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Arroyo-Arce, Stephanny; Guilder, James; Salom-Pérez, Roberto
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Habitat features influencing jaguar *Panthera onca* (Carnivora: Felidae) occupancy in Tortuguero National Park, Costa Rica

Stephanny Arroyo-Arce^{1*}, James Guilder² & Roberto Salom-Pérez³

1. Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional, 1350-3000 Heredia, Costa Rica; sturnina@gmail.com

2. Global Vision International/GVI Costa Rica, 230-60601 Quepos, Costa Rica; jamesguilder@gmail.com

3. Panthera Costa Rica, 8-3870-1000 San José, Costa Rica; rsalom@panthera.org

* Correspondence

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Abstract: Habitat characteristics and human activities are known to play a major role in the occupancy of jaguars *Panthera onca* across their range, however the key variables influencing jaguar distribution in Tortuguero National Park, Costa Rica, have yet to be identified. This study evaluated jaguar occupancy in Tortuguero National Park and the surrounding area. Jaguar detection/non-detection data was collected using digital camera traps distributed within the boundaries of the protected area. Local community members were also interviewed to determine jaguar occurrence in the Park's buffer zone. Occupancy models were then applied to identify the habitat characteristics that may better explain jaguar distribution across the study area. From June 2012 to June 2013, a total of 4 339 camera trap days were used to identify 18 individual jaguars inside the protected area; 17 of these jaguars were exclusively detected within the coastal habitat, whilst the remaining individual was detected solely within the interior of the Park. Interviewees reported 61 occasions of jaguar presence inside the buffer zone, between 1995 and 2013, with 80% of these described by the communities of Lomas de Sierpe, Barra de Parismina and La Aurora. These communities also reported the highest levels of livestock predation by jaguars (85% of attacks). In the study area, jaguar occurrence was positively correlated with the seasonal presence of nesting green turtles *Chelonia mydas*, and negatively correlated with distance to the Park boundary. Our findings suggested that the current occupancy of the jaguar in the study area may be a response to: **1)** the vast availability of prey (marine turtles) on Tortuguero beach, **2)** the decline of its primary prey species as a result of illegal hunting inside the Park, and **3)** the increase in anthropogenic pressures in the Park boundaries. Rev. Biol. Trop. 62 (4): 1449-1458. Epub 2014 December 01.

Key words: *Panthera onca*, marine turtles, human pressures, occupancy models, Tortuguero National Park.

Large mammalian carnivores commonly need vast amounts of space (Cardillo, Mace, Jones, Bielby, & Bininda-Emonds, 2005), and this necessity has driven many of these species to become some of the most threatened in their class (Ceballos, Ehrlich, Soberon Salazar, & Fay, 2005). Successful conservation strategies thus require a detailed understanding of the factors that influence large carnivore abundance, distribution and habitat use, both inside and outside of protected areas. Predators require suitable hunting areas with either high prey abundance or easy prey 'catchability' to fall

within their home ranges (Hopcraft, Sinclair, & Packer, 2005). Such areas ensure the necessary energy requirements are satisfied with, ideally, minimal exposure to the risk of predation (Hayward & Kerley, 2005). Humans commonly hunt large carnivores and an increase in human presence can therefore be considered to equate to an increased predation risk (Wolf & Ale, 2009). Globally, large predators have been shown to demonstrate human avoidance, not only due to the threat of being hunted but also as a result of habitat degradation and a depletion of natural prey species (Whittington, Clair,

& Mercer, 2005; Johnson, Vongkhamheng, Hedemark, & Saithongdam, 2006; Gavashe-lishvili & Lukarevskiy, 2008; Chávez, 2010; Conde et al., 2010).

Across their range, jaguars (*Panthera onca*) take advantage of a relatively large number of prey species (Rabinowitz & Nottingham, 1986; Azevedo, 2008) with large and/or medium-sized prey species often the prominent items in the diets of jaguar populations (Chinchilla, 1997; López-González & Miller, 2002; Núñez, Miller, & Lindzey, 2002; Azevedo, 2008). Some individual jaguars may display selective tendencies with regards larger prey species (Weckel, Giuliano, & Silver, 2006). However, the jaguar is widely perceived as an opportunistic predator (Seymour, 1989; Núñez et al., 2002). This opportunism is considered a strategy to optimize foraging success, and enables jaguars to adapt their hunting behavior in accordance with prey availability. Jaguars will often shift their home ranges and activity patterns, in response to those of an abundant, accessible or more favorable prey (Rabinowitz & Nottingham, 1986; Carrillo, 2000).

Jaguars are also known to occupy a wide range of habitats (Seymour, 1989; Sunquist & Sunquist, 2002). Optimal patches generally incorporate a combination of dense forest cover, close proximity to water and high prey availability. In addition, increased distance from human settlement enhances habitat suitability for jaguars as has been seen with many other large carnivores (Cullen, 2006; Chávez, 2010; Conde et al., 2010). Local declines in the abundance of natural prey, due to illegal hunting or habitat degradation, increase the likelihood of jaguars exploiting suboptimal territories within a human-dominated matrix and heighten the probability of jaguar-livestock conflict (Hoogestijn, Hoogestijn, & Mondolfi, 1993; Núñez et al., 2002). Elevated livestock predation rates result in aggravated levels of jaguar persecution, with more jaguars being killed in retaliation for the economic losses suffered by local community members (Núñez et al., 2002; Hoogestijn & Hoogestijn, 2010).

Previous research on the jaguar population of Tortuguero National Park has fundamentally focused on the burgeoning predator-prey relationship between marine turtles and the jaguar. These studies have documented an increase in marine turtle predation, coinciding with an increase in jaguar presence on Tortuguero beach (Carrillo-Jimenez, Morera-Avila, & Wong-Reyes, 1994; Troëng, 2000; Verissimo, Jones, Chaverri, & Meyer, 2012; Arroyo-Arce, 2013). The recent habitat degradation that has occurred across the Park's buffer zone (Troëng, 2000) may have played a role in driving the jaguars towards the coastal habitat, further compounding jaguar exploitation of the seasonally abundant nesting marine turtles. The aim of this study was to identify the habitat features that are influencing current jaguar distribution inside Tortuguero National Park, as well as across the areas immediately bordering the Park.

MATERIALS AND METHODS

Study site: Tortuguero National Park is located on the Northeastern Caribbean coast of Costa Rica (10°32'28" N - 83°30'08" W, Fig. 1), and encompasses an approximate terrestrial area of 45 755ha. The predominant ecosystem is the Tropical Wet Forest (Holdridge, 1969). Elevation ranges from 0m to 311m above sea level. The average temperature is between 25°C and 30°C, with a mean annual precipitation of 6000mm (Bermudez & Hernandez, 2004). The Park is bordered to the Northwest by Barra del Colorado Wildlife Refuge and Tortuguero Protected Zone. The Western and Southern edges of the Park are bordered by a number of communities that are economically dependent on crop farming (mainly banana and pineapple), extensive livestock farming (meat and milk) and to a lesser extent, tourism (Ling, 2002; Bermudez & Hernandez, 2004).

Four species of marine turtles nest along the Park's 30km stretch of beach, which extends from the Tortuguero River mouth in the North, to the Jalova River mouth in the South.

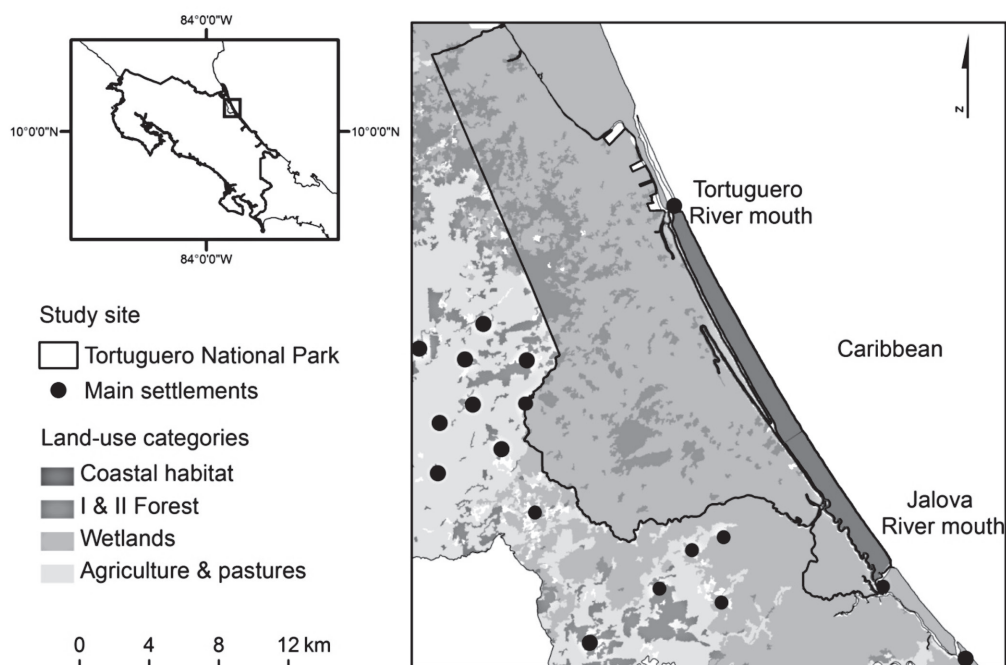


Fig. 1. Tortuguero National Park and its surrounding area, Costa Rica.

The Park is a key nesting site for the endangered green turtle *Chelonia mydas* (Troëng & Rankin, 2005; IUCN, 2013). Green turtle nesting season occurs from June to November with a peak season between mid-July and mid-October (Tiwari, Bjorndal, Bolten, & Bolker, 2006; Atkinson, Nolasco del Aguila, & Harrison, 2011). The Park also hosts a small nesting population of vulnerable leatherback turtles *Dermochelys coriacea* (Troëng, Chacón, & Dick, 2004; IUCN, 2013). Leatherbacks nest predominantly from March through May (Troëng, Harrison, Evans, De Haro, & Vargas, 2007). The critically endangered hawksbill turtle *Eretmochelys imbricata* (Troëng, Dutton, & Evans, 2005; IUCN, 2013) and the endangered loggerhead turtle *Caretta caretta* (Troëng et al., 1998; IUCN, 2013) nest sporadically on Tortuguero National Park beach.

Camera trapping: Jaguar presence in Tortuguero National Park was assessed using camera traps, between June 2012 and June 2013. A total of 25 trap stations were active for

continuous periods of 3-12 months, covering an area of approximately 189km². Of the 25 trap stations, 11 were located within the forest interior and 14 were located within the coastal habitat. Consecutive trap stations were separated by a minimum of 2km (Fig. 2) and each station consisted of one digital camera trap (models Moultrie M100 GameSpy Digital Camera and Covert Reveal 8.0 Game Cam). Cameras were placed 60cm above the ground, in areas where jaguar detection probability was considered to be high (e.g. trails). Cameras were set on a 15s delay between successive photos, and were checked every 15 days to collect memory cards, replace batteries if required and ensure the equipment is still functioning. Each trap station had a scent lure (Calvin Klein's Obsession) placed on a stick in front of the camera trap in an attempt to increase the time jaguars stood in front of the camera; increasing the sharpness of the image and thus facilitating the identification of individuals through their coat pattern. All photographed jaguars were referenced against a pre-existing photographic

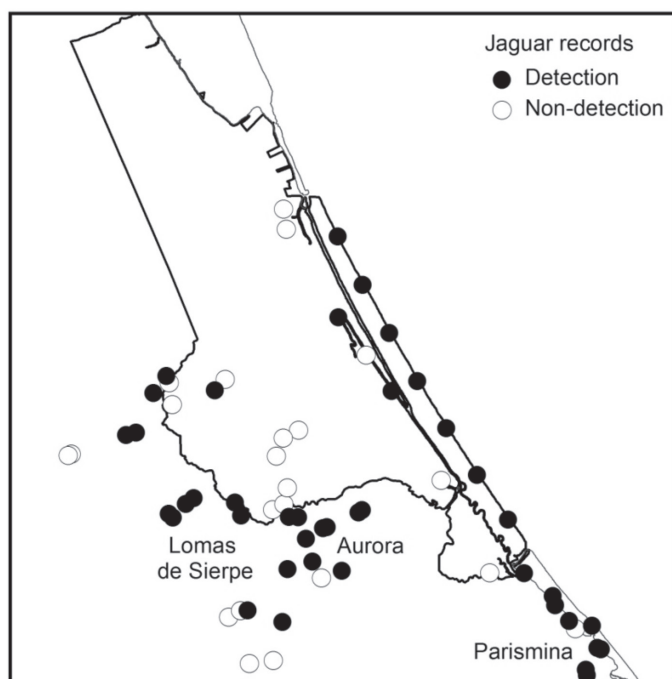


Fig. 2. Jaguar *Panthera onca* records obtained through camera trapping and interviews in Tortuguero National Park and its surrounding area, Costa Rica.

database (Global Vision International, unpublished) for individual identification.

Due to logistical constraints (e.g. flooding, equipment theft, warfare and security concerns), the Northwestern sector of the Park was not surveyed.

Social method: Interviews were conducted between January and March, 2013 in the areas surrounding the Park, specifically the main settlements within the Canton of Pococí (Fig. 1). This area was divided into cells of 5x5km with each cell functioning as a sampling unit. The size of the grid was based on the approximate home range size of the jaguar (Zeller, Nijhawan, Salom-Pérez, Potosme, & Hines, 2011).

The number of interviews per sampling unit (replicates) ranged from one to six. The number of interviews depended on the number of inhabited ranches (e.g. if a sampling unit included eight ranches but only five were inhabited, then only five interviews were

conducted). Interviewees were selected using snowball sampling (Marshall, 1996), allowing us to identify community members who have had some interaction with a jaguar (e.g. sighting, livestock depredation). Interviewees were all required to have lived in the area for a minimum of one year, and had to be able to demonstrate at least a basic knowledge of the local fauna.

Interviews were carried out using the questionnaire and protocol established by Zeller et al. (2011). The interview incorporated questions on jaguar and prey presence, livestock predation, and threats to jaguars and their prey species.

Occupancy modeling: We used site-occupancy models to assess jaguar occurrence across the Tortuguero National Park and its buffer zone using the data collected via camera traps and interviews. These models estimate the probability of occurrence (Ψ) and detection (ρ), and enable the inclusion of habitat covariates

that most likely influence the distribution of the jaguar in the study area (see MacKenzie et al., 2002; MacKenzie et al., 2006; Zeller et al., 2011 for a thorough discussion). Models include effects of covariates in occurrence maintaining a constant probability of detection (e.g. $\Psi(\text{covariate})$, $p(\text{constant})$).

Covariates were selected based on prior knowledge of jaguar ecology and of the study area (Table 1). We limited the number of covariates to those with greater ecological relevance in order to avoid ambiguity (Long, Donovan, Mackay, Ziekinski, & Buzas, 2010). Digital layers for the land-use categories and settlements of Costa Rica were retrieved from the Digital Atlas of Costa Rica (Ortiz, 2008), and analyzed with ArcMap (v 10; Environmental Systems Research Institute, Redlands, CA, USA) software. Marine turtle data was estimated using the pre-existing database (Global Vision International, unpublished).

The best models were selected based on the Akaike Information Criterion adjusted for

small sample sizes (AIC_c). For each model, we computed delta AIC_c (Δ_i) and Akaike weights (w_i) to determine the strength of evidence for each model (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011). Modeling analysis was performed with the program PRESENCE (v 5.7; USGS-PWRC, Laurel, MD, USA).

RESULTS

Camera trapping: After a total of 4 339 camera trap days, we were able to identify 18 jaguars inside Tortuguero National Park. This included 7 males, 9 females, 1 cub and 1 unsexed adult. Jaguars were detected at 44% of the stations. Only one jaguar (female) was detected within the interior of the Park, and this individual was the only one not captured within the coastal habitat. All other individuals were captured exclusively within the surroundings of the coastal habitat (Fig. 2).

TABLE 1
Habitat covariates and *a priori* predictions about their influence on habitat occupancy of jaguars *Panthera onca* in Tortuguero National Park and its buffer zone, Costa Rica

Covariate	Code	Description	Predictions for occupancy
Primary Forest (%)	PF	Percentage of primary forest	Primary forest favors jaguar
Secondary Forest (%)	SF	Percentage of secondary forest	Secondary forest favors jaguar
Wetlands (%)	WE	Percentage of wetlands	Wetlands favors jaguar
Coastal Habitat (%)	CO	Percentage of coastal habitat	Coastal habitat favors jaguar
Pastures (%)	PA	Percentage of pastures	Pastures disfavors jaguar
Plantations (%)	PL	Percentage of plantations	Plantations disfavors jaguar
Distance to main town (km)	Town	Euclidean distance from the nearest town to centroid of a sampling unit	Human presence disfavors jaguar
Distance to the coastal habitat (km)	Beach	Euclidean distance from beach edge to centroid of a sampling unit	Coastal habitat favors jaguar
Distance to the Tortuguero National Park boundary (km)	Park	Euclidean distance from Park edge to centroid of a sampling unit	Tortuguero National Park favors jaguar
Green turtles tracks (%)	Green	Percentage of green turtle <i>Chelonia mydas</i> tracks during the nesting season 2012	Green turtle favors jaguar
Leatherback turtles tracks (%)	Leatherback	Percentage of leatherback turtle <i>Dermochelys coriacea</i> tracks during the nesting season 2012	Leatherback turtle favors jaguar

Green turtle nesting was the only covariate included in the top model explaining jaguar occurrence (Table 2). This model suggests that jaguar occupancy is positively correlated with green turtle nesting in Tortuguero National Park. As expected, the detection probability was higher in those sites where green turtles were present.

Social data: We conducted 42 interviews across 11 different settlements (Fig. 2). Interviewees (98% males) ranged in age from 15-77 years (mean±SD=48±15 years), and had resided in the study area from 1-64 years (mean±SD=25±17 years). The majority of interviewees were engaged in agricultural activities (67%). Sixty-one reports of jaguar presence were documented; 34% from 1995 to 2011, 41% during 2012, and 25% were recorded in the first quarter of 2013.

Distance to the Park boundary was the only covariate included in the top model for the jaguar (Table 2). This model suggested that jaguar occupancy is negatively associated with distance to the limit of the Park. Detection probability was therefore higher in the communities located near the Park edge. Lomas de Sierpe, Barra de Parismina and La Aurora comprised 80% of jaguar presence reports (Fig. 2).

Interviewees (62%) identified hunting of small and medium-sized mammals as the main threat faced by jaguars, with this being more problematic in the communities of Lomas de Sierpe, Barra de Parismina and La Aurora. They also identified livestock predation as the only source of conflict between people and jaguars. Interviewees (40%) reported suffering jaguar predation on livestock and pets, with a total of 19 attacks reported between 1995 and 2013. Approximately 85% of these attacks occurred in the communities of Lomas de Sierpe, Barra de Parismina and La Aurora. A noteworthy case was the small ranch located within the protected area's coastal habitat. This property is situated close to the Jalova River mouth and has yet to be expropriated by the government. A small number of cattle are still present here and although the ranch is located in an area with a high concentration of jaguars, only three livestock depredation events have been reported over the last 15 years (in 2010, 2012 and 2013).

Most interviewees (75%) had a positive attitude toward the jaguar; 20% expressed that jaguar presence had a negative effect on their communities, and 5% had a feeling of indifference towards the species. All interviewees with negative attitudes had lost animals (e.g.

TABLE 2
Top models and untransformed coefficients of covariates for jaguar *Panthera onca* in Tortuguero National Park and its buffer zone, Costa Rica

Sector	Data source	Models	AIC _c ¹	ΔAIC _c ²	AIC _c w _i ³	k ⁴	Untransformed coefficients of covariates (standard errors)		
							Green	Town	Park
Tortuguero National Park	Camera trapping	Ψ (green), p (.)	491.12	0.00	0.31	3	17.25 (10.28)	-	-
		Ψ (town), p(.)	491.66	0.54	0.24	3	-	0.20 (0.12)	-
		Ψ (green+town), p (.)	491.77	0.65	0.23	4	13.79 (10.74)	0.15 (0.13)	-
Buffer zone	Interviews	Ψ(park), p (.)	181.94	0.00	1	3	-	-	-0.40 (0.30)

Covariates: green, percentage of green turtle *Chelonia mydas* tracks during the nesting season 2012; town, euclidean distance from the nearest town to centroid of a sampling unit; park, euclidean distance from Tortuguero National Park edge to centroid of a sampling unit.

¹AIC_c=Akaike Information Criterion.

²ΔAIC_c=difference in AICc value relative to the top model.

³AIC_cw_i=AICc weight.

⁴k=number of parameters in the model.



cattle, pets) to predation. Interviewee data also suggested that at least four jaguars have been killed between 2006 and 2013 in retaliation to the economic losses caused by jaguar depredation of domestic animals.

DISCUSSION

Jaguar occupancy in Tortuguero National Park strongly correlates with the seasonal availability of green turtles nesting on Tortuguero beach. This green turtle nesting population is the largest remaining green turtle rookery in the Atlantic, with an estimated 17 402-37 290 females nesting per year (Troëng & Rankin, 2005). Jaguar selection for the coastal habitat may have passed from generation to generation, as the local population learned to locate and exploit the temporal and spatial fluctuations in prey availability (Rabinowitz & Nottingham, 1986; Gittleman, 1989; Barnes, 1990; Carrillo, Fuller, & Sáenz, 2009). Tortugueros' jaguars appear to now restrict their movement patterns to the coastal habitat during green turtle nesting season in a strategy to maximize the exploitation of a very abundant and attainable prey. Outside of turtle nesting season, results suggest that some individuals will remain within the coastal habitat, whereas others relocate to alternative sectors of the Park or its surrounding areas (Arroyo-Arce, personal observation).

A high presence of jaguars in the coastal habitat could also be related to the habitat degradation that has occurred across the Park's buffer zone as a result of human activity (Troëng, 2000). Anecdotal evidence (M. Zúñiga, personal communication, February 6, 2013) suggests, in the early 1990s, there was an increase in agricultural activities (large-scale banana and pineapple plantations) in the communities located outside the boundaries of the Park. This expansion of the agricultural frontier coincides with the increase in the number of marine turtles predated by jaguars; from four female green turtles in 1997 (Troëng, 2000; Veríssimo et al., 2012) to approximately 300 females in 2013 (Global Vision International, unpublished). Another factor potentially

influencing the jaguar's coastal habitat preference is the possible decline of alternative or primary species (*Tayassu pecari*, *Mazama americana*, *Cuniculus paca* and *Dasyprocta punctata*), due to illegal hunting inside the Park (Troëng, 2000; Veríssimo et al., 2012; Arroyo-Arce, 2013). These anthropogenic pressures may be causing the jaguar to increasingly select marine turtles as prey, and as a direct result, occupy the coastal habitat to a greater extent than the other sectors of the Park.

Communities with higher levels of human-jaguar conflict were located in the Southwest sector of the Park. This was most likely due to their close proximity with the Park boundary where a higher presence of jaguars has been documented; habitat characteristics that have both previously been suggested to increase livestock vulnerability to jaguar predation (Amit, Rojas, Alfaro, & Carrillo, 2009; Michalski, Boulhosa, Faria, & Peres, 2006). These communities were also located in areas where hunting and deforestation were more prevalent. Some authors (Miller & Everett, 1986; Núñez et al., 2002; Hoogestijn & Hoogestijn, 2010) suggest that a decline in prey species, as a result of habitat loss and illegal hunting, could force jaguars to seek food outside the forest habitat and select livestock, or even pets, as an alternative prey. Therefore, if natural prey species were abundant, there would be fewer livestock predation events. The few attacks that have occurred on the farm located inside the Park (a high jaguar and green turtle density area) support this hypothesis. Conflict inside the study area could also be related to the presence of jaguars with limited capabilities to hunt such as cubs, old or injured individuals (Soto et al., 2008; Hoogestijn & Hoogestijn, 2010).

Although most interviewees had a positive perception towards the jaguar, and livestock losses may not seem significant when compared with other studies, there is still a residual feeling of negativity, primarily associated with the loss of livestock or pets. This has led to the persecution of the jaguar as retaliation for economic losses. The elimination of jaguars as a strategy to reduce the conflict constitutes

one of the major threats to the species in Latin America (Hoogestijn & Hoogestijn, 2010), and is one of the main factors related to the disappearance of the species outside protected areas (Nowell & Jackson, 1996).

This study provides the first attempt to determine the factors influencing jaguar occupancy in Tortuguero National Park. The results provide critical information about the interaction of this apex carnivore with local communities and one of its main prey species; marine turtles nesting on Tortuguero beach. This study has highlighted a number of important questions, including: **1)** do jaguars pose a considerable threat to the Tortuguero marine turtle population? **2)** is Tortuguero National Park's jaguar population approaching carrying capacity? **3)** is there a sufficient source of alternative prey species to support the jaguar population?. Further understanding of these issues will be required for an effective management of the local jaguar population, as well as the marine turtle species that nest in Tortuguero National Park.

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RESUMEN

Características del hábitat que influyen en la presencia del jaguar *Panthera onca* (Carnivora: Felidae) en el Parque Nacional Tortuguero, Costa Rica. Las características del hábitat y las actividades humanas juegan un papel importante en la presencia del jaguar *Panthera onca* en toda su área de distribución, sin embargo, las variables clave que influyen en la distribución del jaguar en el Parque Nacional Tortuguero, Costa Rica, aún no se han

identificado. Por lo tanto se evaluó la presencia del jaguar *Panthera onca* en este parque nacional y su área de amortiguamiento. Se recolectaron datos de detección/no detección del jaguar mediante cámaras trampa ubicadas dentro del parque, y se realizaron encuestas en las comunidades del área de amortiguamiento. Posteriormente, se emplearon modelos de ocupación para identificar los atributos del hábitat que mejor explicaban la presencia del felino en el área. Se identificaron 18 jaguares dentro del parque, de los cuales 17 estuvieron exclusivamente en el hábitat costero. En el área de amortiguamiento, las comunidades con una mayor presencia del felino (Lomas de Sierpe, Barra de Parismina y La Aurora) coincidieron con las zonas más conflictivas, en relación a la cacería y la depredación de jaguar sobre el ganado. La probabilidad de ocupación del jaguar se incrementa a medida que aumenta la presencia de la tortuga verde *Chelonia mydas*, y disminuye conforme la distancia al límite del parque se incrementa. Nuestros resultados indican que la actual presencia del jaguar se debe a: **1)** la alta disponibilidad de presas (tortugas marinas) en el hábitat costero, **2)** la disminución de las principales especies presa como resultado de la cacería y **3)** al incremento de las actividades humanas en el área de amortiguamiento del parque.

Palabras clave: *Panthera onca*, tortugas marinas, presiones humanas, modelos de ocupación, Parque Nacional Tortuguero.

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