



Original investigation

Spatial requirements of jaguars and pumas in Southern Mexico

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ABSTRACT

Understanding how large felids use space is essential for the design of conservation plans that are required for their survival. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and they are sympatric throughout the entire range of the jaguar. However, there is very little information about the spatial requirements of these two species in the tropical rainforests of Central America. Using satellite GPS collars, we compared the spatial ecology of jaguars and pumas in a tropical rainforest in southern Mexico. We found that jaguars had home ranges that were 2–6 times larger than those of pumas. The mean annual home range was $181.4 \pm 4.0 \text{ km}^2$ for female jaguars and $431.6 \pm 152.6 \text{ km}^2$ for males. Annual home range for the only female puma tracked was 34.3 km^2 , and $72.0 \pm 85.2 \text{ km}^2$ for males. Jaguars and pumas with overlapping home ranges showed little overlap of core areas and avoided using the same sites at the same time, which suggested that territoriality and avoidance were in play. Further evidence of avoidance was derived from our observation that pumas exhibited greater movement during the lightest periods of the day and jaguars moved most during the darkest. This temporal separation probably facilitates coexistence. Our data suggest that habitat destruction and fragmentation has more severe effects on jaguars than on pumas. According to our estimates, patches of at least 180 km^2 of primary forest are required to meet the annual spatial requirements of female jaguars. Thus, to conserve jaguars in this region, large tracts of primary forest should be preserved. Importantly, this population of jaguars depends on the adequate preservation of connectivity between natural reserves in Mexico and Guatemala.

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Introduction

Understanding the details of how large felids use space is essential to develop and implement effective conservation plans for these species. Large felids require large home ranges for their survival and, thus, they exist at low population densities (Carbone and Gittleman, 2002; Woodroffe and Ginsberg, 1998). Diverse factors determine the patterns of space use of solitary large felids. Variables that dictate home range in these animals include body size (Carbone et al., 2007, 2005; Gittleman and Harvey, 1982; Gittleman, 1985; Jetz et al., 2004), prey availability (Herfindal et al., 2005; Marker and Dickman, 2005; Odden and Wegge, 2009; Schmidt, 2008), habitat suitability (Broomhall et al., 2003; Conde et al., 2010; Spong, 2002), and sociality (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Goodrich et al., 2010; Logan and Sweanor, 2001; Seidensticker et al., 1973). Additionally, interac-

tions between species, in particular other large carnivores, can influence patterns of space use. Co-occurring species of large carnivores may use different habitat types, actively avoid using the inhabited sites, or segregate their space use temporally (Bhattarai and Kindlmann, 2012; Foster et al., 2013; Harmsen et al., 2009; Odden et al., 2010; Scognamiglio et al., 2003; Sollmann et al., 2012). Landscape configuration and connectivity are critical aspects that determine the space use in large felids as well (Colchero et al., 2011; Conde et al., 2010; de la Torre et al., in press; Zeilhofer et al., 2014).

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are the largest felids in the Neotropics, and are sympatric throughout the entire range of the jaguar. As with most large species of Carnivora, jaguar and puma populations are declining due to habitat destruction and human persecution (Ripple et al., 2014; Treves and Bruskotter, 2014; Woodroffe and Ginsberg, 1998). The present distribution of jaguars ranges from northern Mexico to northern Argentina, with some individuals occasionally reaching the southern portions of the United States (Arizona and New Mexico) (Sanderson et al., 2002; Sunquist and Sunquist, 2009). Throughout their range, jaguars occupy diverse habitat types, which include

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tropical rainforests, mangroves, wet grasslands, arid scrublands, and pine oak forests (Sanderson et al., 2002).

In comparison, pumas are found in an even wider range of habitat types and they have a larger distribution that ranges at present from Patagonia to Northern British Columbia (Sunquist and Sunquist, 2009). Pumas are smaller in areas where they live in sympatry with jaguars, and their body size is larger in areas outside the jaguar's distribution (Iriarte et al., 1990). Although jaguars are larger than pumas, there is overlap in their size and the size of prey they can hunt effectively and, thus, they are potentially competing species. Several studies have examined interactions between these species in areas of sympatry. It appears that coexistence between jaguars and pumas is facilitated by differential habitat use, active avoidance, temporal segregation of space, or by differential prey use (Aranda and Sánchez-Cordero, 1996; Emmons, 1987; Foster et al., 2010a, 2013; Harmsen et al., 2009; Novack et al., 2005; Nuñez et al., 2000; Romero-Muñoz et al., 2010; Scognamillo et al., 2003; Sollmann et al., 2012).

Recently, there have been significant advances in understanding jaguar and puma ecology in tropical ecosystems (Carvalho and Pezzuti, 2010; De Angelo et al., 2011; Di Bitetti et al., 2010; Foster et al., 2010a, 2010b, 2013; Harmsen et al., 2011, 2010, 2009; Hernández-saintmartín et al., 2013; Romero-Muñoz et al., 2010; Rosas-Rosas and Bender, 2012; Rueda et al., 2013; Scognamillo et al., 2003; Sollmann et al., 2012; Soto-Shoender and Main, 2013). However, information about spatial requirements, movement behavior, and the impact of habitat destruction is still lacking. Thus, current conservation and management plans for these species in Neotropical ecosystems suffer from insufficient information.

The aim of this study is to describe and compare the spatial ecology of jaguars and pumas in a tropical rainforest with heavy human activity in southern Mexico. Using GPS telemetry, we documented home range size, movement patterns, and interactions between jaguars and pumas. This is the first study that presents data on jaguars and pumas that were tracked simultaneously using GPS radio-telemetry, and the results presented in this study illustrate differences in the space use between these species that have not been documented previously. We were interested to know the home range characteristics of jaguars and pumas in the tropical rainforests of southern Mexico, to describe the spatial organization of both species, and to describe how jaguars and pumas share space when they coexist. Because home range size in large predators is determined by body size and energetic requirements (Gittleman and Harvey, 1982; Gittleman, 1985), we predicted that home range areas and movement rates will be greater in jaguars than in pumas. Given that coexisting felids show temporal segregation in their space use and actively avoid the same sites (Bhattarai and Kindlmann, 2012; Harmsen et al., 2009; Romero-Muñoz et al., 2010; Odden et al., 2010; Scognamillo et al., 2003), we predicted that jaguars and pumas with overlapping home ranges would show little overlap at core home range areas and they would avoid using sites at the same time.

Material and methods

Study site

Our study area was in the Greater Lacandona Ecosystem (GLE) in southeastern Mexico. This region contains the largest remaining portion of tropical rainforest in Mexico. Found in the most biodiverse region of Mexico, the GLE is a valuable natural resource and is part of what is called the 'Mayan Forest', given its important cultural associations (de la Torre and Medellín, 2011; Medellín, 1994). Despite importance for conservation of numerous species, the GLE continues to be subjected to anthropogenic destruction.

Of its original 1,500,000 ha of rainforest, 2/3 has been lost due to human impact in the past 40 years (Jong et al., 2000; Mendoza and Dirzo, 1999).

There are seven Natural Protected Areas (NPAs) within the GLE. These cover the largest forested areas of this region: Montes Azules (3312 km²), Lacantún (619 km²), Bonampak (48 km²), Yaxchilán (26 km²), Chan-kin (122 km²), Naha (38 km²), and Metzabok (33 km²) (Fig. 1). Our study area was in the north of GLE and covered approximately 2500 km², including Yaxchilán (Usumacinta river as the border with Guatemala on the north), Bonampak, Lacantún, and Montes Azules NPAs (Fig. 1). The study area also encompassed the Sierra la Cojolita, a tract of natural habitat in the north of GLE that is protected by local communities. Three indigenous communities inhabit the Mexican part of our study area: Lacanja Chansayab (~1000 people), Nueva Palestina (~20,000), and Frontera Corozal (~15,000). The main economic activities in this region include ranching, farming, and ecological and archeological tourism. The climate is hot (mean of 25 °C) and the mean rainfall per year is 2800 mm, with the greatest concentration in June–September, and the lowest in March–April (reviewed O'Brien (1998)).

Data collection

We captured jaguars and pumas using foot snares (Frank et al., 2003). At the site of each snare trap we also placed a VHF radio transmitter to monitor if traps were triggered (Halstead et al., 1995). Traps were checked every 4 h throughout the night and, depending on weather conditions, several times during the day. All capture and handling protocols followed the American Society of Mammalogists' IACUC guidelines (Sikes et al., 2011).

Upon capture, we immobilized animals using medetomidine (0.06 mg/kg) combined with ketamine (3.5 mg/kg) using a dart fired from a CO₂ pistol or rifle. While immobilized, we examined individual body condition and determined sex. We estimated age based on coat color, tooth wear (Stander, 1997), and gum-line recession (Laundré et al., 2000). Body mass and linear measurements were recorded. Weight was recorded using a portable scale.

We used satellite global positioning system (GPS) collars (i.e., Telonics® GEN IV, model TGW-4580). We programmed GPS collars to acquire a location every 4.8 h (4 locations/day), and to send data through the ARGOS system every 4 days. All collars included a programmable release mechanism (model CR-2a, Telonics®), and we scheduled the drop-off mechanism to release 12–14 months after capture. The GPS collars were recovered when possible using the locations that were obtained after their release through the ARGOS system and by searching the VHF pulse of the collars using a receiver.

Data analysis

For all analysis, we used only the 3D GPS fixes that were obtained by the collars, which are locations calculated from four or more GPS satellites that provided a location estimate for the GPS/ARGOS system with a typical accuracy of 2–10 m. For comparisons with other studies, we estimated annual home range size using 95% minimum convex polygon estimations (Mohr, 1947). However, to provide a more precise description of the home range use of jaguars and pumas, we also used the 50% and 95% fixed kernel estimators (Worton, 1989). We defined the core area within a home range as the area enclosed by the 50% isopleth. To prevent under-smoothing in kernel estimates, we utilized the rule-based ad hoc method of Kie (2013). We used the package "adehabitat HR" (Calenge, 2013) for R 3.1.1 (R Core Team, 2016) to estimate minimum convex polygons and kernel home ranges. We evaluated if the home range sizes were influenced by the number of fixes that were obtained per individual using Pearson's correlation analysis, and we tested if

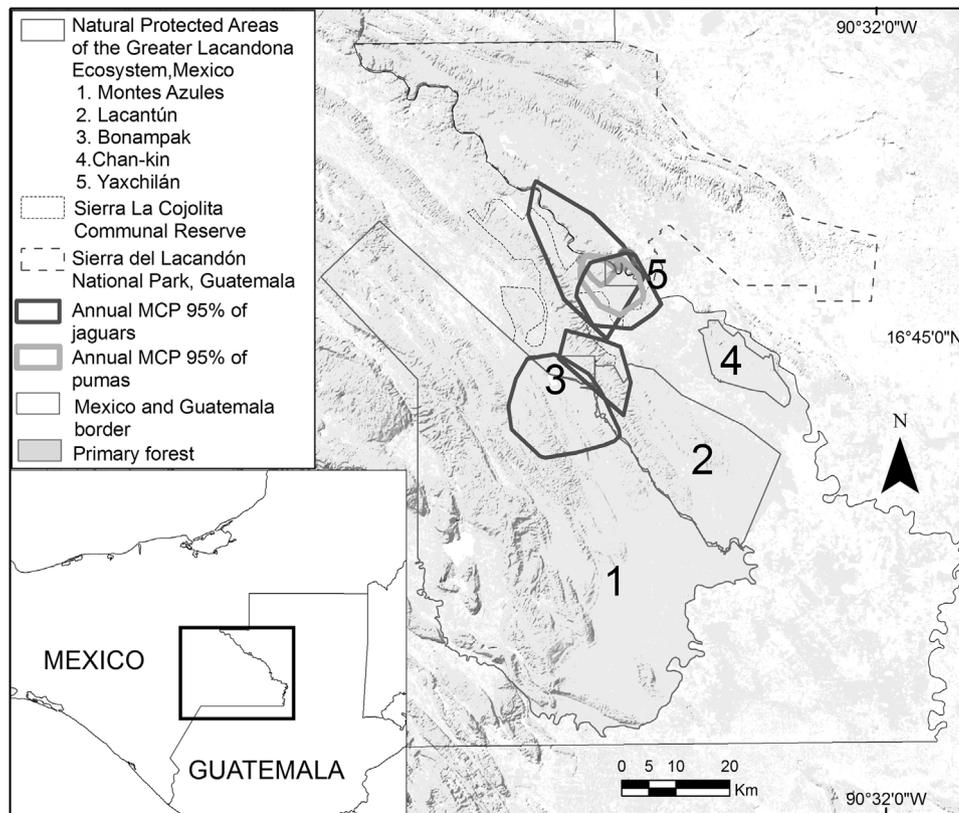


Fig. 1. Location of the study area in the Greater Lacandona Ecosystem (GLE), Chiapas, Mexico. The dark grey polygons represent the 95% Minimum Convex Polygons of the jaguars that were tracked in this study and the light grey polygons represent the pumas that were tracked.

the home ranges of jaguars were larger than those of pumas using the Student's *t*-Test.

We evaluated spatial and dynamic interactions among jaguars and pumas. We calculated three indices of distribution overlap using the fixed kernel estimator to quantify overlap of shared space used for individuals that were tracked simultaneously: the volume of intersection (VI – Seidel, 1992), Bhattacharyya's affinity (BA – Bhattacharyya, 1943), and the utilization distribution overlap index (UDOI – Fieberg and Kochanny, 2005). The VI index gives the minimum joint space use between two utilization distributions. The BA is a product based on two utilization distributions. The BA measures the affinity between two individuals, and it assumes that individuals use space independently of one another. The UDOI is a product-based index of degree of joint space use similar to Hurlbert's (1978) index of niche overlap. UDOI assumes that animals use space independently of one another. Index values in VI, BA, and UDOI range from 0 (for two home ranges with no overlap) to 1 (for two home range with the same utilization distribution), but the UDOI index can be >1 if the two utilization distributions are distributed non-uniformly and if they have a high degree of overlap. Therefore, UDOI index values <1 indicated less overlap relative to uniform space use, whereas values >1 indicated higher than normal overlap relative to uniform space use (Fieberg and Kochanny, 2005). The VI and BA statistics are most appropriate for quantifying the degree of similarity of two utilization distribution estimates, and the UDOI index is most appropriate for quantifying shared space use. We used the function “kerneloverlap” in the “adehabitat HR” package for R 3.1.1 to estimate the BA, VI, and UDOI indices.

To evaluate whether jaguars and pumas with overlapping home ranges avoided simultaneous use of the same space, we used the proximity analysis (Prox) of Bertrand et al. (1996). The proximity analysis determines the proportion of simultaneous fixes (ST),

which are proximal fixes based on a given distance threshold (*dc*). The Prox index is calculated as: $Prox = ST/dc$. We defined the distance threshold between two simultaneous fixes as 2.5 km and we defined the temporal threshold between simultaneous fixes as 24 h. We chose these wide thresholds to provide distance and time intervals that were sufficiently large to determine conservatively that tracked cats were not using the same space simultaneously. We only included in this analysis the simultaneous fixes between the tracked animals that were obtained during the same time slot as defined previously. Furthermore, we used the movement correlation coefficient (*Cr*) to measure the level of dynamic interaction (correlation) between the pairs of jaguars and pumas with overlapping home ranges. This statistic is essentially the Pearson's correlation statistic formulated for use of movement data, and it is sensitive to interaction to both direction of movement and displacement (Shirabe, 2006). Additionally, we used the Minta's temporal interaction coefficient (L_{ixn}) to test how two animals tracked simultaneously utilize an area shared between the two individuals (Minta, 1992). The Minta's temporal interaction coefficient is based on a contingency table that compares the observed frequency of those fixes that are simultaneous and within or outside the shared area to expectations based on the proportions of area that overlap, and use Chi-square statistic to examine the significance between the observed and expected use of shared areas. When L_{ixn} is near 0, it indicates that both animals use the shared area randomly with regard the other individual. When $L_{ixn} > 0$, both animals use the shared area simultaneously more often, and when $L_{ixn} < 0$, it is an indication of avoidance (Minta, 1992). We defined 24 h as a temporal threshold between simultaneous fixes in the Minta's temporal interaction coefficient. We used the package “wildlifeDI” (Long et al., 2014) for R 3.1.1 to perform the proxim-

ity analysis, the movement correlation coefficient, and the Minta's temporal interaction coefficient.

To determine rate of movement of both species, we used only the sequential locations that we obtained every 4.8 h. For all sequential locations, we calculated the distance traveled from the *initial location* to *final location* during the time intervals of 4.8 h, and then we calculated the distance travelled in km/h. The mean distance travelled per hour (km/h) was used as a response variable in comparisons among individuals and between species during different seasons and day periods using a linear mixed model. Species, sex, season, and day periods were treated as fixed effects, and individual as a random effect. We defined "dry season" as November–April and "rainy season" as May–October. To define day periods, we classified the day between the sunrise to sunset (0500 h–1659 h), and the night between the sunset to the sunrise (1700 h–0459 h). Because samples that we obtained from the sequential locations spanned both day and night, in our model we assigned each sequential location based on the percentage of day and night that was included in the elapsed time between sequential locations to obtain a better representation of day periods. We defined three categories of day periods: "light" ($\geq 66.6\%$ of day), "dark" ($\geq 66.6\%$ of night), and "light and dark" (< 66.6 and $> 33.3\%$ of day or night). We used likelihood ratio test to evaluate the significant differences between the different linear mixed models constructed with the different fixed effects defined. We used the lme4 library (Bates et al., 2014) for R 3.1.1 to perform the linear mixed effect models.

Results

We successfully deployed satellite global positioning system collars on four jaguars and three pumas (Table 1). A total of 2523 3D GPS fixes were obtained from the collared animals (1134 from jaguars and 1389 from pumas). Mean horizontal error was 5.01 ± 4.61 m for jaguar localizations and 5.88 ± 6.13 m for pumas. The fix success of the GPS collars was very low for most of the individuals probably due to the closed forest canopy (Table 1). We only recovered three of the collars deployed (JF15, JM04, and PF18). We could not recover three collars (JF05, PM19, PM20), because after the release mechanisms were activated, we did not obtain fixes through the ARGOS satellite system to search for these collars. We also never found the VHF in the field to search for these collars after the release mechanism was activated. Additionally, we lost the signal of jaguar male JM11 after five months of tracking through the ARGOS satellite system. Thus, data presented for animals JF05, JM11, PM19, and PM20 corresponded only to data obtained through the ARGOS satellite system. Animals JF05, PM19, and PM20 were tracked for an entire year, and jaguar JM11 was tracked for five months (Fig. 2 and Table 1).

The home range sizes of the individuals that were tracked when plotted against the number of months of tracking indicated that our sampling effort to describe the annual home range sizes of jaguars and pumas was adequate (Fig. 2). Home range size varied ($t_4 = 2.66$; $P < 0.05$) between jaguars and pumas; jaguars inhabited larger home ranges compared to pumas (Fig. 3; Table 1). The mean annual home range for female jaguars that was estimated using the 95% fixed kernel was $181.4 \pm 4.0 \text{ km}^2$ and for male jaguars it was $431.6 \pm 152.6 \text{ km}^2$ (Table 1). Annual home range using the 95% fixed kernel for the only female puma that we tracked was 34.3 km^2 , and the mean annual home range of male pumas was $72.0 \pm 85.2 \text{ km}^2$ (Table 1). There was no correlation between the home range size and the number of fixes obtained per individual ($R^2 = 0.033$, $P = 0.94$).

Jaguars shared part of their home ranges with conspecifics at 95% fixed kernels. Home range overlap between the individuals (with data for the sexes pooled) ranged from 0.09 to 0.41, as indi-

Table 1
Estimated annual home range sizes of jaguars and pumas in the northern Greater Lacandona Ecosystem, Chiapas, Mexico.

Animal ID	Species	Sex	Age class	Weight	Minimum Convex Polygon (95%) km ²	Fixed Kernel (95%) km ²	Fixed Kernel (50%) km ²	Total number of locations	Fix success (%)	Period tracked
JF05	<i>P. onca</i>	♀	Adult	34	133.3	184.2	40.2	88	4.8	January 2012–January 2013
JF15	<i>P. onca</i>	♀	Adult	33	156.2	178.6	40.4	393	21.6	August 2012–August 2013
JM04	<i>P. onca</i>	♂	Adult	50	280.1	322.3	71.1	576	31.6	January 2012–January 2013
JM11	<i>P. onca</i>	♂	Adult	55	296.2	540.9	142.6	72	4.0	August 2012–January 2013
PF18	<i>P. concolor</i>	♀	Adult	22	20.9	34.3	8.2	852	46.8	March 2013–March 2014
PM19	<i>P. concolor</i>	♂	Juvenile	27	7.6	11.7	3.7	270	14.8	March 2013–March 2014
PM20	<i>P. concolor</i>	♂	Adult	32	82.2	132.3	35.0	267	14.7	March 2013–March 2014

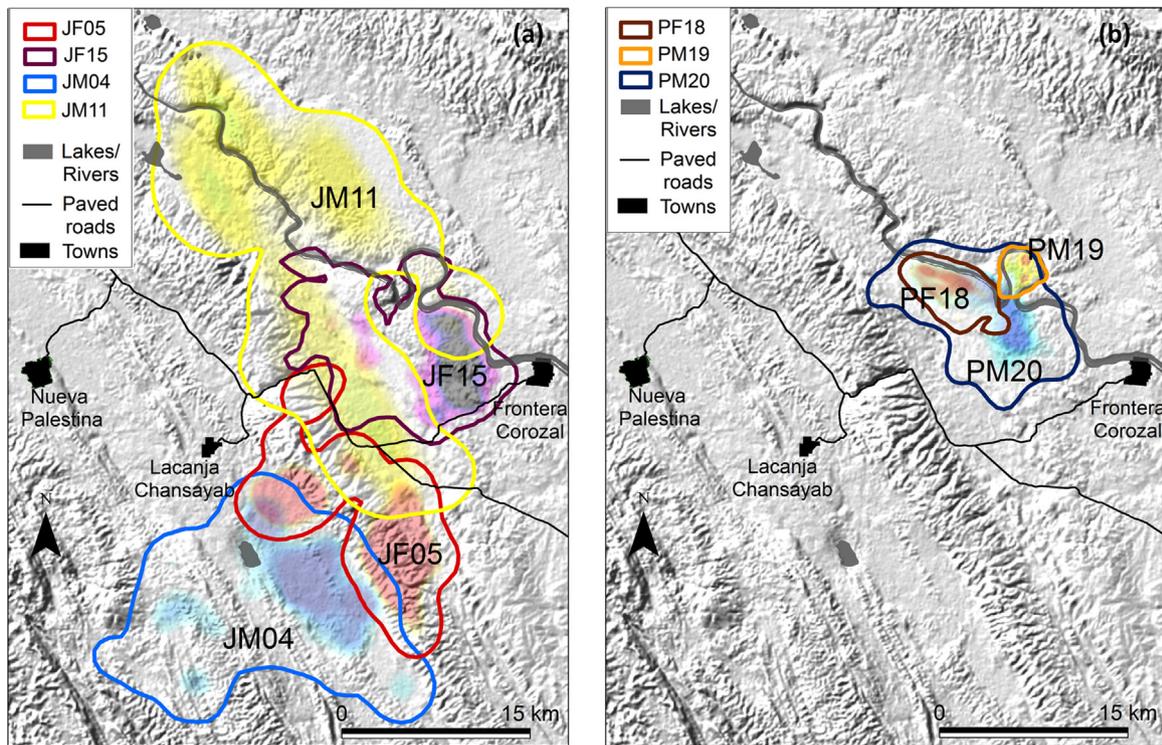


Fig. 3. (a) Annual home ranges of jaguars as estimated using 95% fixed kernels in the Greater Lacandona Ecosystem (GLE). (b) Annual home ranges of pumas using 95% fixed kernels. The color gradient reflects areas of high (greater color intensity) and low (less color intensity) use according to the observed distribution of big cat utilization.

Table 2

Percentage of overlap at 95% and 50% of the fixed kernel, using the UDOI, VI, and BA indexes, for jaguars and pumas with adjacent or overlapping home ranges.

Types of interactions		Individuals pairs	95% UDOI	50% UDOI	95% VI	50% VI	95% BA	50% BA
Jaguars adjacent	males	JM04–JM11	0.00	0.00	0.00	0.00	0.00	0.00
	females	JF05–JH15	0.00	0.00	0.01	0.00	0.02	0.00
Jaguars overlapping	female-male	JF05–JM04	0.09	0.00	0.18	0.02	0.28	0.02
		JF05–JM11	0.05	0.00	0.12	0.00	0.22	0.00
		JF15–JM11	0.20	0.00	0.23	0.00	0.41	0.00
		PM19–PM20	0.07	0.00	0.08	0.00	0.24	0.00
Pumas overlapping	males	PM19–PM20	0.07	0.00	0.08	0.00	0.24	0.00
	female-male	PF18–PM20	0.35	0.04	0.31	0.08	0.53	0.19
Jaguars – Pumas overlapping	female jaguar– female puma	JF15–PF18	0.08	0.00	0.08	0.00	0.25	0.00
	female jaguar– male puma	JF15–PM19	0.02	0.00	0.02	0.00	0.12	0.00
		JF15–PM20	0.50	0.00	0.40	0.04	0.63	0.05

cated by all three indices of overlap (Table 2). However, very little of this overlap was observed in core areas (0–0.02 – Table 2). For pumas (sexes pooled), home range overlap between individuals ranged from 0.07 to 0.53 as determined by the three indices of overlap, and overlap of core areas ranged from 0 to 0.19 (Table 2). Proximity analysis (Prox) indicated that jaguars with overlapping home ranges avoided occupying the same sites at the same time (Table 3). Mean percentage of simultaneous fixes between jaguars

below the threshold was almost zero (0.003 ± 0.005). The movement correlation coefficients (Cr) indicated that movements of jaguars with overlapping home ranges were random with respect to neighboring jaguars, based on the low values of the correlation coefficients that we obtained (Table 3). Minta's temporal interaction coefficient (L_{ixn}) indicated no attraction or avoidance to shared areas of jaguars with overlapping home ranges (Table 3). On the other hand, pumas showed nearest distances in simultaneous fixes

Table 3

Results of the proximity analysis (Prox), the movement correlation coefficient (Cr), and the Minta's temporal interaction coefficient (L_{ixn}) for jaguars and pumas with adjacent or overlapping home ranges.

Types of interactions		Individuals pairs	Simultaneous fixes	Prox	Cr	L_{ixn}	$L_{ixn} p$
Jaguars adjacent	males	JM04–JM11	35	0	–0.23	–	–
	females	JF05–JH15	20	0	–0.03	–1.53	0.85
Jaguars overlapping	female-male	JF05–JM04	52	0.01	–0.19	–0.22	0.57
		JF05–JM11	6	0.00	0.20	–	–
		JF15–JM11	31	0.00	0.19	0.01	0.98
		PM19–PM20	59	0.16	0.04	0.27	0.85
Pumas overlapping	males	PM19–PM20	59	0.16	0.04	0.27	0.85
	female-male	PF18–PM20	135	0.24	0.02	–	–
Jaguars – Pumas overlapping	female jaguar– female puma	JF15–PF18	83	0.03	–0.10	0.77	0.16
	female jaguar– male puma	JF15–PM19	21	0.04	–0.45	–0.95	0.75
		JF15–PM20	14	0.07	0.09	–0.15	0.87

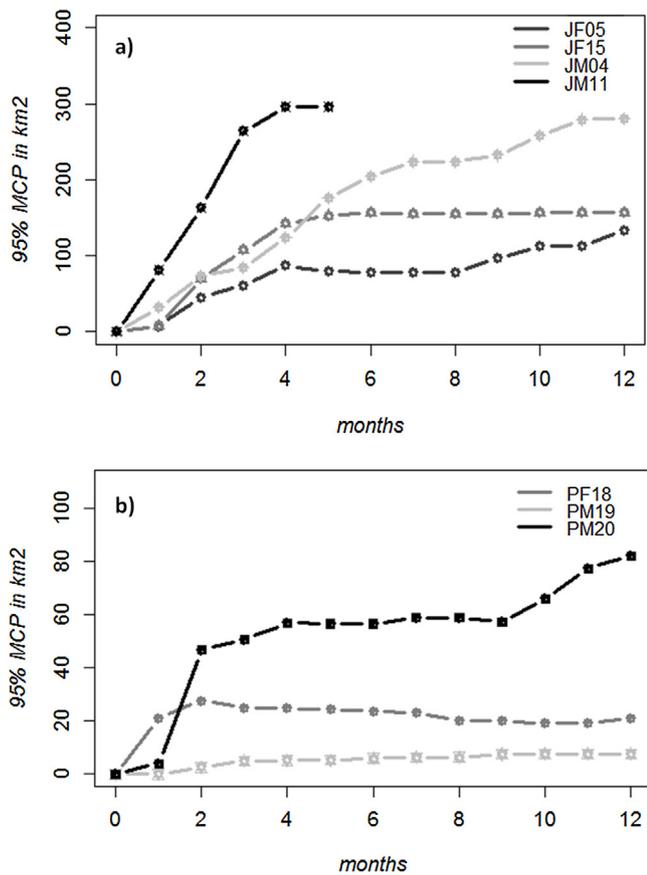


Fig. 2. The 95% Minimum Convex Polygon home ranges of jaguars (a) and pumas (b) that were tracked in the Greater Lacandona Ecosystem (GLE) obtained by cumulative sequential samples and then plotted versus the number of months tracked. The graphs show that home range sizes stabilized before the 12 months of tracking for most individuals. This indicated the adequacy of our sampling effort to describe the annual home range sizes of jaguars and pumas in our study area.

between conspecifics, but their movements were random relative to neighboring pumas and they did not show attraction or avoidance to shared areas with other pumas.

Jaguars and pumas shared space at the home range level, because home range overlap of jaguars and pumas that were tracked simultaneously ranged from 0.02 to 0.63 (Table 2). However, little overlap was observed in core areas (ranged from 0 to 0.05 – Table 2). Mean percentage of simultaneous fixes below the distance threshold between female jaguar JF15 and three pumas was very low (0.04 ± 0.02). The movement correlation coefficients indicated that movements of jaguars and pumas that shared the space were random with respect to the movement of other individuals with the exception of a pair (JF15 and PM19), where the correlation coefficient showed little avoidance ($Cr = -0.45$). Minta's temporal interaction coefficient indicated no attraction or avoidance to shared areas for all the pumas that had overlapping home ranges with jaguars (Table 3).

A total of 1114 sequential locations were obtained from the seven tracked animals (435 from jaguars and 679 from pumas). We did not detect differences between the mean rate travelled by jaguars and pumas, or between sexes and seasons. However, movement rates varied among different day periods between species ($X^2 = 25.29$, $P < 0.0001$). Jaguar movements were greater during the “light & night” ($0.161 \text{ km/h} \pm 0.027$) and “night” periods ($0.160 \text{ km/h} \pm 0.019$) than during the “light” period ($0.140 \text{ km/h} \pm 0.019$), and puma movements were greater during the “light period” ($0.173 \text{ km/h} \pm 0.025$) than during the “night”

($0.121 \text{ km/h} \pm 0.024$) and “light & night” ($0.116 \text{ km/h} \pm 0.039$) periods.

Discussion

We found noteworthy differences in space use between the two largest neotropical felids, jaguars and pumas. Average home range size of jaguars was 2–6 times larger than that of pumas in GLE. However, we did not find differences in the mean rate travelled by these species. Although jaguars used larger home ranges than pumas, movement rates within their home range were similar in both species. Larger home range sizes of jaguars are likely due to their larger body mass. At our study site, male jaguars were 1.68 times heavier than male pumas and female jaguars were 1.60 times heavier than female pumas. Allometric relationships between body mass and home range size have been well-documented (Harestad and Bunnell, 1979; Lindstedt et al., 1986; McNab, 1963). Such patterns are due in part to the metabolic requirements of larger species. Higher metabolic demands may result in increased spatial requirements or time expenditures for the search and pursuit of correspondingly larger prey (Carbone et al., 2007; Gittleman and Harvey, 1982; Gittleman, 1985). Further evidence of greater jaguar metabolic demands comes from other studies that have documented that jaguars often take larger prey relative to pumas, and that pumas hunt a wider spectrum of prey than jaguars (Emmons, 1987; Novack et al., 2005; Nuñez et al., 2000; Rabinowitz and Nottingham, 1986; Scognamiglio et al., 2003).

Jaguars and pumas with overlapping home ranges demonstrated a low degree of spatial overlap in the core area, which suggested that they had areas of exclusivity within their home range (Azevedo and Murray, 2007). Furthermore, our proximity analysis results showed that even though jaguars and pumas had overlapping home ranges, they tended to avoid the same sites temporally (Harmsen et al., 2009; Scognamiglio et al., 2003). We interpret these results as evidence of spatial and temporal avoidance between jaguars and pumas. Spatial segregation that is observed in solitary felids implies territoriality, because core areas are usually associated with regions of high resource concentration (Azevedo and Murray, 2007; Nuñez, 2006; Plowman et al., 1998; Samuel et al., 1985). Spatial territoriality affects the interactions of jaguars and pumas, and it could facilitate the coexistence of these sympatric species through resource partitioning (Azevedo and Murray, 2007; Harmsen et al., 2009; Romero-Muñoz et al., 2010; Scognamiglio et al., 2003). Scent marking using scat, scrapes, or urine may provide spatial and temporal information and, thereby, reduce the probability of confrontation, and these signs may help to maintain exclusive territories and the sharing of space simultaneously (Harmsen et al., 2009; Nuñez, 2006). A caveat to these results is that other individuals that were not tracked in our study could have occupied the area simultaneously unbeknown to us.

We documented a temporal separation of activity between jaguars and pumas in GLE. Jaguars were more active during periods that included the nighttime and pumas were more active during the daytime. Differences in their activity patterns, which may be due to avoidance behavior, could allow for the coexistence of these sympatric felids in tropical forests (Foster et al., 2013; Romero-Muñoz et al., 2010). Temporal separation between coexisting felids also could be facilitated by differences in the activity patterns of their main prey (Emmons, 1987; Foster et al., 2013; Karanth and Sunquist, 2000; Ramesh et al., 2012; Sunquist and Sunquist, 1989).

Our results differed from other studies that have tracked both species simultaneously. Nuñez (2006) and Scognamiglio et al. (2003) reported similar home range areas for jaguars and pumas in dry tropical forest of Mexico and in Los Llanos, Venezuela. In the trop-

ical rainforest of Calakmul, Mexico, pumas used larger areas than jaguars (Chávez, 2006). Jaguar home ranges in other studies ranged from 10 to 125 km² in females and from 25 to 625 km² in males (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Ceballos et al., 2002; Chávez, 2009; Crawshaw and Quigley, 1991; Nuñez, 2006; Rabinowitz and Nottingham, 1986; Schaller and Crawshaw, 1980). However, other studies that estimated jaguar home ranges using GPS tracking yielded similar results to our own (Chávez, 2009). In the case of pumas, home range estimates are limited in number in neotropical ecosystems, but estimates in other studies ranged from 35 to 161 km² in females and 62 to 763 km² in males. Our home range estimates for pumas were similar to those from the dry tropical forest in the Mexican Pacific, the Venezuelan Llanos, and temperate areas in South America, but our estimates were smaller than those that were estimated for temperate and arid areas of North America (Chávez, 2006; Dickson and Beier, 2002; Franklin et al., 1999; Logan and Sweanor, 2001; Nuñez, 2006; Scognamiglio et al., 2003; Spreadbury et al., 1996). Home ranges of both species vary throughout their geographic range, and this variability is likely a reflection of plasticity in the movement of these species in response to resource availability. In these species, home range sizes were inversely related to abundance and availability of prey (Crawshaw and Quigley, 1991; Logan and Sweanor, 2001; Rabinowitz and Nottingham, 1986).

Home ranges of male jaguars were 2.3 times larger than those of female jaguars, and home ranges of male pumas were 2.0 times larger than those of female pumas. Both species are solitary except for periods of mating and breeding. Usually, females have smaller home ranges than males, and the home ranges of males include and overlap with the home ranges of several females (Cavalcanti and Gese, 2009; Logan and Sweanor, 2001; Rabinowitz and Nottingham, 1986; Schaller and Crawshaw, 1980; Seidensticker et al., 1973). Home ranges of females must contain sufficient prey to meet the energetic requirements that raising cubs demands (Eisenberg, 1986; Logan and Sweanor, 2001; Sandell, 1989). Another factor that determines space use in solitary female felids is the availability of safe refuges for offspring (Fuston et al., 2001; Nuñez, 2006). On the other hand, home ranges of males must be large enough to cover the home ranges of several females that could serve as mates, and to defend their territory from other males that would kill their cubs (Cavalcanti and Gese, 2009; Eisenberg, 1986; Ferguson et al., 2009; Goodrich et al., 2010).

We recognize that our results could be biased by the low number of individuals that we tracked. This sample size probably is not representative of the population of jaguars and pumas of our study area. In fact, we tracked only one female puma and her behavior could be atypical. However, our data suggest that jaguars required larger areas compared with pumas to meet their spatial requirements in southern Mexico. This has important implications for the conservation plans for these species at the landscape scale, because habitat destruction and fragmentation would have more severe effects on jaguars than on pumas. Although jaguars and pumas do not use sites exclusively that are covered completely with forest, they preferred primary forest in contrast to modified environments that were associated with human activities (Colchero et al., 2011; Conde et al., 2010; Cullen et al., 2013; Dickson et al., 2005; Foster et al., 2010a). According to our estimates, decision-makers and managers would need to conserve primary forest patches of at least 180 km² to meet the annual spatial requirements of a female jaguar in the south of Mexico. The GLE landscape is a mosaic of primary forest that is surrounded by a mixture of human-modified habitats (crops, pastures, paved roads, and towns). To ensure the long term conservation of jaguars in this important region, large extensions of primary forest should be guaranteed and deforestation should be controlled completely.

Additionally, two jaguars and one puma tracked in this study repeatedly crossed the Usumacinta River into Guatemala. These observations suggest that jaguars and pumas of the GLE in Mexico and Sierra del Lacandon National Park in Guatemala belong to the same population. The jaguar population of GLE has been identified as a crucial source population that is required to secure the future of this species in the Mayan Forest, and adequate preservation of this population depends on maintaining the connectivity between the Natural Protected Areas of GLE in Mexico with those located in the Guatemalan Mayan Forest (de la Torre and Medellín, 2011; de la Torre et al. in press). The Sierra La Cojolita is a large tract of forest that is outside protected areas of the GLE, and it is absolutely critical for maintaining the connectivity in this landscape. We believe firmly that the Sierra La Cojolita should be incorporated into the regional strategy to conserve jaguars. We suggest that human land use activities in this area should be compatible with conservation of natural habitats, that payments for ecosystem services to halt deforestation should be enacted, and that a management plan should be developed in conjunction with the local communities. Only in this way can we guarantee the connectivity of the Mayan Forest landscape and the long-term conservation of this bi-national population of jaguars.

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