



Sex matters: Modeling male and female habitat differences for jaguar conservation

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ABSTRACT

Competition for mates, cub rearing, and other behaviors differ between males and females in large carnivores. Although these differences can be reflected in patterns of habitat use, gender has rarely been incorporated into habitat models. We evaluated differences in habitat use between male and female jaguars in the Mayan Forest of the Yucatan Peninsula by modeling occupancy as a function of land cover type, distance to roads, and sex. Nested models were fitted to high-spatiotemporal resolution satellite (GPS) telemetry, controlled for temporal autocorrelation, and eliminated selection bias of pseudo-absences using a semi-non-parametric bootstrap. Although both male and female jaguars prefer tall forest, short forest was also preferred by females but avoided by males. Whereas females significantly avoided roads, males didn't and ventured into low-intensity cattle ranching and agriculture. Females' preference for intact forests and against roads led to their habitat being fragmented to a greater degree than that of males. Models that ignored sexual differences failed to capture the effect of roads and agriculture on jaguar habitat use, blurred the distinction of use between short and tall forest, and underestimated fragmentation of female jaguar habitat; but incorporating these differences increased precision of habitat maps and allowed the identification of potential jaguar-human conflict areas associated with male's use of cattle and agricultural lands. Specifying sex differences increases the power of habitat models to understand landscape occupancy by large carnivores, and so greater attention should be paid to these differences in their modeling and conservation.

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1. Introduction

Human encroachment on the last remaining wildernesses has challenged the long-term conservation of large carnivores (Woodroffe, 2000). These species are in global decline due to habitat loss, fragmentation, and hunting for fur trade and livestock protection (Weber and Rabinowitz, 1996; Ogada et al., 2003). However, despite dramatic decreases in large carnivore populations worldwide, still little is known about many species' environmental requirements and their associated habitat losses.

Large carnivores frequently exhibit sexually distinct social behaviors and spacing patterns, especially those associated with gestation and parental care (Wilson, 1975; Crook et al., 1976;

Eisenberg, 1981). Female cheetahs (*Acinonyx jubatus*), for example, tend to show stronger preference than males for denser vegetation types, which provide greater protective cover, higher densities of prey, and lower densities of competitors and cub predators (Broomhall et al., 2004). In addition, some species show clear sexual differences in their response to roads (Mace et al., 1996; Maehr, 1997; Kerley et al., 2002; Gaines et al., 2005). For example, roads are avoided and thereby delineate territories of female Florida panther (*Puma concolor coryi*), but males cross roads more frequently and therefore suffer higher mortality rates from car collisions (Maehr, 1997). Likewise, studies on livestock depredation show that higher mobility of males and possible differences in diet preferences lead to males being the primary culprits for most attacks, resulting in a higher number of males killed by local people (Linnell et al., 1999). Although females have greater energy requirements during gestation and lactation periods, males have larger home ranges, possibly as a result of males' farther dispersion and mate-seeking behaviors (Lindstedt et al., 1986).

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In recent decades, habitat models have become a key tool for the design of conservation policies worldwide (Pearce and Ferrier, 2000; Gavashelishvili and Lukarevskiy, 2008). However, despite known sex-related differences in large carnivores, these models usually fail to incorporate gender as a variable. Although a few habitat models of large carnivores do focus on modeling females alone (e.g., Mace et al., 1996; Gaines et al., 2005), the majority of habitat models typically ignore sex as an explanatory variable (e.g., Palma et al., 1999; Schadt et al., 2002; Linkie et al., 2006; Matthew et al., 2006; Klar et al., 2008).

When behavioral differences do exist between the sexes, disregarding them in models can blur behavioral preferences between the sexes and bias their estimation toward that of the more frequently observed sex. For those species for which there are significant intersexual differences specifically in habitat use, lack of discrimination could result in underestimating important environmental factors for one sex while overestimating them for the other.

To evaluate gender differences in habitat use, we developed a model that discriminates male and female preferences in jaguar (*Panthera onca*) habitat occupancy. We tested the hypothesis that males are more tolerant to human activity than females, as reflected in the probability of their occurrence as a function of land-use type and proximity to roads. In particular, we predict that: (1) both will use undisturbed forests as their preferred cover type; but (2) males will occur with higher probability in human-dominated land-use types (i.e., low-intensity agriculture and rangeland) and in closer proximity to roads than females.

This analysis quantifies the distribution and fragmentation of available habitat for male and female jaguars in the Mayan Forest region and identifies likely human-jaguar conflict zones for the development of conservation policies. This study therefore describes the habitat use of one of the least studied large carnivores in the world, and provides a fundamental tool for wildlife conservation and management in a region where pressure from infrastructure projects is rapidly increasing.

2. Methods

2.1. Study area and species

This study was conducted in the Mayan Forest, which holds the largest jaguar population and the largest patch of tropical forest in Central America. The area is one of the priority jaguar conservation units (JUC) defined by the Wildlife Conservation Society Jaguar Conservation Program (Sanderson et al., 2002).

Located in the core of the Mayan Forest, the study area includes central and northern Belize, a large portion of the Mexican states of Campeche and Quintana Roo, and the majority of the Petén of Guatemala. The region is covered predominantly by tropical semi-deciduous forest, with an average annual rainfall of 1350 mm, a pronounced dry season between February and June, and relatively flat topography ranging between 0 and 700 m above mean sea level (Holdridge et al., 1971; Pennington and Sarukhan, 2005). The area also contains subtropical moist forest (Holdridge et al., 1971) composed of two subtypes; (1) tall forests, found in areas of greater relief and characterized by a high, closed tree canopy; and (2) short forests, which are mostly seasonally inundated dry-deciduous (i.e., "raingreen") lowland alluvial forests with short, relatively open canopies and dense understories (Novack et al., 2005). The region also includes secondary vegetation which growing on abandoned lands previously cleared for slash and burn agriculture (Ucan et al., 1999) and swamps, which are classified as Mesoamerican palustrine vegetation (García and Secaira, 2006).

Agriculture and cattle ranching are practiced at varying intensities in the region. Low-intensity agriculture and cattle grazing are

dominant, especially in the communal forests and lands (ejidos) and bordering legally protected areas. Broad-scale, mechanized agriculture and cattle grazing are rare and extremely localized.

The jaguar is the largest Neotropical felid and the third largest cat worldwide, but it is the least studied of the big cats. The species is considered near threatened (IUCN, 2009), and although it has a wide distribution from Mexico to Argentina, the species maintains only 54% of its historical range (Kinnaird et al., 2003). Jaguars are solitary, generalist predators, with foraging strategies for selected prey species (Weckel et al., 2006).

Conflict between jaguars and humans is increasing. Male jaguars are responsible for approximately 70% of cattle predation in the region. This results in greater male mortality due to hunting by humans (Rabinowitz, 1986).

2.2. Jaguar data

We captured jaguars in the borders of Calakmul Biosphere Reserve and the Caoba forestry Ejido (Mexico) during the dry seasons of 2001–2007 and in the borders of the Mayan Biosphere Reserve (Guatemala) during the 2006–2007 dry seasons. The captured jaguars were chemically anaesthetized using a projectile dart (Ceballos et al., 2002), examined for general body condition, measured, weighed, and fitted with GPS collars (Televilt, Lindesberg, Sweden, see URL <http://www.televilt.com>). The GPS collars were programmed to record animal positions at varying time intervals over 2–12 months, depending on collar battery life. Most of the individuals were recaptured the year following their initial capture to recover data and replace collars.

We used a total of 5246 high-resolution GPS points from three females captured in Ejido Caoba and three males captured at the limits of the Calakmul and Mayan Biosphere Reserves (Fig. 1). All the individuals captured were adults, with ages ranging from 4 to 10 years old. None of the jaguars were captured close to broad-scale mechanized agriculture and broad-scale ranching activities.

Temporal autocorrelation among locations can lead to biased estimates of environmental effects and inflated parameter variances, making comparisons between alternative models difficult (Lennon, 1999). We avoided this by calculating the cross-correlations of latitude and longitude within serial jaguar locations at lags from 1 h to 7 days (Legendre and Legendre, 1998) and filtered points based on an empirical cross-correlation threshold of 0.3 (i.e., 72 h). This resulted in a sample size of 444 independent observations of jaguar presence 218 points for females and 226 points for males. A random sample of 10,000 pseudo-absences were selected from the minimum convex polygon enclosing each individual's full (unfiltered) GPS trail, buffered by 10 km using the Hawth's Analysis Tools extension in ArcMap 9.1 (Beyer, 2004).

2.3. Landscape data

We obtained geospatial environmental data from the Selva Maya Zoque y Olmeca database (García and Secaira, 2006), including vegetation, population centers, and roads for the year 2000. We included in our analysis only selected paved and unpaved roads with high traffic, since small trails are known not to affect the behavior of large carnivores (Mladenoff and Sickley, 1998; Zarza et al., 2007). Based on previous studies (Chavez Tovar, 2006; Zarza et al., 2007; Conde, 2008), we used three variables that could potentially influence jaguar occurrence in the region: land cover (L), distance to roads (R), and sex (S). Preliminary analysis indicated that road type (i.e. paved versus non-paved), vegetation, seasonality, and elevation did not significantly affect jaguar habitat use (Conde, 2008). Although elevation has been a significant variable to model jaguar and other large carnivore habitat (Gaines et al., 2005; Mace et al., 1996; Hatten et al., 2005), we did not include

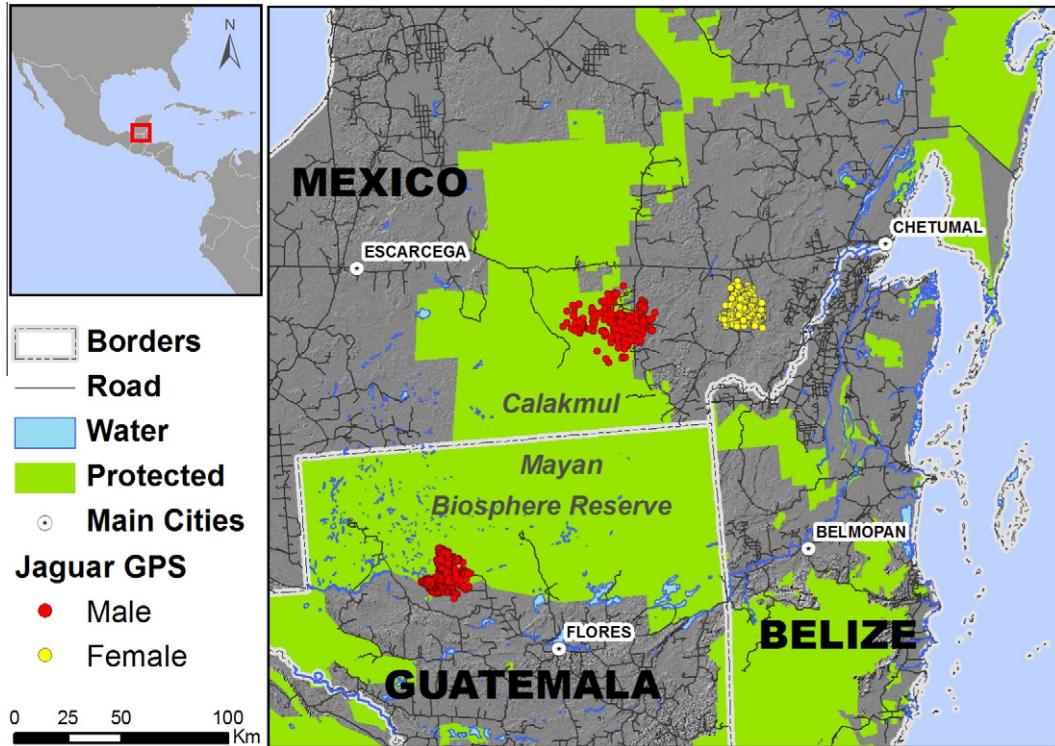


Fig. 1. Study area and jaguar GPS points (three females in the Ejido Caoba, one male in Calakmul and two males in the Mayan Biosphere Reserve).

it in models because of the lack of variation in the study area (100–400 m a.s.l.). Five general land cover types were defined: tall forest, short forest, swamp, secondary vegetation, and agriculture-cattle, which included low-intensity, non-mechanized cattle ranching and agricultural land. Other variables that had Spearman's rank correlation >0.6 with these selected variables were not included in the model (Wilson, 1975; Fielding and Haworth, 1995; Klar et al., 2008). For instance, distance to population centers and human population densities were not included due to their strong correlation with road proximity.

2.4. Statistical analyses

We used a generalized linear model (GLM) to infer the probability of jaguar occupancy as a function of sex and environmental variables (Pearce and Ferrier, 2000; Rhodes et al., 2006; Klar et al., 2008). This modeling framework assumes that habitat preferences are revealed by individual selection of sites versus a random draw of the available landscape (Manly et al., 2002), using randomly selected points as “pseudo-absences”. These models differ from symmetric presence-absence models in that they do not assume that certain areas are never used, but instead that locations where presence was not recorded are merely uninformative (Pearce and Ferrier, 2000; Boyce et al., 2002).

The model's dependent variable was represented by the set of presence and pseudo-absence points. We assigned to each point i the indicator function y_i , where

$$y_i = \begin{cases} 1 & \text{if presence} \\ 0 & \text{if pseudo-absence,} \end{cases} \quad (1)$$

and we modeled the probability of jaguar presence at each site i as a Bernoulli process, $y_i \sim \text{Bernoulli}(p_i)$, with probability of occurrence p_i . We used a logit-link function to relate this probability to the covariates described above:

$$\ln\left(\frac{p_i}{1 - p_i}\right) = \mathbf{z}_i \mathbf{b}, \quad (2)$$

where \mathbf{z}_i is the vector of covariates for point i and \mathbf{b} is the vector of parameters linking \mathbf{z}_i to the probability p_i . We tested a total of eight nested models that included land cover types (L), distance to roads (R), and interactions between the first two terms and sex (i.e. S:R and S:L, respectively). Thus, R is a continuous variable associated with the slope in Eq. (2), and the categorical variables L and S relate to the intercepts.

To avoid spurious results in parameter estimation due to a biased random selection of pseudo-absences, we performed a “semi-” non-parametric bootstrap (SNPB), randomly selecting (with replacement) the same number of pseudo-absences as the number of jaguar presences out of the 10,000 random locations per jaguar range (see data collection section). We ran the analysis with 2000 different sets of pseudo-absence points (i.e. SNPB steps) and stored the resulting estimates, out of which we calculated mean values as well as standard errors and confidence intervals for each parameter.

We used Akaike's Information Criterion (AIC) for model selection, which incorporates a measure of model goodness-of-fit and a penalization based on the number of parameters (Akaike, 1974). We then compared the models hierarchically, counting the number of times each model had the lowest AIC out of the 2000 SNPB steps. A model consistently showing the lowest AIC of all competing models indicates not only that it best explains the data, but also that it is robust despite the selection of pseudo-absences.

To quantify similarities between parameter estimates for the different land cover types (L), we used the Kullback–Liebler (K–L) divergence (Burnham and Anderson, 2001), a distance function that evaluates the similarity between two probability distributions. Let a and b be two parameters with distributions $P_a(x)$ and

$P_b(x)$ to be compared; the K-L distance between a and b , D_{ab} is calculated as

$$D_{ab} = \int_{-\infty}^{\infty} P_a(x) \log \left(\frac{P_a(x)}{P_b(x)} \right) dx = E \left[\log \left(\frac{P_a}{P_b} \right) \right]. \quad (3)$$

Thus, D_{ab} is equal to the expected value of the log-ratio between both distributions with P_a as the reference distribution. As a result, when the distributions are similar, D_{ab} will tend to 0 (i.e., when $a = b$, then $D_{ab} = 0$). Because K-L divergence is not symmetric, we calculated both K-L distances, D_{ab} and D_{ba} .

2.5. Model validation and habitat prediction

The model assigns a continuous probability of jaguar occurrence to each raster cell. To identify an optimal threshold at which to discriminate (binary) habitat from non-habitat, we calculated the Receiver Operating Characteristic (ROC) of the selected model. ROC analysis tests a range of probabilities, at which a prediction \hat{y}_i is assigned to each point i such that $\hat{y}_i = 0$ (i.e. non-habitat) when the calculated probability is below the threshold and $\hat{y}_i = 1$ (i.e. habitat) otherwise. It then compares these predictive variables to the actual y_i (i.e. presence-pseudo-absence points) and calculates the proportions of true positives (where $\hat{y}_i = y_i = 1$) and false positives (where $\hat{y}_i = 1$ and $y_i = 0$). The probability at which the proportion of true positives is maximized and false positives is minimized is selected as the threshold for habitat-non-habitat (Pearce and Ferrier, 2000). We obtained threshold probabilities and proportions of true positives and false positives for each SNPB step and calculated means and confidence intervals for each one of these measures. We used this mean threshold to create separate binary habitat maps for males and females over the study area.

Model validation was based on the Kappa statistic (Cohen, 1968), using a random sample of independent presence and pseudo-absence points (i.e. those not used to train the model). Kappa is

a measure of the accuracy improvement of the model over that expected by chance (Cohen, 1968; Guisan and Zimmermann, 2000), and is appropriate when the proportions of positive and negative cases is similar (Fielding and Bell, 1997), in this case the number of presences and pseudo-absences. We calculated the mean value and 95% confidence interval for Kappa and used Landis and Koch classification to determine model reliability (Landis and Koch, 1977).

To further assess the predictive capabilities of the model, we used 149 radio-telemetry locations from five different jaguars (i.e. animals that were not used to develop the model): one adult male and three adult females captured at the east edge of the Calakmul Biosphere reserve and one adult female captured in the Ejido Caoba (Fig. 2). We calculated the percentage of these independent jaguar points that matched our predicted habitat for all 2000 sets of estimates from the selected model.

2.6. Habitat fragmentation

Habitat fragmentation was quantified by calculating total number of patches, maximum patch size, and mean patch size. We also counted the number of patches between 100–1000, 1000–10,000 and 10,000–100,000 km² and tallied the percentage of each category that was inside vs. outside protected areas. These metrics were compared between the best-fit model (that included sex) and the model that did not include sex. The R statistical analysis software was used for all statistical analyses (R Development Core Team 2008).

3. Results

3.1. Jaguar habitat

Habitat selection by jaguars is significantly different between males and females. The model including the interactions between

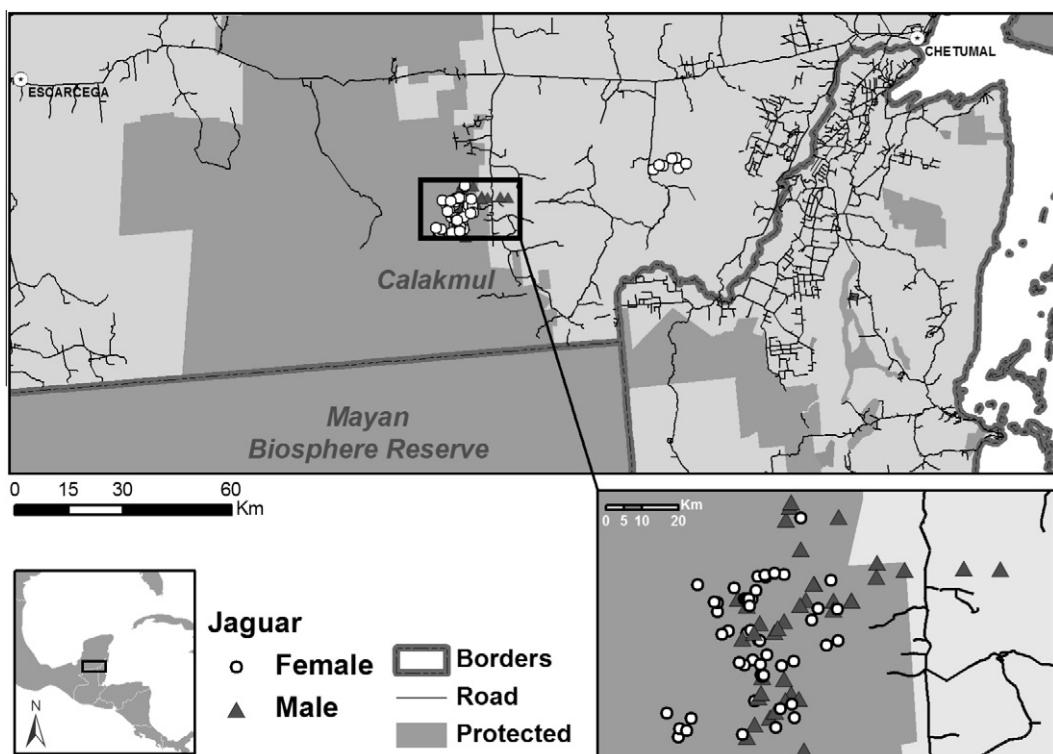


Fig. 2. Independent data set of five jaguars collared with radio-telemetry (three females and one male in Calakmul and one female in the Ejido Caoba).

sex and road distance (S:R) and between gender and land cover (S:L) had the lowest AIC score in 93% of SNPB steps (Table 1). The two “runner-up” models both incorporated S:L interaction, stressing important gender differences in habitat use. The model that excluded sex ranked 6th overall.

Both males and females showed strong selection for tall forests (Fig. 3), but this is the only similarity in their habitat use (Table 2). Females preferred—but made little distinction between—short and tall forests, as shown by their similar, positive parameter distributions (Kullback–Leibler distances $D_{(\text{tall f., short f.})} = 2$, $D_{(\text{short f., tall f.})} = 1$; Fig. 3). Females strongly avoided the two disturbed land covers (i.e., agriculture-cattle and secondary vegetation), for which the distributions of preference were similarly negative ($D_{(\text{agr., sec.})} = 0.6$, $D_{(\text{sec., agr.})} = 0.4$; Fig. 3). There was also a clear difference in female selection of forests from the disturbed land covers, with no overlap between their parameter distributions ($60 < D < 90$). In contrast, males equally avoided agriculture-cattle, secondary vegetation, swamps, and short forest, all with negative parameters and a relatively high overlap between their distributions ($D < 5$, Fig. 3). However, they showed strong preference for tall forest, whose parameter distribution was positive and dissimilar to the other land cover types ($D > 10$). Nonetheless, males showed a tendency to use agriculture-cattle areas in proportion to their availability, since this parameter's 95% confidence interval included zero.

The effect of roads on the probability of occurrence for jaguars also indicated important differences between sexes (slope parameter in Eq. (2) and Table 2). The probability of occurrence for females significantly increased away from roads, whereas roads had a negligible effect on male occurrence (Fig. 4). When comparing the selected model (S:L + S:R) with the best model ignoring gender (L + R), the effect of roads on the probability of occurrence was lost, while short forests appeared as a preferred cover type together with tall forest (Fig. 4).

Table 1

Percentage of trials in which models showed the lowest AIC value (i.e. rank 1), the second lowest (rank 2), and so forth until the 8th lowest value (rank 8). Rows are sorted in increasing order based on the final ranking as shown in the second column. The model variables were: (R) roads distance; (L) land-use (tall forest, short forest, swamps, secondary, agriculture-cattle); (R:S) interaction between sex and road distance; and (L:S) interaction between land-use and sex.

Model	Final rank	AIC ranks (% times per rank)							
		1	2	3	4	5	6	7	8
S:L + S:R	1	93	5	2					
S:L	2	7	78	15					
S:L + R	3		17	83					
L + S:R	4			75	17	8			
L	5			24	61	15			
L + R	6			1	22	77			
S:R	7					68	32		
R	8					32	68		

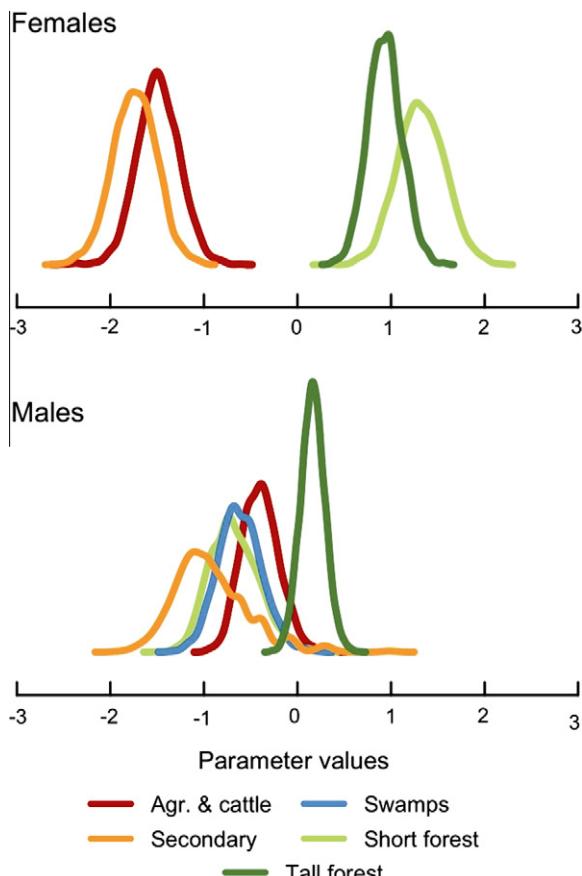


Fig. 3. Distributions of the selected model's parameters linking the logit of the probability of jaguar occurrence to land cover type for males and females at 5 km from the roads. These distributions were derived from the 2000 SNPB steps. The y-axis was omitted for display clarity.

The selected model reliably predicts jaguar habitat, based upon independent validation. The cross-validation area under the ROC curve for females was 0.84 (± 0.70 , 0.95) for true positive and 0.52 (± 0.45 , 0.58) for false positive, and for males was 0.77 (± 0.52 , 0.88) for true positive and 0.51 (± 0.45 , 0.56) for false positive, indicating reasonable discrimination at a probability threshold of occurrence of 0.44 (± 0.30 , 0.58) for females and of 0.53 (± 0.40 , 0.59) for males (Pearce and Ferrier, 2000). The Kappa statistic from the 2000 SNPB iterations fell consistently on what is considered a substantial agreement value based on Landis and Koch's (1977) criteria, with a mean of 0.77 (± 0.74 , 0.80). Assuming that Kappa statistics often underestimate model accuracy in presence-availability models (Boyce et al., 2002), our results indicate that the selected model is therefore highly reliable. Moreover, the validation based on independent radio-telemetry data points of five jaguars not used to develop the model shows that the percentage of data points that were correctly predicted ranged from 85.5% to 96.4%, which includes data points of three females captured in a protected area.

Since the probabilities associated with tall forest and agriculture fell above the ROC threshold for males' habitat, we distinguished two types of habitat for this sex: (i) optimal habitat, characterized by tall forest; and (ii) habitat-conflict areas in agriculture-cattle land-use type (Fig. 5). In agriculture-cattle areas, we expect the propensity of cattle depredation by jaguars and hunting of jaguars by people to be higher. These high conflict areas accounted for 8.6% of males' habitat, with a total of 6378.4 km².

The selected model predicted that the region contained similar coverage of male and female jaguar habitat (Table 3; Fig. 5). However, females had more than twice as many patches as males within the range of 100–10,000 km², and the largest patch of female habitat was more than 10,000 km² smaller than the largest male patch, suggesting a far greater degree of habitat fragmentation for females than males. The model that ignored gender (L + R) yielded a similar total habitat area for females, but it predicted a lower level of fragmentation and overestimated the largest patch size, closer to the largest male habitat patch.

Table 2

Mean and 95% confidence intervals (2.5% and 97.5%) for parameter estimates from the selected model. All values correspond to the linear model that links the probability of occurrence in logit scale (i.e. logit (p_i)) to the covariates. The intercepts are associated with land cover and the slopes to distance to roads (km).

Sex	Slope (distance to roads km)			Intercepts (land cover)			
	Mean	2.5%	97.5%	Types	Mean	2.5%	97.5%
Females	0.129	0.0565	0.203	Agriculture-cattle	-2.784	-3.217	-2.340
				Sec. veg.	-3.034	-3.510	-2.570
				Short forest	0.021	-0.450	0.543
				Tall forest	-0.364	-0.712	-0.002
				Swamps	-	-	-
Males	-0.014*	-0.040	0.017	Agriculture-cattle	-0.270	-0.620	0.146
				Sec. veg.	-0.834	-1.434	0.076
				Short forest	-0.563	-0.998	-0.005
				Tall forest	0.297	0.042	0.555
				Swamps	-0.492	-0.917	-0.013

* Denotes non-significant slopes (i.e. not different from 0).

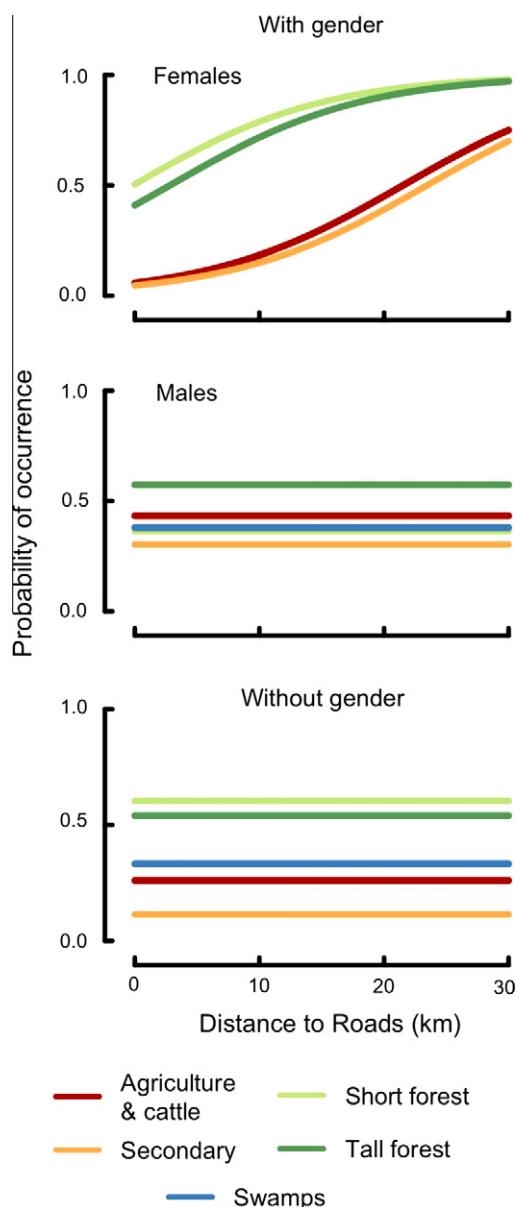


Fig. 4. Probability of male and female jaguar occurrence based on land cover and distance to roads, comparing the selected model (above) with the model without sex (below). The slopes show the change in probability of jaguar occurrence given the distance to roads and the intercept is defined by the land cover types, representing the species land cover preferences.

4. Discussion

4.1. Jaguar habitat inferences

Although largely ignored in wildlife habitat modeling, there are strong differences in habitat use between male and female jaguars. Both sexes selected tall forests and avoided swamps and secondary growth; but males avoided short forests while females preferred them, selecting short and tall forests with similar levels of preference. Also, males used low-intensity agriculture and cattle lands more than females, which are approximately 9% of male's habitat. Short forests are seasonally inundated and support a densely vegetated understory (Ucan et al., 1999). These conditions are generally avoided by human hunters, allowing target species to persist in greater numbers in areas surrounded by high hunting pressure, including communal lands (Reyna-Hurtado and Tanner, 2005) and the edges of protected areas (Rivera pers. communication). During the dry season, when short forests are no longer inundated, we expect female jaguars to use these areas for their greater prey abundance and denser cover, two factors conducive to rearing cubs. Similarly, Broomhall et al. (2004) found that female cheetahs used dense woodlands more frequently than males, areas which had greater prey densities and whose vegetation structure provided refuge from cub predators.

Roads are an important but variable constraint on jaguar movement. Female jaguars avoided roads while males seemed unaffected by them. Similar gender differences in road-avoidance have been found in other large carnivore species. Mace et al. (1996) found that female grizzly bears (*Ursus arctos*) in Montana (USA) occupied ranges with sparser road densities than males, and Maehr (1997) found that roads significantly restricted habitat of female Florida panthers (*Puma concolor coryi*). These marked sexual differences could respond to the restrictive movement of jaguar females, compared to that of males (Schaller and Crawshaw, 1980) as well as to the reduction of female survivorship and reproductive success near roads, as shown for Amur tigers (*Panthera tigris*) (Kerley et al., 2002). Therefore, it is not surprising that roads not only limited habitat for female jaguars, but were also an important factor in fragmenting it.

In contrast, the higher tolerance of males to human-modified landscapes can increase their exposure to antagonistic interactions with local human inhabitants. For instance, mortality due to direct persecution and hunting as well as car collisions is considerably higher in male carnivores (Maehr, 1997; Linnell et al., 1999; Rabenowitz, 1986).

All models were fit based on a small number of jaguars, with males captured in the borders of protected areas and females captured in ejidos (communal lands) with higher road density and

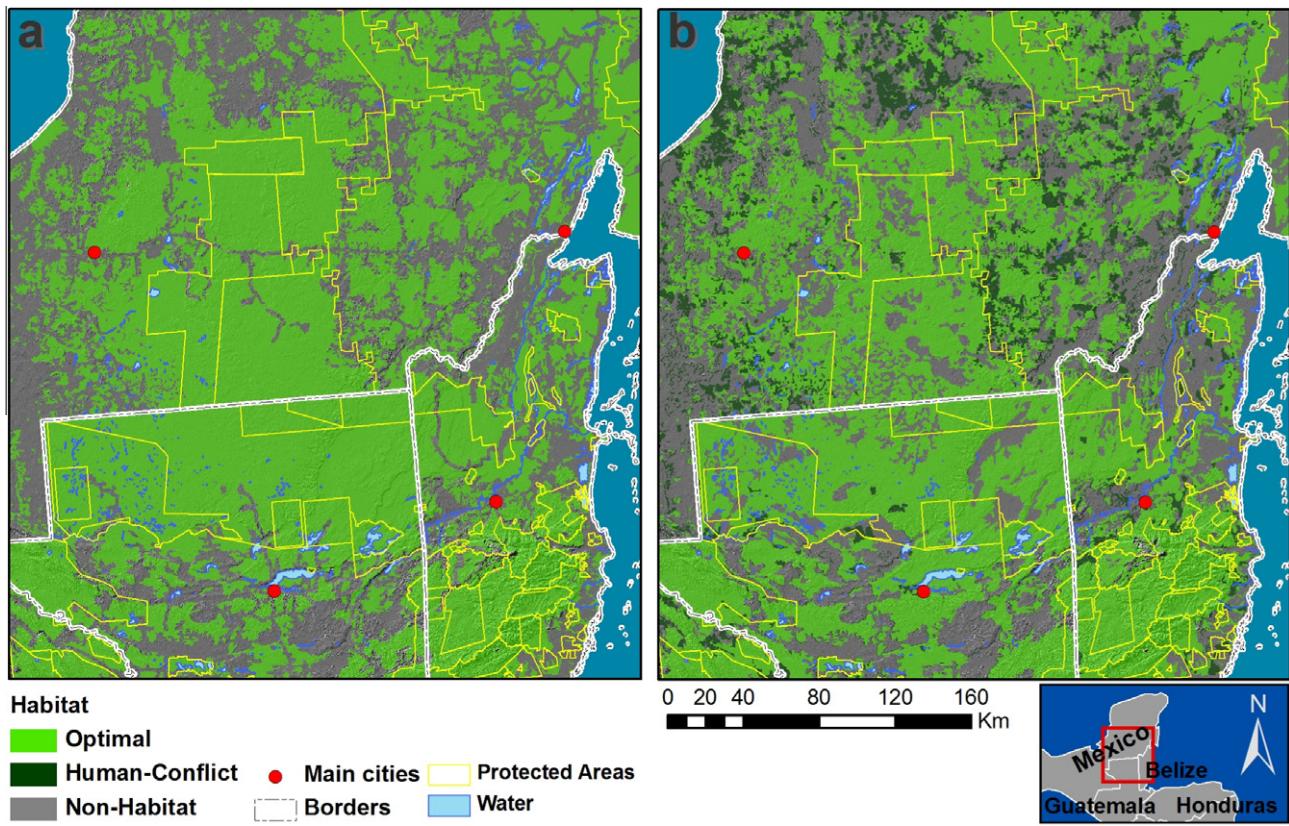


Fig. 5. Habitat maps for female (a) and male (b) jaguars in the study area.

Table 3

Male and female jaguar habitat patch metrics for the model that includes sex differences and the model without this differences. Patch areas are in km².

Sex	Total area	Patch metrics			Patch number by size and category			
		Number of patches	Largest patch area	Average patch area	<100	100–1000	1000–10,000	10,000–100,000
Female	76927.34	616	43,679	124.8	568	42	5	1
Males	73147.94	527	57,297	138.8	510	14	2	1
Without	77309.66	354	55,451	218.3	334	15	4	1

more productive land-use types. Although at first glance the observed differences in habitat selection between sexes might appear to be due to a sampling bias, further inspection suggests that such an artifact is unlikely. Assuming a dominant sampling bias, females should appear as having a greater tolerance to roads and low-scale agriculture, since they are more exposed to these landscape features. However, regardless of the greater availability of protected areas within male home ranges, males still significantly used the communal lands outside de protected area (Fig. 1) which are areas with high human influence – whereas females significantly limited their habitat use to the remaining pristine patches of forest in the region. Perhaps more convincingly still, the selected model accurately predicted a set of independent radio-telemetry locations, which included data points from three females captured inside the Calakmul protected area (Fig. 2).

Nonetheless, it is important to note that sampling bias is always a consideration in studies with such small samples. We fit our model on only six jaguars and thus the model is expected to have limited ability to depict individual variations. For example, females' habitat use is expected to change during lactation and cub rearing, while males are expected to disperse to a more widely during their juvenile years than as adults. Resolving such fine detail in movement and habitat preference patterns will require more

observations of a greater number of individuals, and over longer periods of time. Nevertheless, our model was able to accurately predict the locations of five jaguars that were independently-collected using radio-telemetry methods.

4.2. Conservation and management implications

Ignoring sex-related differences in environmental preferences diminishes the ability of habitat models to inform management of jaguars and other large carnivores. For example, our models that did not incorporate sex failed to capture the effect of roads and low-intensity agriculture and cattle ranching on jaguar habitat use, blurred the distinction in their use between short and tall forest, and greatly underestimated fragmentation of female jaguar habitat. So clearly those models ignore basic ecological traits that differ among sexes and that have strong conservation implications. In contrast, sex-specific models more finely resolved the complex habitat requirements of these large carnivores, potentially leading to more effective conservation policies. The selected model discriminated male use of low-intensity agriculture and cattle, explaining the greater exposure of male jaguar to human activities and more frequent occurrence of cattle predation by males than by females (Rabinowitz, 1986; Linnell et al., 1999). Identification of

these conflict zones could be an important tool to identify key areas for the development of management plans to reduce human-jaguar conflicts.

Identifying conflict zones could facilitate efforts by local communities, NGOs and governments to reduce cattle predation and jaguar mortality in the region. The identification of both habitat and conflict zones is a strong guidance for the development of alternative conservation-development projects, beyond merely subsidizing cattle ranching and agriculture. For instance, the Mexican Ministry of Agriculture and Livestock recently launched a new program named "PROGRAN" (Sustainable Livestock, Beekeeping, and Land Management Program), which includes a Cattle Insurance Program for local landowners to minimize the impact of large carnivore predation (SAGARPA, 2009). PROGRAN could benefit from a model capable of identifying areas more likely to need attention. In this area it could be useful to apply results from previous studies that have outlined alternatives to reduce cattle predation by jaguar and puma, including: impeding the ability of livestock to enter forests, installing electric fences around maternity pastures, and excavating water retention ponds specifically for prey, among others (Hoogesteijn et al., 1993; Polisar et al., 2003).

Other regional plans, such as the Puebla – Panama Plan, which is lead by Mexico, involve the incursion of roads through protected areas to interconnect cities and archeological centers (Conde, 2008). Our results suggest that the planned roads and their subsequent land-use changes will further reduce and fragment female jaguar habitat and increase the number of jaguar-human conflicts zones in the region. Although small-scale agriculture and cattle ranching did not appear to significantly limit male habitat use in this study, the effect of larger and/or more intensive agriculture and livestock operations needs to be further explored. This is especially important given the potential increase of these land uses due to the different development plans in the region. Given the questionable economic and ecological effects of road investments in the Mayan forest (Conde et al., 2007), we suggest that transport investments should be focused to modernize the existing road network instead of the construction of new roads. The construction of roads that will bisect the Mayan Biosphere Reserve will significantly fragment the largest patch of tropical forest in Central America, which in turn will have strong repercussions not only on jaguar populations but in many other species in a key region for biodiversity conservation worldwide.

The future of the Jaguar and many other species in the largest remaining tropical forest North of Colombia depends on a better understanding of their requirements and needs. Our study provides solid conservation management lessons that are a building block for the long-term conservation of these unique forests and its magnificent biodiversity, including jaguars.

5. Conclusions

Sex-specific behaviors result in different patterns of habitat use between male and female jaguars. Whereas females avoid human-dominated areas, male jaguars are more general in their habitat use. These differences in behavior and environmental preference lead to different spatial patterns of habitat as well, with the habitat specificity of females leading to a less extensive, more fragmented habitat distribution than for males. Specifying sex in habitat modeling better informs policies to avoid further habitat loss and fragmentation and could allow more precise identification of carnivore-human conflicts areas. Our results identify areas for the development of community-based programs to reduce cattle predation, and show that the construction of roads inside the Mayan Biosphere Reserve will severely fragment the largest patch of jaguar habitat in Central and North America.

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