

# Coexistence of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a tropical forest in south-eastern Mexico

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## Abstract

*Coexistence of jaguars (Panthera onca) and pumas (Puma concolor) in a tropical forest in south-eastern Mexico.* The biological ranges of the jaguar (*Panthera onca*) and puma (*Puma concolor*) overlap in the Yucatan Peninsula, corresponding to the most important population of jaguars in Mexico. The goal of this study in the El Eden Ecological Reserve (EER) was to investigate the factors that permit these two predators to coexist in the dense vegetation of medium-stature tropical forest and secondary forest in the north-eastern Yucatan Peninsula. We assessed their spatial and temporal overlap using Pianka's index, and evaluated their habitat use by applying occupancy models. A total sampling effort of 7,159 trap-nights over 4 years produced 142 independent photographic records of jaguars, and 134 of pumas. The felids showed high to very high overlap in their use of different vegetation (0.68–0.99) and trail types (0.63–0.97) and in their activity patterns (0.81–0.90). However, their peak activity patterns showed some temporal separation. Time of day, particularly for peak activity time, was the best predictor to explain the coexistence of the felids in this habitat. While occupancy models showed that the presence of potential prey species and vegetation type could predict the presence of felids in the study area. Natural disturbances during 2010 (hurricane) and 2011 (fire) drastically changed habitat use and activity patterns, resulting in pumas and jaguars adjusting their resource-use and activity pattern through a strategy of mutual evasion.

Keys words: Big cats, Activity pattern, Habitat use, Prey, Occupancy models

## Resumen

*Coexistencia del jaguar (Panthera onca) y el puma (Puma concolor) en un bosque tropical del sureste de México.* La distribución del jaguar (*Panthera onca*) y el puma (*Puma concolor*) se superponen en la Península de Yucatán, donde se encuentra la población más importante de jaguares en México. El objetivo de este estudio, realizado en la Reserva Ecológica El Eden, fue estudiar los factores que permiten que estos dos depredadores coexistan en la densa vegetación de la selva mediana tropical y los bosques secundarios del noreste de la península de Yucatán. En el estudio se evaluó la superposición en el tiempo y el espacio utilizando el índice de Pianka y se analizó el uso que hacen del hábitat estas dos especies mediante modelos de ocupación. Un esfuerzo de muestreo total de 7.159 noches/trampa durante cuatro años produjo 142 registros fotográficos independientes de jaguares y 134 de pumas. Los félidos mostraron una superposición alta o muy alta en el uso de vegetación (0,68–0,99) y los tipos de senderos (0,63–0,97) y en sus patrones de actividad (0,81–0,90). Sin embargo, sus picos de actividad muestran una cierta separación temporal. El momento del día, en particular para los picos de actividad, fue el factor que mejor explicaba la coexistencia de los félidos en este hábitat. Los modelos de ocupación mostraron que la presencia de presas potenciales y el tipo de vegetación podrían predecir la presencia de félidos en la zona del estudio. Las perturbaciones naturales acaecidas durante 2010 (huracán) y 2011 (incendio) cambiaron drásticamente el uso del hábitat y los patrones de actividad de forma que los pumas y los jaguares adaptaron el uso de los recursos y sus patrones de actividad mediante una estrategia de evasión mutua.

Palabras clave: Grandes felinos, Patrón de actividad, Uso del hábitat, Presas, Modelos de ocupación

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## Introduction

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) occur sympatrically in their neotropical ranges, with both species experiencing continued range contractions resulting from habitat loss and fragmentation, and anthropogenic activities including direct persecution (Sanderson et al., 2002; Scognamillo et al., 2003). Most jaguar studies focus on their central and southerly populations, and tropical biomes, while their more northerly populations in the Yucatan Peninsula in south-eastern Mexico are poorly known (Faller et al., 2007; Chávez, 2010). Pumas have been widely studied throughout the most northerly parts of their range, particularly temperate and continental parts of the USA and Canada, but little is known of their tropical (Foster et al., 2010a) and Mexican populations (Monroy-Vilchis and Soria-Díaz, 2013). Furthermore, the majority of coexistence studies on these felids are from humid tropical and sub-tropical forests (Nuñez et al., 2002; Scognamillo et al., 2003; Foster et al., 2010a; Faller et al., 2007) and semiarid regions (Astete et al., 2017; Gutierrez-González and López-González, 2017).

The coexistence of two similar-sized carnivores has stimulated research into the mechanisms that allow them to partition resources, including specialization in their temporal and spatial use of prey or habitats (Carothers and Jaksic, 1984; Linnel and Strand, 2000; Donadio and Buskirk, 2006; Foster et al., 2013). Complex interactions between coexisting jaguars and pumas are related to their habitat and prey use (Woodroffe, 2001; Scognamillo et al., 2003; Foster et al., 2010a, 2010b; Sollman et al., 2012). Evidence to support this includes their differential use of vegetation, particular densely vegetated habitats (Hanski, 1994; Creel and Creel, 1996; Durant, 1998; Fedriani et al., 1999; Maffei et al., 2004; Chávez, 2010; Di Bitetti et al., 2010; Foster et al., 2013) and temporal differences that facilitate evasion (Aranda and Sánchez-Cordero, 1996; Romero-Muñoz et al., 2010) such as different activity regimes to help avoid conflict (Paviolo et al., 2009; Di Bitetti et al., 2010; Foster et al., 2013; Hernández-Saint Martín et al., 2013; Ávila-Nájera et al., 2016). Examples of dietary specialization include the dominant species—usually considered to be the jaguar (Sollman et al., 2012)—selecting larger prey, and changes to niche breadth seen from differential prey selection by size, age and taxa (Gittleman, 1985; Aranda, 1994; Karanth and Sunquist, 1995; Aranda and Sánchez-Cordero, 1996; Taber et al., 1997; Karanth and Nichols, 1998; Nuñez et al., 2000; Scognamillo et al., 2003; Chávez, 2010; Di Bitetti et al., 2010; Foster et al., 2013).

The many small reserves and protected areas in the Yucatan Peninsula, Mexico, form patches of interconnected natural habitat (Pozo et al., 2011) where sympatric jaguar and puma populations occur in a landscape mosaic dominated by semi-natural environments and human activity (Zarza et al., 2007). Camera traps are increasingly used in ecological and behavioural studies of large nocturnal predators that roam widely over their extensive home ranges (Nuñez

et al., 2002; Chávez, 2010; Foster et al., 2013). In the present study we used camera trap evidence to investigate which factors permit jaguar and puma to coexist in the tropical forest of the El Eden Ecological Reserve (EER) in the north-eastern Yucatan Peninsula. We assessed the degree of overlap in their resource-use (spatial and temporal) and applied occupancy models (MacKenzie et al., 2006) to evaluate how differences in their habitat use and activity regimes allow them to coexist. We tested the hypotheses that different habitat components directly affect the temporal and spatial occurrence of jaguars and pumas, and that flexibility in their daily activity patterns and habitat use allow them to minimize their interactions with each other, and avoid direct competition.

## Material and methods

### Study area

The El Eden Ecological Reserve covers an area of 3,077 ha of the northernmost tropical forests of North America, and is congruent with the larger Yum Balam Protected Area (Navarro et al., 2007) (fig. 1E). It consists mainly of medium stature tropical forest (MSTF) with secondary forest (acahual) being the dominant tree species described (Schultz, 2003).

### Fieldwork

Camera traps operating 24 h/d were deployed in July–September 2008, October–December 2010, May–July 2011, and August–November 2012 (Cuddeback expert, Capture, Capture IR, Moultrie and Wildview), and images were downloaded every 15 days. Traps were sited using the Mexican National Census of the jaguar and its prey design (CENJAGUAR) (Chávez et al., 2007), with up to three cameras placed 1.5–3 km apart in 9 km<sup>2</sup> plots. At least one site per plot had paired cameras to capture images of both sides of any animal that triggered the trap. Cameras were placed along forest paths, firebreaks and minor roads, and were re-positioned each year across the two dominant vegetation types (MSTF and secondary forest), as shown in figure 1A–1D.

### Camera trap analysis

We identified individual jaguars by their coat patterns and markings, and pumas by their scars, coloration patterns, and body shape (Kelly et al., 2008). Photographs were grouped by trap site to perform the analyses. Photographs were considered as independent events (1) when the same individual was photographed again more than 30' later, (2) when different individuals could be distinguished in consecutive photos, (3) when several individuals were clearly identifiable in a single photo and (4) when individuals could not be identified in consecutive photos, in which case a new event was recorded after 3 h (Ávila-Nájera et al., 2016). All records were placed into one of three time classes: nocturnal (20:00–06:00 h), diurnal

(08:00–18:00 h) or crepuscular (06:00–08:00 h and 18:00–20:00 h) (Gómez et al., 2005).

Any cameras > 1.5 km apart were considered as independent sampling units, and assumed to be equally accessible to all felids. The cameras were grouped by vegetation type (MSTF and secondary forest) and site characteristics (forest path, firebreak or road).

### Statistical analyses

The overlap in activity pattern and habitat use was estimated via Pianka's Index (Pianka, 1973), where 0 indicates no overlap and 1 is complete overlap in resource use. All tests and graphics were calculated using the R statistical package (version 3.1.0).

To understand changes or differences in the proportion of sites occupied by jaguars and pumas, the imperfect detection of these species had to be taken into account as this can result in some occupied sites appearing to be unoccupied. We estimated the probability of occupancy ( $\psi$ ) and detection ( $p$ ) of jaguar and puma based on their detection rates from the 70 sampling days in 2008 and 2012. These data were used to run occupancy models for each species and each sampling period or year (MacKenzie et al., 2006). The models that we considered assume that occupancy was either constant across sites  $\psi$  or varied by site according to the variables  $\psi$  (type of prey, prey interactions, co-predators, vegetation type or trail type). Detectability was either constant across both years and sites or varied according to features of the camera trap site (path type, vegetation type or co-predators). Final model selection used Akaike's Information Criteria for small sample size (AICc) to identify the most parsimonious model, balancing model fit and parameter precision, where models with lower AICc are considered best.

It should be mentioned that the reserve was affected by a hurricane in September 2010 and by a fire that occurred outside EER in May 2011. The results reported therefore take these changes into account in the environment.

## Results

A total sampling effort of 7,159 trap nights over the four years produced 142 independent photographic records of jaguars and 134 of pumas.

### Habitat use by felids

During the study most jaguars were recorded in secondary forest (80%) as seen in 2008, 2010 and 2012 (95%, 62% and 75% respectively), although the majority of sightings in 2011 were from MSTF (71%). The only significant differences in jaguar habitat use were seen in 2008 ( $\chi^2 = 21.88$ ,  $p < 0.05$ ) and 2011 ( $\chi^2 = 159.98$ ,  $p < 0.05$ ). Pumas occurred in both forest types, and used secondary forest and MSTF roughly equally in 2008 (54% and 46% respectively), but were seen more often in MSTF in 2010 and 2011 (75% and 53% respectively) and more often in secondary

forest in 2012 (78.6%). The only significant differences in puma habitat use occurred in 2008 ( $\chi^2 = 8.22$ ,  $p = 0.02$ ) and 2011 ( $\chi^2 = 159.9$ ,  $p < 0.05$ ).

More jaguars were seen on roads (67%–88%) than on forest paths (20%) or firebreaks (13%), and difference in the type of trail used by jaguars in 2008 was significant ( $\chi^2 = 36.88$ ,  $p < 0.05$ ) and 2011 ( $\chi^2 = 228.76$ ,  $p < 0.05$ ). However, pumas were mainly seen on forest paths (46%–75%) and roads (44%), with only 10% recorded on firebreaks. In 2012, only 21% of puma records were from forest paths. There was a significant difference in the type of trail used by pumas in 2011 ( $\chi^2 = 228.76$ ,  $p < 0.005$ ) and 2012 ( $\chi^2 = 9.10$ ,  $p = 0.03$ ).

### Activity patterns of felids

Both felids were predominantly crepuscular–nocturnal (jaguar 69% and pumas 64%) although about a third of all sightings were diurnal (fig. 2). Their activity patterns differed between the years, with less nocturnal and more diurnal activity in 2010, and predominantly nocturnal jaguar activity (86%) with no crepuscular sightings in 2011, compared with 48% nocturnal and 17% crepuscular records for puma. There were significant differences in the activity patterns of jaguars in 2011 ( $\chi^2 = 176.67$ ,  $p > 0.00$ ) and 2012 ( $\chi^2 = 1.32$ ,  $p > 0.01$ ) and of pumas in 2008 ( $\chi^2 = 1053.77$ ,  $p > 0.00$ ), 2011 ( $\chi^2 = 176.67$ ,  $p > 0.00$ ) and 2012 ( $\chi^2 > 1053.77$ ,  $p > 0.00$ ).

### Spatial and temporal overlap of felids

The felids showed a high to very high overlap in the use of vegetation and path types (0.63–0.99), particularly in 2011 and 2012. There was also a very high overlap in their activity patterns (0.81–0.90) in most years (table 1).

### Occupancy models

The best occupancy model for pumas was in 2008 (0.68 with 0.30–0.88 CIs, and an AIC of 234.76 and AIC Wgt of 0.96), and was mainly explained by the presence of collared pecaries and by vegetation type (table 2). However, pumas were also affected by the presence of jaguars, which when included as a variable, produced a model for 2012 which had the lowest AIC value (184.17).

However, for both years and all variables selected, none of the models or variables (AIC,  $\Delta$ AIC and AIC Wgt) predicted the presence of jaguar in the EI Eden. The models with the lowest AIC are shown in table 2. However, the  $\Delta$ AIC values showed no difference between the models.

## Discussion

### Habitat use by felids

Jaguars were seen on all trail types but were more frequently seen on roads, while pumas used paths,

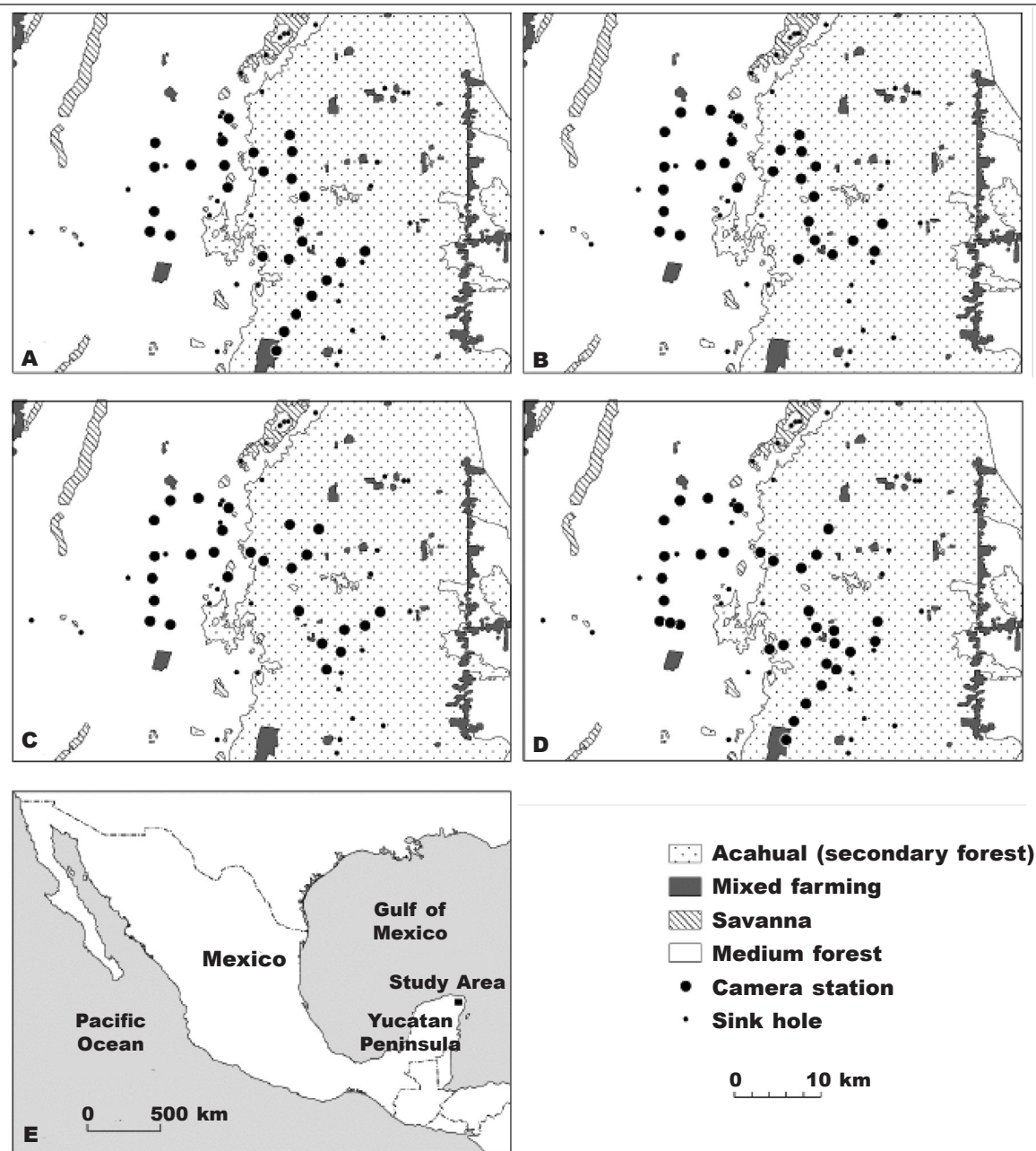


Fig. 1. Camera trapping stations (black circles) at the El Eden Ecological Reserve, Quintana Roo, Mexico plotted by year of study with the major vegetation types: A, 2008; B, 2010; C, 2011; D, 2012.

Fig. 1. Estaciones de trapeo con cámaras (círculos negros) en la Reserva Ecológica El Edén, en Quintana Roo, México, por año de estudio con los principales tipos de vegetación: A, 2008; B, 2010; C, 2011; D, 2012.

firebreaks and roads according to availability, although this changed following the fire. In other studies, jaguars frequently use roads because they facilitate movement and scent marking (Maffei et al., 2004), although male jaguars are more likely to use roads than females (Conde et al., 2010; Maffei et al., 2011). Pumas also take advantage of roads to move around their home ranges, but the proximity to fire damage

combined with the high presence of co-predators like jaguars may have made them less favorable to pumas in 2011. Normally the roads in EER have little human traffic, but the fire in 2011 resulted in firefighters and people hired to put out the fires frequently travelling on the roads and around the reserve, creating high levels of disturbance. The secondary forest surrounding many roads in EER is extremely dense, so

Table 1. Overlap in resource use (Pianka Index) between jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the El Eden Ecological Reserve, Quintana Roo, Mexico: CI, confidence interval.

Tabla 1. Superposición en el uso de recursos (índice de Pianka) entre el jaguar (*Panthera onca*) y el puma (*Puma concolor*) en la Reserva Ecológica El Edén, en Quintana Roo, México: CI, intervalo de confianza.

|                       |      | Median overlap<br>(Pianka's Index) | SD   | CI<br>2.5% | CI<br>97.5% |
|-----------------------|------|------------------------------------|------|------------|-------------|
| Vegetation type       | 2008 | 0.68                               | 0.11 | 0.45       | 0.87        |
|                       | 2010 | 0.75                               | 0.18 | 0.35       | 1.00        |
|                       | 2011 | 0.90                               | 0.10 | 0.64       | 1.00        |
|                       | 2012 | 0.99                               | 0.01 | 0.95       | 1.00        |
| Path type             | 2008 | 0.63                               | 0.11 | 0.40       | 0.83        |
|                       | 2010 | 0.76                               | 0.17 | 0.35       | 0.99        |
|                       | 2011 | 0.90                               | 0.10 | 0.64       | 1.00        |
|                       | 2012 | 0.97                               | 0.03 | 0.89       | 1.00        |
| Activity pattern      | 2008 | 0.90                               | 0.07 | 0.73       | 0.99        |
|                       | 2010 | 0.88                               | 0.11 | 0.59       | 1.00        |
|                       | 2011 | 0.81                               | 0.11 | 0.56       | 0.96        |
|                       | 2012 | 0.88                               | 0.08 | 0.71       | 0.99        |
| Two-hour time periods | 2008 | 0.67                               | 0.10 | 0.46       | 0.85        |
|                       | 2010 | 0.28                               | 0.14 | 0.04       | 0.60        |
|                       | 2011 | 0.28                               | 0.15 | 0.04       | 0.61        |
|                       | 2012 | 0.64                               | 0.10 | 0.43       | 0.83        |

roads are highly likely to be used by both felids, as is common in other parts of their range (Dickson and Beier, 2002; Harmsen et al., 2010; Rodríguez-Soto et al., 2013), although pumas generally prefer small paths with high tree cover elsewhere in Mexico (Lira and Naranjo, 2003).

Although we observed changes in the jaguars use of resources, secondary forests were used consistently to a greater or lesser extent over the study period. In more humid tropical forests, dense horizontal and vertical vegetation cover is thought to be essential for their permanency (Scognamillo et al., 2003; Conde et al., 2010), but while both forms of vegetation are present in EER they were not significant factors in the occupancy models. After the fire in 2011, the area immediately around the perimeter was damaged and cameras recorded less activity; both species are known to be sensitive to changes in the level of human activity, and prey and co-predator abundance (Carrillo, 2000; Novack et al., 2005; Haines, 2006; McLoughlin et al., 2010; Foster et al., 2013). Environmental changes following natural or anthropogenic disturbances are therefore likely to effect the interactions between puma and jaguar, and may result in changes in behaviour and resource use.

#### Activity patterns of felids

Jaguars in the El Eden were active 24 h/d although they were mainly crepuscular and nocturnal, with most activity occurring early in the morning, as in the southern Yucatan Peninsula (Chávez et al., 2007). We observed two nocturnal activity peaks, and most crepuscular activity occurred around dusk. Jaguars' activity patterns vary across their range and are thought to be influenced by the activity patterns of their prey (Carrillo, 2000; Scognamillo et al., 2003). For example, some jaguars are predominately diurnal (Rabinowitz and Nottingham, 1986; Álvarez-Castañeda and Patton, 2000; Maffei et al., 2004; Harmsen et al., 2009; Maffei et al., 2011; Foster et al., 2013) and least active at midnight (Maffey et al., 2004) as are their most important prey such as *Mazama* sp. and *Tayassu* sp. (Barrientos and Maffei, 2000).

Pumas at EER were also active 24 h/d, and they were mainly cathemeral. There was a strong positive association between peak puma activity and that of their main prey (nine-banded armadillos, collared peccaries and red brocket deer) and a negative temporal association with jaguars, suggesting a possible copredator evasion strategy (Ávila-Nájera et al., 2018b). Similar activity patterns have been

Table 2. Occupancy models for jaguar (*Panthera onca*) and puma (*Puma concolor*) in the El Eden Ecological Reserve, Quintana Roo, Mexico in 2008 and 2012: AIC, Akaike's information criteria for small sample sizes;  $\psi$ , occupancy probability;  $p$ , detection probability.

Tabla 2. Modelos de ocupación del jaguar (*Panthera onca*) y el puma (*Puma concolor*) en la Reserva Ecológica El Edén, en Quintana Roo, México en 2008 y 2012: AIC, criterio de información de Akaike para muestras pequeñas;  $\psi$ , probabilidad de ocupación;  $p$ , probabilidad de detección.

| Year          | Predictor variables  | AIC    | $\Delta$ AIC | AIC Wgt |
|---------------|--|--------|--------------|---------|
| <b>Jaguar</b> |  |        |              |         |
| 2008          | $\psi$ (white tailed deer), $p$ (vegetation)   | 233.7  | 0.00         | 0.24    |
|               | $\psi$ (puma), $p$ (vegetation)  | 233.7  | 0.07         | 0.23    |
|               | $\psi$ (pecari), $p$ (vegetation)  | 234.63 | 0.93         | 0.15    |
|               | $\Psi$ (red brocket deer), $p$ (vegetation)  | 234.91 | 1.21         | 0.13    |
| 2012          | $\Psi$ (coati*white tailed deer*red brocket deer*pecari), $p$ (vegetation)                   | 300.35 | 0.00         | 0.37    |
|               | $\Psi$ (.), $p$ (vegetation)   | 301.41 | 1.06         | 0.22    |
|               | $\Psi$ (.), $p$ (trail)  | 301.41 | 1.06         | 0.22    |
|               | $\Psi$ (.), $p$ (.)  | 302.92 | 2.57         | 0.10    |
| <b>Puma</b>   |  |        |              |         |
| 2008          | $\Psi$ (pecari), $p$ (vegetation)  | 234.76 | 0.00         | 0.96    |
|               | $\Psi$ (.), $p$ (type_trail)   | 241.52 | 6.76         | 0.03    |
|               | $\Psi$ (.), $p$ (vegetation)   | 241.52 | 6.76         | 0.03    |
|               | $\Psi$ (coati+armadillo+opossum+white tailed deer+red brocket deer+pecari), $p$ (vegetation) | 259.25 | 24.49        | 0.00    |
|               | $\Psi$ (.), $p$ (jaguar)   | 261.79 | 27.03        | 0.00    |
|               | $\Psi$ (.), $p$ (.)  | 265.22 | 30.46        | 0.00    |
| 2012          | $\Psi$ (.), $p$ (jaguar)   | 184.17 | 0.00         | 0.45    |
|               | $\Psi$ (vegetation), $p$ (jaguar)  | 186.17 | 2.00         | 0.16    |
|               | $\Psi$ (coati*white tailed deer*red brocket deer*pecari), $p$ (jaguar)                       | 186.17 | 2.00         | 0.16    |
|               | $\Psi$ (red brocket deer), $p$ (jaguar)  | 186.17 | 2.00         | 0.16    |
|               | $\Psi$ (pecari+red brocket deer+white tailed deer), $p$ (jaguar)                             | 190.74 | 6.00         | 0.02    |
|               | $\Psi$ (.), $p$ (.)  |        |              |         |

reported in other Mexican studies (Hernández–Saint Martin et al., 2013). However, in other parts of their range pumas are predominantly crepuscular with peak activity between 02:00 and 10:00 h (Hernández–Saint Martin et al., 2013) and in a tropical forest in the south of Mexico, pumas are more diurnal and jaguars are nocturnal (De la Torre et al., 2017). Other studies show a negative influence of human activity on puma activity (Chávez, 2010; Foster et al., 2010; Rodríguez–Soto et al., 2013). Pumas have become more nocturnal in order to avoid human contact and as a result of human impact are absent or considered to be endangered in parts of Mexico where they used to be abundant (Chávez, 2010). To ensure their sustainable and long-term survival. We therefore need to understand how best to conserve them in protected areas like EER in the south of Mexico.

#### Spatial and temporal overlap of felids

This camera trapping survey of sympatric jaguar and puma populations in the El Eden found evidence of their coexistence in a relatively small reserve consisting mainly of MSTF in North Eastern Yucatan. Despite the high degree of overlap in both habitat and resource–use, there were some differences in peak activity times and association with other species, including a jaguar evasion strategy by pumas. This has also been seen in their sympatric populations in tropical areas (Scognamillo et al., 2003; Di Bitetti et al., 2010) and between other coexisting large felids (Ramesh et al., 2012). The differences between habitat use over the four years in EER also suggests flexibility in how they use shared resources, and includes changes in habitat–use following disturbances

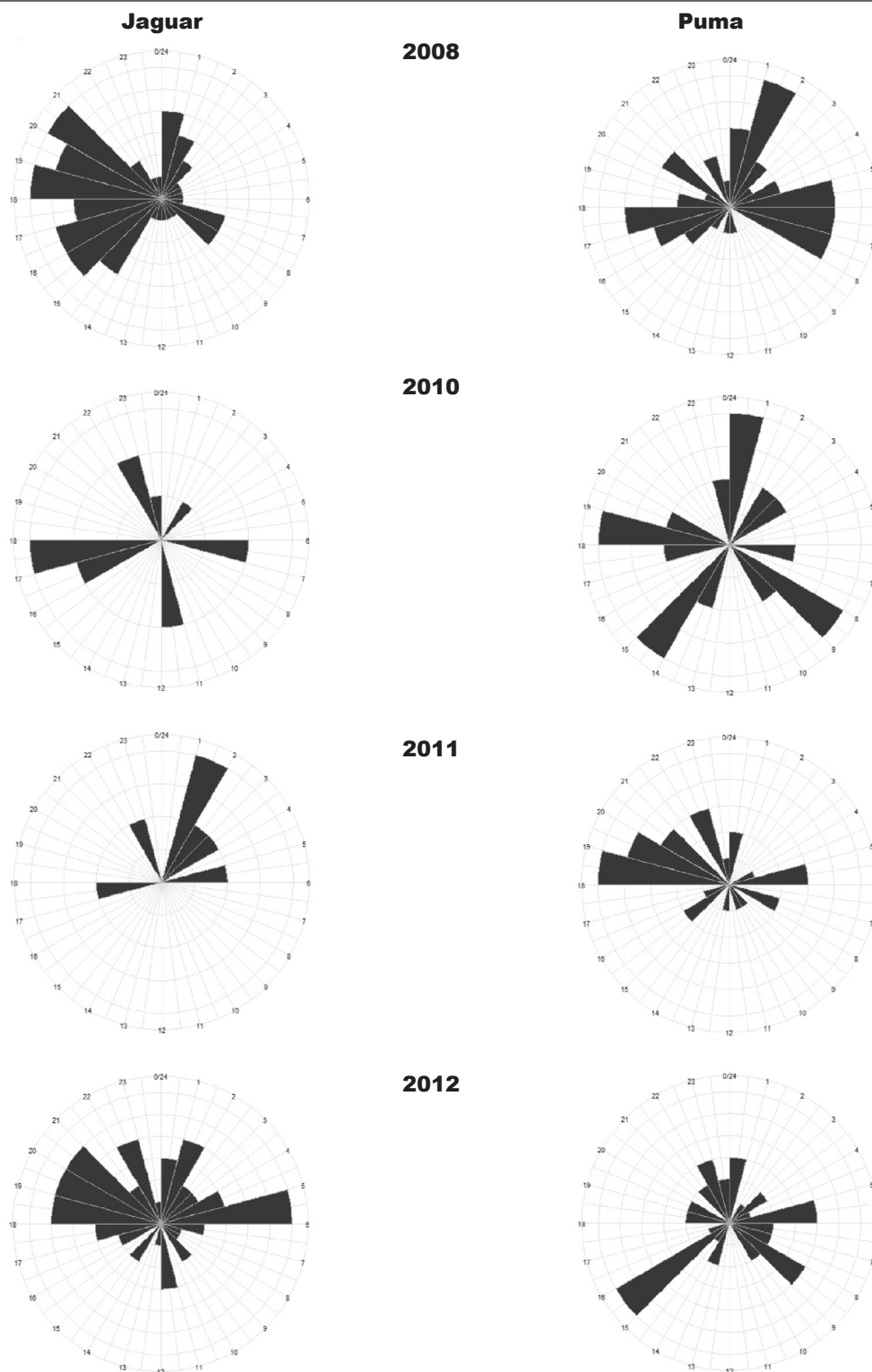


Fig. 2. Activity patterns of jaguars (*Panthera onca*) and pumas (*Puma concolor*) based on camera trap records from the El Eden Ecological Reserve, Quintana Roo, Mexico, plotted by study year (2008, 2010, 2011 and 2012).

Fig. 2. Patrones de actividad del jaguar (*Panthera onca*) y el puma (*Puma concolor*) basada en registros de cámaras en la Reserva Ecológica El Edén, en Quintana Roo, México por año de estudio (2008, 2010, 2011 y 2012).



such as Hurricane Karl in September 2010 and a fire around the reserve in May 2011.

#### Occupancy model

The environmental variables that influence the presence of the jaguar and its resource–use patterns vary across its range. In Belize, Davis et al. (2010) found that jaguars were positively associated with canopy height, length of trails and the presence of small birds and large mammals. However, in the El Eden, the year of study had a significant impact on all the models tested. Sightings of all species in the El Eden decreased following the disturbances in 2010 and 2011, and may in part explain this effect. However in The Reserve, distance to water bodies did not affect jaguar or puma occurrence because water is available throughout the year and is not a limiting factor, unlike in other parts of their range (Davis et al., 2010). In addition, secondary forest was positively associated with jaguar sightings. This is probably because many of the roads are in the secondary forest, where jaguars can move more easily and hence find prey, as seen by Davis et al. (2010) in Belize.

Another strong predictor of puma and jaguar presence in the study was the activity pattern and spatial overlap of prey species (Ávila–Nájera et al., 2016). Similarly important prey occur throughout the jaguar's geographic range (Ceballos et al., 2005; Chávez et al., 2007; Davis et al., 2010; Harmsen et al., 2010; Romero–Muñoz et al., 2010).

In the El Eden, the most frequently recorded species in the camera traps during the study, for example in 2011, were humans (unpublished data), and human activity was a significant negative factor in predicting jaguar and puma sightings, agreeing with similar findings by Davis et al. (2010). Many researchers have noted the negative impact of humans on the presence of jaguars, and there is evidence of significant hunting and poaching in the Calakmul region of the Yucatan (Ceballos et al., 2005). In addition, subsistence hunting depletes prey availability because hunters favour the same species as the felids (Chávez, et al 2007; Ávila–Nájera et al., 2011; Foster et al., 2014).

Predators select habitats as a result of the complex interactions between factors including their population density and the presence of other predators, as well as the abundance and diversity of prey and the level of human activity (Hojnowski et al., 2012; Foster et al., 2014). In EER, slight differences in peak activity time, and dietary preferences (Ávila–Nájera et al., 2018a, 2018b) facilitate the coexistence of two large predators despite the high overlap in their resource use. Studies in other ecosystems have also reported differential habitat use by coexisting predators (Johnson et al., 1980; Davis et al., 2010; Sollmann et al., 2012) along with a positive dependence upon each other (Gutierrez–González and López–González, 2017). However, this has not been previously reported for these felids in Mexico, which generally show complete overlap in their habitat–use and diet in dry deciduous tropical forest in western Mexico (Núñez et al., 2002).

None of the variables used in the occupancy models were able to predict the presence of jaguar in the reserve. This may suggest that they use it as a corridor to travel between larger reserves, since they require extensive areas of home range, and the protected natural areas and surrounding areas serve as important biological corridors that encourage biodiversity conservation (Domínguez, 2009). In contrast, in 2008, puma occupancy was dependent on one of its main prey, the collared peccary, although the 2012 model depended on both its copredator (which it avoided) and prey abundance. All the occupancy models tested suggest that pumas are occasional residents in the EER, and that their presence is associated with that of their prey, such as peccaries. However, this remains untested.

In conclusion, the factors that allow jaguars and pumas to coexist in EER are the differences in their activity patterns, especially their peak activity times, as well as their diets (the latter tested in a previous investigation within the reservation), as reported in previous studies from similar habitats in this region. However, natural perturbations like hurricanes and fire triggered changes in the habitat use and activity pattern of both felids. This showed that they were able to modify their behaviour and the level of interaction in order to avoid contact with each other. However, several aspects require deeper analysis, such as individual interactions between males and females of the same species or co–predators.

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