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ABUNDANCE AND ACTIVITY PATTERNS OF MEDIUM-SIZED FELIDS (FELIDAE, CARNIVORA) IN SOUTHEASTERN MEXICO

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Abstract—We compared abundance and activity patterns of medium-sized felids in the neotropics. We used 29 camera traps to record species in the region of Los Chimalapas, Oaxaca, Mexico, during 2011–2013. We estimated population size with the capture-recapture model (Cormack-Jolly-Seber model). We assessed the differences in activity patterns between species through the Mardia-Watson-Wheeler test. *Leopardus pardalis*, *Leopardus wiedii*, and *Puma yagouaroundi* were recorded by cameras. The population size of *L. wiedii* was high in comparison with *L. pardalis*, which presented a medium abundance compared to other regions. *Puma yagouaroundi* individuals were relatively rare, likely due to a difference in habitat selection. We provide evidence that in the southeastern region of Mexico there is a significant *L. wiedii* population despite the presence of *L. pardalis*.

Resumen—Comparamos la abundancia y el patrón de actividad de felinos de talla media en el neotrópico. Usamos 29 estaciones de trampas cámara para registrar especies en la región de Los Chimalapas, Oaxaca, México, durante 2011–2013. Estimamos el tamaño poblacional a través del modelo de captura-recaptura (modelo Cormack-Jolly-Seber). Evaluamos las diferencias en el patrón de actividad entre las especies a través de la prueba de Mardia-Watson-Wheeler. *Leopardus pardalis*, *Leopardus wiedii* y *Puma yagouaroundi* fueron registrados por las cámaras. El tamaño poblacional de *L. wiedii* fue alto en comparación de *L. pardalis*, quien presentó una abundancia media en comparación de otras regiones. Individuos de *P. yagouaroundi* fueron relativamente raros, posiblemente debido a una diferencia de selección de hábitat. Proporcionamos evidencia de que en el sureste de México se encuentra una población considerable de *L. wiedii*, aun en presencia de *L. pardalis*.

In terrestrial ecosystems, apex predators have a significant influence on structure and functionality through a top-down control process (Steneck, 2005; Ritchie and Johnson, 2009). However, medium-size predators or mesopredators also contribute to the dynamics of ecosystems through diverse interactions. Both groups may affect other species in two ways: 1) lethal encounters may directly affect population size or 2) apex predators may control mesopredators through intraguild interactions (Ritchie and Johnson, 2009; Lourenço et al., 2014). In response to these interactions, species might change habitat use or alter foraging behavior and activity to diminish lethal encounters with the dominant species (Elmhagen and Rushton, 2007; Ritchie and Johnson, 2009; Lourenço et al., 2014).

In the neotropics, there are two apex predators: jaguar (*Panthera onca*, 37–158 kg) and puma (*Puma concolor*, 35–71 kg). Both species have suffered major declines due to habitat loss, overexploitation, and hunting by humans. Because of this, in some original areas of distribution, these predators are no longer present (Salom-Pérez et al., 2007). There are eight medium-sized felids (species larger than 1 kg) in this region and the dominant species is the ocelot (*Leopardus pardalis*, 11–16 kg). This species is the most-studied by wildlife biologists compared to felids of similar size. Other species such as the margay (*Leopardus wiedii*, 3–6 kg), the jaguarundi (*Puma yagouaroundi*, 3–8 kg), Geoffroy's cat (*Leopardus geoffroyi*, 2–8 kg), and the oncilla (*Leopardus tigrinus*, 1.5–3.5 kg) are little-studied due to their cryptic behavior (Cuellar et al., 2006; de Oliveira et al., 2010; de Oliveira and Pereira, 2014).

Within the assemblage of felids, *L. wiedii* is the most arboreal of the felids in the neotropics. Its present distribution ranges from Mexico to the north of Argentina and Paraguay (de Oliveira, 1998). This species eats arboreal mice, squirrels, birds, amphibians, and reptiles (de Oliveira, 1998; Sunquist and Sunquist, 2002; Bianchi et al., 2011) and sleeps and rests primarily in trees; consequently its presence depends on dense vegetation (de Oliveira, 1998; Sunquist and Sunquist, 2002; but see Di Bitetti et al., 2010).

Puma yagouaroundi is largely sympatric with *L. wiedii* and *L. pardalis*. It is distributed from the south of the United States to the center of Argentina. It is medium-sized and lives in a variety of vegetation types, although it prefers the edges or semiopen areas surrounding tropical forests, scrubs, or chaparrals (de Oliveira, 1998; Sunquist and Sunquist, 2002). It has diurnal habits and consumes a variety of prey such as mice, birds, reptiles, and arthropods (Sunquist and Sunquist, 2002). Like *L. wiedii* it is a little-studied species (Maffei et al., 2007; Bianchi et al., 2011; Charre-Medellín et al., 2012). Members of this species are difficult to identify at an individual level as they do not have a spot pattern like *L. wiedii* or *L. pardalis*, and it is therefore difficult to estimate their population size (de Oliveira, 1998; Maffei et al., 2007; Caso et al., 2008).

Population size of *L. pardalis* varies across its geographic distribution (Di Bitetti et al., 2008; de Oliveira et al., 2010). In some regions *L. pardalis* is considered by researchers to be abundant compared to other medium-sized felids (Di Bitetti et al., 2008). *Leopardus wiedii* and *L. tigrinus* are considered more abundant where *L. pardalis* is scarce or absent (Vanderhoff et al., 2011; Carvajal-Villarreal et al., 2012; Oliveira-Santos et al., 2012). In contrast, in other areas where *L. pardalis* is more abundant, these species are less abundant (Di Bitetti et al., 2010). Also it has been suggested by Oliveira-Santos et al. (2012) that these species might alter their activity pattern in areas where *L. pardalis* or other large felids occur together. This temporal segregation could be an important mechanism that allows for coexistence among felids (Di Bitetti et al., 2010).

Five out of the six felid species in Mexico inhabit the southeastern region of the country: two large-sized species, *P. concolor* and *P. onca*; and three medium-sized species, *L. wiedii*, *L. pardalis*, and *P. yagouaroundi*. Wildlife biologists do not know population sizes of medium-sized felids in those regions where they coexist. However, researchers expect population sizes of *L. wiedii* and *P. yagouaroundi* to be low (Caso et al., 2008; Payan et al., 2008), particularly in regions where *L. pardalis* is abundant (Cuellar et al., 2006; de Oliveira et al., 2010). Our objective for this study was to compare the abundance of medium-sized felids and their activity patterns. We only analyzed medium-size felids due to taxonomic and size similarity. Activity patterns would suggest a strategy of reducing interference competition and allowing for coexistence. Knowledge of these factors is crucial to comprehending the factors that enable coexistence between mesopredators (Ritchie and Johnson, 2009; Oliveira-Santos et al., 2012).

Materials and Methods—*Study Area*—The study site was located in the Los Chimalapas region (17°9′13″N, 94°21′13.6″W), in the state of Oaxaca, southeastern Mexico. This is part of the Selva Zoque, a region prioritized for conservation by the states of Oaxaca, Veracruz, and Chiapas (Fig. 1). The vegetation type is tropical rainforest. The climate is warm-humid with an average annual temperature of 22–26°C, and an average annual precipitation of 2,000–2,500 mm (Trejo, 2004).

Field Sampling—We installed a total of 29 permanent sampling stations from March 2011 to June 2013. We placed unbaited camera traps at a height of 30 cm above the ground. Seven sampling stations included two cameras to record both sides of organisms, for individual recognition. Due to topographical conditions and the varying home ranges of each species, the distance interval between traps ranged from 0.5–1.5 km with a total area of 22 km^2 (Fig. 1). The traps were active 24 h and programmed with a 0.3–1-min delay. We used the Wildgame IR4 4-megapixel digital game-scouting camera (Wildgame Innovations, Los Angeles, California). We used this model for the first 10–12 months of sampling. We changed traps when they were damaged. We substituted the damaged traps (100%) with the ScoutGuard SG550/SG550V (HCO Outdoors Products, Norcross, Georgia), and Bushnell Trophy Cam models (Bushnell Outdoor Products, Overland Park, Kansas). Both models remained active 14–16 months. We deposited photographs in the Colección de Referencia de Mamíferos del Laboratorio de Ecología Animal of the Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca, Instituto Politécnico Nacional.

Data Analysis—In order to ensure that all events were independent and to avoid pseudoreplication (Tobler et al., 2008), we considered all photographs taken by each sampling station within a 1-h span as a single record. We calculated relative abundance as the number of single records of felids in 100 camera-days. In order to estimate population size and density, we identified each individual of *L. wiedii* and *L. pardalis* according to spot patterns (Trolle and Kéry, 2003; Maffei et al., 2005). We determined if the population was statistically open or closed with the program CloseTest (Stanley and Richards, 2005). We estimated abundance using the Corman-Jolly-Seber probabilistic model (Lebreton et al., 1992; Santos-Moreno et al., 2007; Pérez-Irineo and Santo-Moreno, 2014). We used the program MARK version 8.0 (White and Burnham, 1999) for the construction and analysis of the models.

The Corman-Jolly-Seber model estimates only two parameters: survival probability (Φ) and capture probability (p). Both parameters can vary or remain constant over time, so there are four candidate models: 1) both parameters constant (Φp); 2) constant Φ and p varying through time (expressed in years: 2011, 2012, and 2013; Φp_t); 3) Φ varying over time and constant p ($\Phi_t p$); and 4) both Φ and p vary over time ($\Phi_t p_t$; Lebreton et al., 1992; Table 1). The best model was selected using the quasi-Akaike information criterion (Burnham and Anderson, 2002).

Once we selected the final model, we estimated population size (N) as the number of identified organisms divided by the probability of capture (Lindenmayer et al., 1998). Population size was extrapolated for an area of 100 km^2 in order to make comparisons between species. We calculated the effective area in accordance with Karanth and Nichols (1998), and used the mean maximum distance traveled by the individuals on two or more occasions. As the distance between traps is short and might result in dependence between records, we used the Moran index (I) to evaluate spatial autocorrelation between camera trap records (Sokal and Oden, 1978). We carried out the

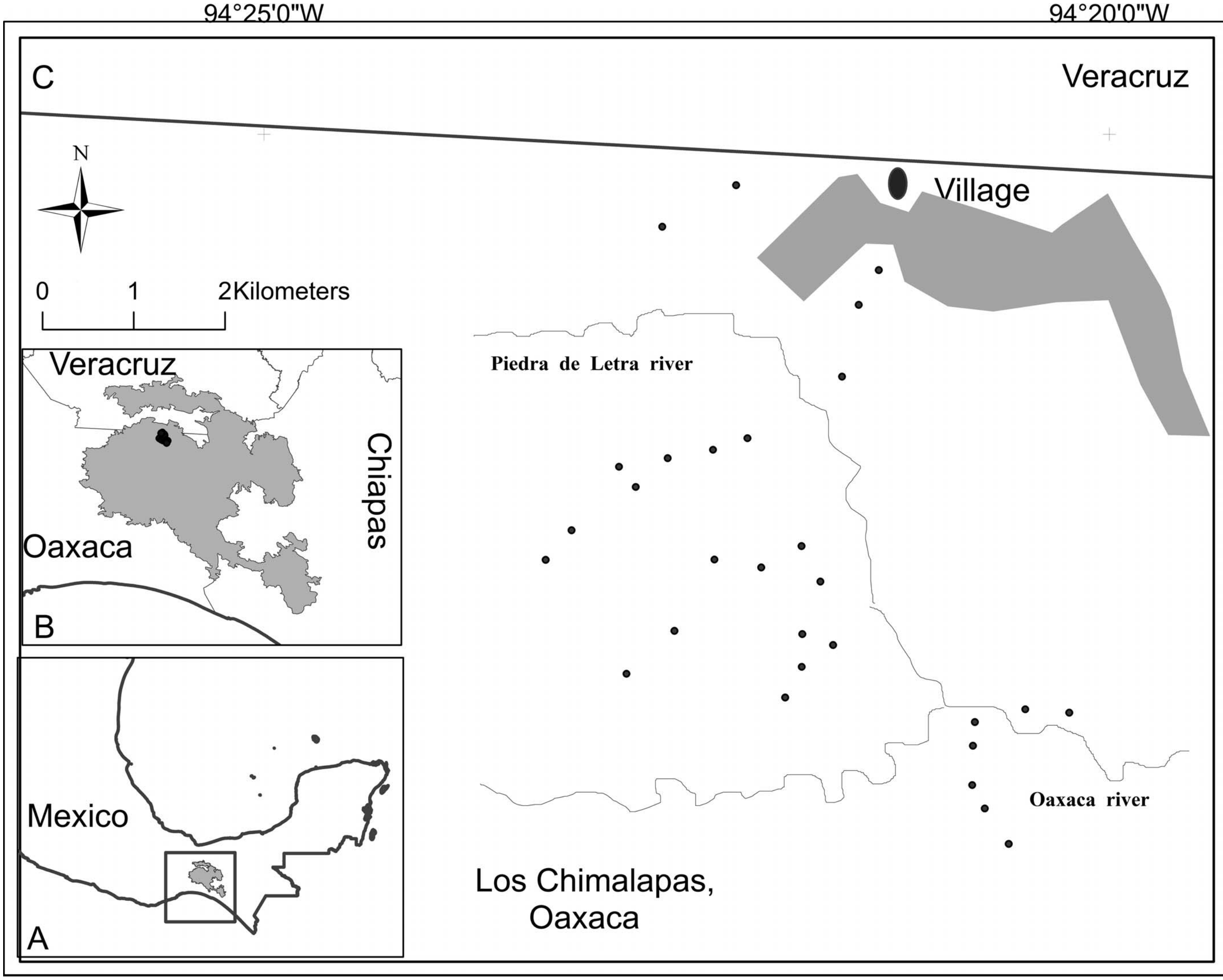

Fig. 1—(A) Los Chimalapas region in southeastern Mexico where we assessed density and abundance of medium-sized felids. (B) The gray area shows the Selva Zoque-La Sepultura Priority Terrestrial Region between Oaxaca, Veracruz, and Chiapas. (C) Gray polygons show livestock areas and points indicate the positions of the camera traps within the tropical rainforest.

Table 1—Corman-Jolly-Seber capture-recapture models for *Leopardus wiedii* and *Leopardus pardalis* in the region of Chimalapas, southeastern Mexico, during 2011–2013. QAICc = quasi-Akaike information criterion, ΔQAICc = difference of QAICc values between the best and the respective model. QAICc weight = relative contribution of each model in respect to the sum of all of the models. The four candidate models were built according to whether one or both parameters (Φ and p) vary or remain constant over time. For example, the best model ($\Phi_t p$) indicates that the survival probability (Φ) varies over time: Φ_{2011}, Φ_{2012} and Φ_{2013}. In contrast capture probability (p) is constant, so there are four parameters.

Species	Model	QAICc	ΔQAICc	QAICc weight	No. of parameters
Leopardus wiedii	$\Phi_t p$	92.9	0	0.484	4
	Φp	93.4	0.435	0.389	2
	$\Phi_t p_t$	97	4.027	0.066	6
	Φpt	97.1	4.123	0.061	4
Leopardus pardalis	$\Phi_t p$	120.71	0	0.751	4
	$\Phi_t p_t$	123.8	3.103	0.159	6
	Φp	125.3	4.629	0.074	2
	Φp_t	128.4	7.705	0.015	4

TABLE 2—Number of records and density of felids at Los Chimalapas, southeastern Mexico, 2011–2013.

	Puma yagouaroundi	*Leopardus wiedii*	*Leopardus pardalis*
No. of records	7	78	112
Relative abundance[a]	0.082	0.914	1.313
Individuals	—	11	9
Abundance ± *SE*	—	36 ± 0.06[b]	20 ± 0.08[c]
Density (CI)[d]	—	68 (57–79)	22 (17–32)
Total area (km^2)		53[e]	89[f]
Capture probability ± *SE*		0.30 ± 0.06	0.44 ± 0.07

[a] The relative abundance was number of records in 100 trap-days.
[b] The estimated abundance of *L. wiedii* was based on the best model (Φ_tp) of Corman-Jolly-Seber capture-recapture models.
[c] The estimated abundance of *L. pardalis* was based on the best model (Φ_tp).
[d] The unit for density was individuals/100 km^2; CI = 95% confidence interval.
[e] The buffer used for the calculation of the total area was mean maximum distance traveled = 1.4 km (*SD* = 0.1).
[f] The buffer used for the calculation of the total area was mean maximum distance traveled = 2.6 km (*SD* = 0.8).

tests with the program ArcGis version 9.3 (ESRI, Redlands, California).

In order to describe activity patterns, we divided the 24-h period into hour-long segments, and classified each independent record within those intervals. Daytime was defined as lasting from 0600–2000h and night from 2000–0600h. We evaluated the significance of the difference of activity patterns between species using the Mardia-Watson-Wheeler (W) test (Zar, 1999). We carried out the tests with the program Oriana version 4 (Kovach Computing Services, Anglesey, United Kingdom). The level of significance of all the tests was $P \leq 0.05$.

RESULTS—In 8,529 trap-days, we obtained 78 records of *L. wiedii*, 112 of *L. pardalis*, and 7 of *P. yagouaroundi*. Additionally, *P. concolor* (n = 42 records) and *P. onca* (n = 44) were recorded by the traps. *Leopardus pardalis* showed higher relative abundance (1.31 records/100 trap-days) in comparison with other felids (Table 2). We did not analyze *P. yagouaroundi* due to the low quantity of data. All records of this species were taken during the day. Of the total *L. wiedii* records, we used 40 to identify 11 individuals and discarded 38 records due to poor photographic quality. Of these 11 identified individuals of *L. wiedii*, seven were female, two male, and two of indeterminate sex. A total of 45% of these individuals (n = 5) remained in the zone for 1 month and the mean residence time was 5.7 ± 1.59 months. One female of *L. wiedii* had the longest residence time (14 months). Of the 112 records of *L. pardalis*, we used 59 records to identify nine individuals. Three individuals were female, five were male, and one undetermined. We observed five of nine ocelots (55%) during a single month, and the mean residence time was 7.44 ± 2.8 months.

The camera-trap records were independent for each year ($I_{2011} = 0.015$, $P = 0.84$; $I_{2012} = 0.125$, $P = 0.64$; $I_{2013} = -0.012$, $P = 0.65$) and for all years combined ($I = 0.095$, $P = 0.66$). For *L. pardalis* and *L. wiedii*, the test results indicated a demographically open population ($\chi^2_{L.\ wiedii} = 31.07$, $df = 13$, $P = 0.00$; $\chi^2_{L.\ pardalis} = 223.47$, $df = 20$, $P = 0.00$), and according to the best model (Table 1), the estimated abundance for *L. wiedii* was 36 individuals and the density was 68 individuals/100 km^2 (Table 2). According to the best model (Table 2), estimated abundance for *L. pardalis* was 20.13, and density was 22 individuals/100 km^2 (Table 2).

For *L. wiedii*, 80% of all records were at night, with peak activity from 0100–0200h, whereas 50% of records of *L. pardalis* were at night, with peak activity from 0100–0600h (Fig. 2). The activity patterns of *L. wiedii* and *L. pardalis* were significantly different ($W = 17.43$, $P < 0.05$).

DISCUSSION—The assemblage of felids at Los Chimalapas includes three medium-sized and two large-sized species, all recorded in this study. We obtained a number of records suitable for estimating population densities of *L. pardalis* and *L. wiedii*. Even the most conservative density estimations of *L. wiedii* (68 individuals/100 km^2; Table 2) were still greater than the density estimated for *L. pardalis* in Los Chimalapas (22 individuals/100 km^2; Table 2). *Leopardus pardalis* had a medium abundance in this region in comparison with other regions of South America where density estimates up to 160 individuals/100 km^2 have been reported (Di Bitetti et al., 2008).

In contrast to *L. pardalis*, few density estimates exist for *L. wiedii*: 12.14 individuals/100 km^2 at Sierra Nanchititla, central Mexico (López, 2010) and 19 individuals/100 km^2 in the tropical dry forest in Bolivia (Cuellar et al., 2006). In the region of Misiones, Argentina, *L. wiedii* has fewer records, even fewer than *L. tigrinus*, which is a smaller species (Di Bitetti et al., 2010). In other regions, researchers have recorded *L. wiedii* in greater numbers and this has been attributed to the absence of *L. pardalis* (Vanderhoff et al., 2011; Carvajal-Villarreal et al., 2012). However, this pattern must be considered with caution, because the rate of photographic records does not always accurately reflect abundance of species (Jannelle et al., 2002), and therefore the low proportion of records does not necessarily indicate low abundance, especially in dense forest. In our study, *L. wiedii* was present in lower relative abundance, but we identified more individuals of *L. wiedii* than *L. pardalis*.

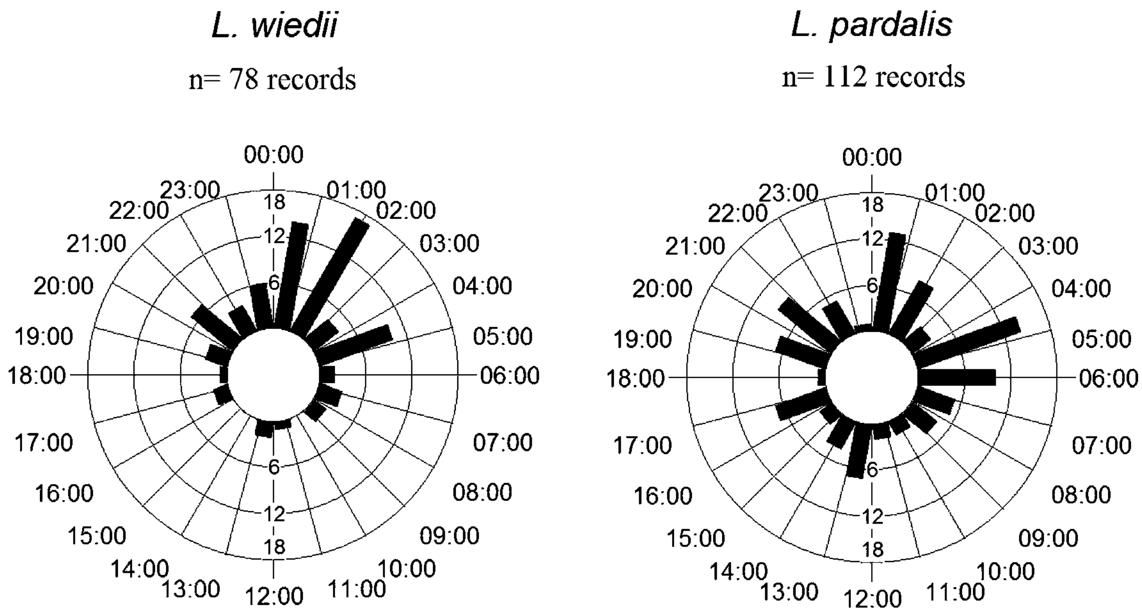

Fig. 2—Activity patterns of *Leopardus wiedii* and *Leopardus pardalis* in the region of Los Chimalapas, southeastern Mexico. The bars indicate the frequency of single records per hour, and the internal circles indicate the value of frequency.

A possible explanation of the relationship between the densities of these species is the "ocelot effect" (de Oliveira et al., 2010). Under the ocelot effect small felids have a lower density in regions where *L. pardalis* is abundant and only reach high abundance in regions where the ocelot is absent or scarce. That is, when *L. pardalis* is the principal mesopredator, it negatively influences the populations of several felids and affects the structure of the assemblage (de Oliveira et al., 2010; de Oliveira and Pereira, 2014). The effect diminishes in cases where predator abundance is low, and other smaller species may use more resources with a low risk of negative interactions (Steneck, 2005; Ritchie and Johnson, 2009; de Oliveira et al., 2010). However, the prediction of the ocelot effect was not supported in the region of Chimalapas: the density of *L. wiedii* was greater than that of ocelots. *Puma yagouaroundi* was relatively rare, but likely due to this species' preference for the edge of forests and open areas (Sunquist and Sunquist, 2002; Caso et al., 2008). In contrast, *L. pardalis* frequents vegetation-dense zones (Sunquist and Sunquist, 2002). We placed camera traps inside the vegetation and maybe this was the reason that *P. yagouaroundi* was recorded so infrequently.

Beside intraguild predation, the relatively large population density of medium-sized felids may be explained by factors such as environment quality. The arboreal structure and dense vegetation provide a wide availability of refuge and prey. The region of Los Chimalapas is well preserved and has low human activity; it is a heterogeneous region, with steep topography and dense forest (Salas et al., 2001; Martínez, 2012). As was mentioned for *L. pardalis* (Pérez-Irineo and Santos-Moreno, 2014), the quality of the environment and the availability of prey might affect population size; therefore a bottom-up control process might determine felid population patterns.

Both species, *L. pardalis* and *L. wiedii*, are primarily nocturnal (de Oliveira, 1998; Sunquist and Sunquist, 2002), but in this study *L. pardalis* had diurnal and nocturnal activity with the same frequency (50%), and differences in activity pattern between species were significant. Activity patterns of felid species may be the result of negative interactions (de Oliveira et al., 2010; Oliveira-Santos et al., 2012). However, they might also reflect a response to behavioral differences and prey preferences.

The lack of knowledge about mesopredator density and their interactions is a critical problem to understanding the patterns of abundance. This study showed that the prediction of the ocelot effect was not supported in the region of Los Chimalapas. There are possibly other explanations for observed density patterns of medium-sized felids than intraguild predation (difference in habitat selection, behavioral or bottom-up control process).

Researchers previously believed it to be difficult to find viable *L. wiedii* populations outside of the Amazonian region (Payan et al., 2008), but this study provides evidence that in the southeastern region of Mexico there is a considerable population of *L. wiedii* coexisting with *L. pardalis*. Both species are a prioritized conservation species in Mexico (Valenzuela and Vázquez, 2007), are listed as Endangered (SEMARNAT, 2010) and *L. wiedii* is cataloged as Near Threatened at an international level (Payan et al., 2008). *Puma yagouaroundi* and *L. wiedii* are poorly studied species (Downey, 1994; Bianchi et al., 2011; Carvajal-Villarreal et al., 2012; Valenzuela-Galván et al., 2013), and both coexist with *L. pardalis* in southeast

Mexico. There is no formal governmental conservation scheme in place in the region of Los Chimalapas, although there are voluntary community initiatives that contribute to conservation of the tropical forest and the presence of felids. The presence of these predators may ensure the health of these communities of vertebrates in tropical environments.

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