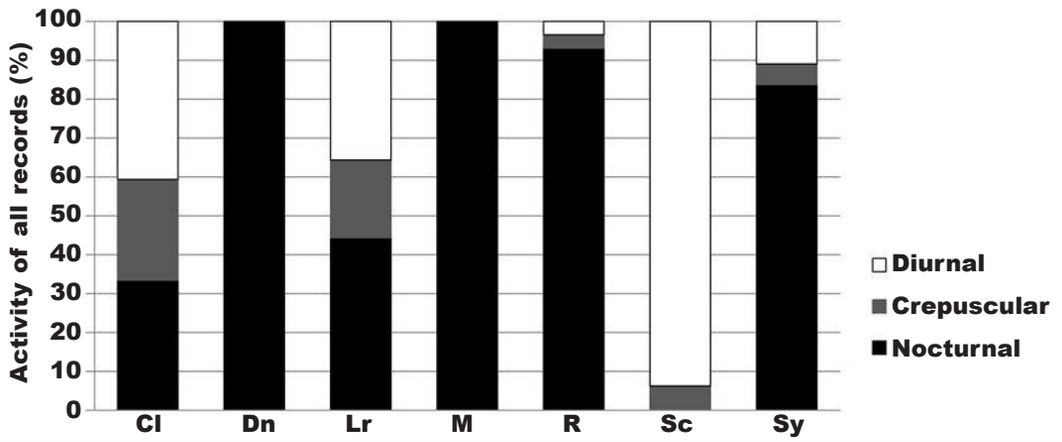

Fig. 2. Frequency histogram showing the percentage of records for three activity patterns (diurnal, crepuscular and nocturnal) of two predators, bobcat (Lr, *Lynx rufus*) and coyote (Cl, *Canis latrans*), and their potential prey species (Dn, *Dasypus novemcinctus*; M, Mephitidae; R, Rodentia; Sc, *Sciurus* sp.; Sy, *Sylvilagus* sp.) recorded over 12 months using camera traps in Pico de Orizaba National Park, Veracruz, Mexico.

Fig. 2. Histograma de frecuencias que muestra el porcentaje de registros de tres patrones de actividad (diurnos, crepusculares y nocturnos) de los dos depredadores, el lince (Lr, Lynx rufus*) y el coyote (Cl,* Canis latrans*) y de sus presas potenciales (Dn,* Dasypus novemcinctus*; M, Mephitidae; R, Rodentia; Sc,* Sciurus *sp.; Sy,* Sylvilagus *sp.) registradas durante 12 meses usando cámaras–trampa en el Parque Nacional Pico de Orizaba, Veracruz, en México.*

prey species. Throughout the year, the two predators exhibited mainly cathemeral activity: *L. rufus* (45; 20.7 %), and *C. latrans* (27; 11.5 %) (number of total independent photographs/percentage of total photographs). However, the potential prey were mostly nocturnal: *Sylvilagus* sp. (37; 17.1 %), Mephitidae (Hooded skunk, *Mephitis macroura* (10; 4.6 %), hog–nosed skunk, *Conepatus leuconotus* (3; 1.4 %), striped hog–nosed skunk, *Conepatus semistriatus* (1; 0.5 %), *Dasypus novemcinctus,* nine–banded armadillo (3; 1.4 %), and rodents (28; 13.4 %). The few diurnal species were *Sciurus* sp. (Peters's squirrel, *Sciurus oculatus* (40; 18.4 %) and Mexican grey squirrel, *Sciurus aureogaster* (24; 11.1 %). Figure 2 shows the frequency of total records grouped by AP for the two predators and the main prey species (Rodentia, Mephitidae, *Sciurus* sp., *Sylvilagus* sp. and *D. novemcinctus*).

The temporal overlap in the total activity recorded for *L. rufus* and *C. latrans* ($\hat{\Delta}$ = 0.80) (fig. 3) was high, particularly between 02:00–06:00 h, and at 16:00 and 20:00 h. This overlap was slightly higher in the rainy season ($\hat{\Delta}$ = 0.79) than in the dry season ($\hat{\Delta}$ = 0.60) (table 1). The APs of the two predators and potential prey species (table 1) differed, with the highest annual temporal overlap between the predators and prey occurring between *C. latrans* and rodents ($\hat{\Delta}$ = 0.80), and for *L. rufus* with *Sylvilagus* sp. ($\hat{\Delta}$ = 0.58). The temporal overlap between *C. latrans* and rodents was higher in the rainy season ($\hat{\Delta}$ = 0.79) than in the dry season ($\hat{\Delta}$ = 0.60), while the temporal overlap between *L. rufus* and *Sylvilagus* sp. was slightly higher in the dry season ($\hat{\Delta}$ = 0.59) than in the rainy season ($\hat{\Delta}$ = 0.52).

Records for the total and separate wet and dry season for the four species with the highest temporal overlaps (*L. rufus, C. latrans, Sylvilagus* sp. and rodents, see table 1) are plotted in figure 4. There was little seasonal variation in the number of *L. rufus* records, with peak activity occurring between 04:00–06:00 h and 17:00–20:00 h, and fewer records in the hottest time of day (09:00–14:00 h). There were more records for *C. latrans* in the rainy season (n = 22) than in the dry season (n = 5), and coyotes were active throughout the day in the rainy season. *Sylvilagus* sp. had the highest number of records for a single species in the rainy season (n = 31), most of these being nocturnal (active between 19:00–04:00 h). Most rodent activity occurred in the rainy season (n = 25), and was mainly nocturnal (fig. 4).

Discussion

Niche segregation results from the distribution of resources, including temporal resource segregation between competing species. The two predators in this study can show marked variation in their circadian rhythms (Romero–Muñoz et al., 2010, Hernández–SaintMartin et al., 2013), as seen from their APs in this study, despite a high overall temporal overlap. Some studies show that the AP of predators is not totally conditioned by the

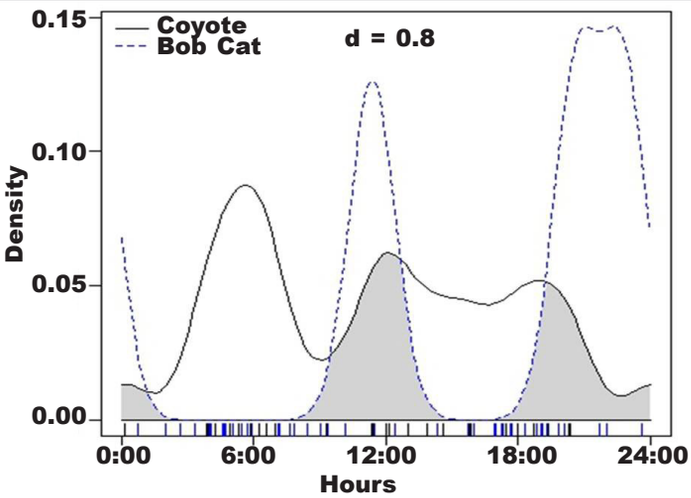

Fig. 3. Overlap in the activity patterns (Δ) of bobcat (*Lynx rufus*) and coyote (*Canis latrans*) in the Pico de Orizaba National Park, Veracruz, Mexico. Density is the frequency of records from January to December 2017 using camera traps.

*Fig. 3. Traslape de los patrones de actividad (*Δ*) del lince (*Lynx rufus*) y el coyote (*Canis latrans*) en el Parque Nacional Pico de Orizaba, en México. Density es la frecuencia de registros tomados de enero a diciembre de 2017 por fototrampeo.*

Table 1. Overlap coefficient values ($\hat{\Delta}$) for two species of predator, bobcat (*Lynx rufus*) and coyote (*Canis latrans*), and their potential prey (grouped by order or family) in the Pico de Orizaba National Park, Mexico.

Tabla 1. Valores del índice de solapamiento ($\hat{\Delta}$*) entre dos especies depredadoras, el lince (*Lynx rufus*) y el coyote (*Canis latrans*) y sus presas potenciales (agrupadas en orden o familia) en el Parque Nacional Pico de Orizaba.*

	Overlap coefficient ($\hat{\Delta}$)		
Species tested	Global	Rain	Dry
Bobcat–coyote	0.80	0.80	0.60
Bobcat–lagomorphs	0.58	0.52	0.59
Bobcat–armadillos	0.29	0.26	–
Bobcat–squirrels	0.39	0.44	0.37
Bobcat–skunks	0.57	0.50	0.45
Bobcat–rodents	0.57	0.50	0.45
Coyote–lagomorphs	0.50	0.48	0.38
Coyote–armadillos	0.35	0.36	–
Coyote–squirrels	0.49	0.56	0.33
Coyote–skunks	0.45	0.21	0.39
Coyote–rodents	0.80	0.79	0.60

activity of their prey (Elizalde–Arellano et al., 2012), with temporal segregation acting as an important mechanism to help carnivores avoid intraguild predation (Fedriani et al., 2000; Monterroso et al., 2014; Ávila–Nájera et al., 2016). However, other factors, such as human or natural disturbances, can significantly alter mammal behaviour (Monroy–Vilchis and Soria–Díaz, 2013; Ramesh and Downs, 2013; Ávila–Nájera et al., 2018), although high levels of activity at the hottest time of day are thought to be associated with reproduction in predatory species (Halle, 2000; Heurich et al., 2014). The AP of a species can thus be considered a complex response to its biotic or abiotic environment, especially where it interacts with other species (Halle, 2000).

In this study, *L. rufus* and *C. latrans* had cathemeral habits. *L. rufus* was most active around 04:00–06:00 h and 17:00–19:00 h, as seen by Elizalde–Arellano et al. (2014), although it is thought to be mainly nocturnal like its main prey, lagomorphs (Aranda, 2002). However, in PONP *C. latrans* was active throughout the day, with peak activity between 05:00 and 06:00 h. This finding is similar to that in a study by González et al. (1992), who also found its diet was more omnivorous in spring–summer when it ate fruits and become mainly diurnal, spending less time searching for nocturnal prey.

An overlap in activity between predator and prey may reflect that predators hunt when their prey are most active (Lima, 2002; Hernández, 2008; Romero–Muñoz et al., 2010), and could account for the high overlap between bobcat and lagomorph records in PONP, as reported by Hamilton and Hunter (1939), Leopold and Krausman (1986) and Aranda (2002).

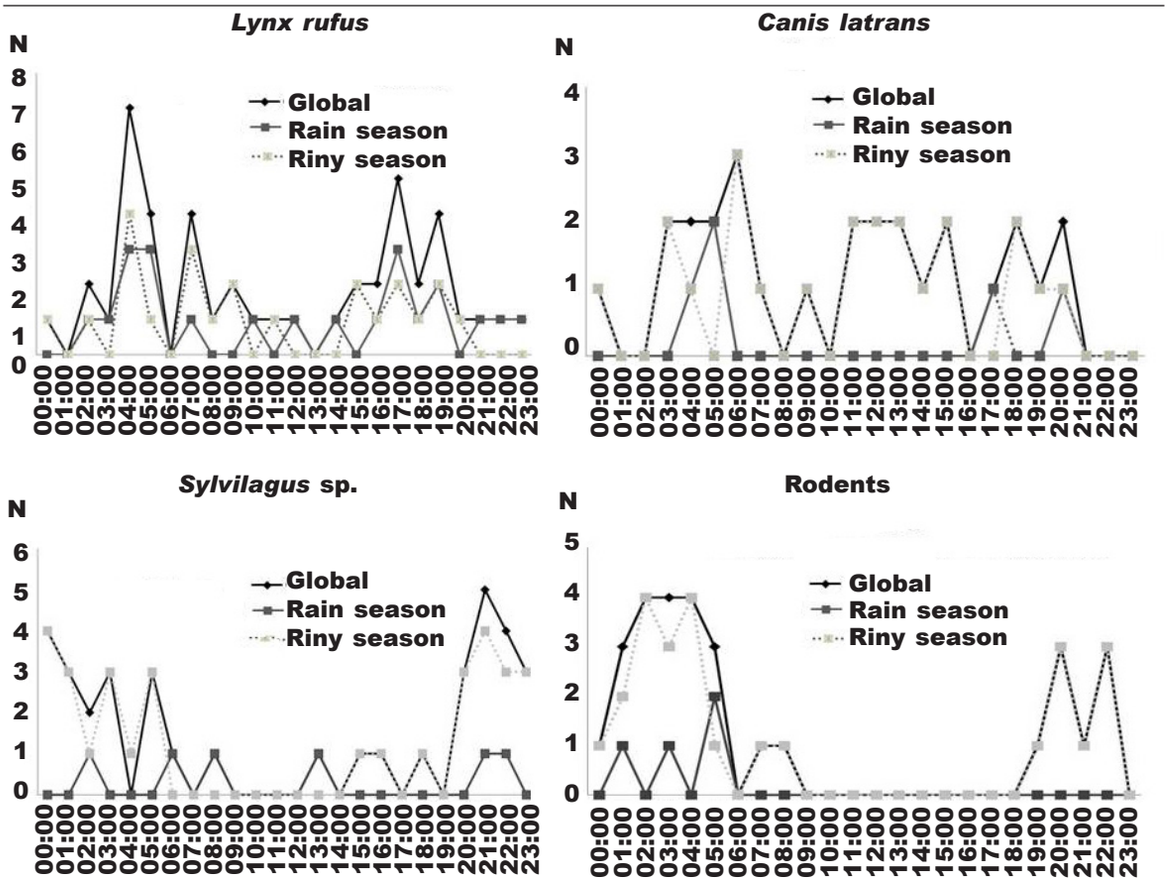

Fig. 4. Annual total, dry and rainy season records of activity of two predators, *Lynx rufus* and *Canis latrans*, and their most frequently recorded prey items, *Sylvilagus* sp. and rodents, in the Pico de Orizaba National Park, Veracruz, Mexic: N, number of records.

Fig. 4. Registros de dos depredadores, Lynx rufus *y* Canis latrans*, y sus presas más frecuentemente registradas,* Sylvilagus *sp. y roedores por temporada de secas y lluvias, en el Parque Nacional Pico de Orizaba, Veracruz, México: N, número de registros.*

Alternatively, predators may hunt opportunistically (Emmons, 1987), which could explain the partial overlap in activity between both predatory species and squirrels in PONP. Squirrels were found to be a component of the bobcat's diet in another Mexican study (Aranda, 2002), and may have been under recorded by the camera traps because of their arboreal habit. Finally, predators may also hunt when their prey are least active (Sunquist, 1981; Emmons, 1987; Romero–Muñoz et al., 2010), and in PONP, skunks showed little overlap with the activity of the two predators (0.2) but are an important prey item elsewhere (Cruz–Espinoza et al., 2010).

Neither *C. latrans* nor *L. rufus* are globally considered endangered, and both are widely distributed (Kelly et al., 2016). However, populations of *L. rufus* could be at risk because of hunting and illegal trade, despite being on Appendix I and II of CITES (Kelly et al., 2016). In PONP they are also at risk of forest fires (with frequent records from 1876 to 2011, particularly in the spring [97 %]), and decreasing rainfall (Cerano–Paredes et al., 2016). There is also considerable habitat loss due to clandestine logging and over use/harvesting of forest resources (Ávila et al., 1994).

In conclusion, the activity of bobcats and coyotes shows low temporal segregation, with their peak activities occurring at different times in PONP. However, both species can be active at any time of day and have a high temporal overlap across the year. This preliminary study shows that even a limited number of cameras can capture significant data about predatory species, especially those that are difficult to observe because they are rare or sparsely distributed or because they avoid human activity and have cathemeral or nocturnal habits. Small–scale studies of this type can add to the quality and quantity of records of poorly known predatory species, providing information concerning how their APs are impacted by their interactions with other species, including humans, and by disturbance and environmental change.

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