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Population trends and site occupancy estimations of a jaguar population
in a heterogeneous landscape in the Selva Maya in Mexico

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Universidad Autónoma de Querétaro
Facultad de Ciencias Naturales

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Que como parte de los requisitos para obtener
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Presenta:
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Dirigido por:
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Querétaro, Qro. A 08 de Mayo del 2023

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por

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Resumen

Determinar la tolerancia que los grandes carnívoros como el jaguar (*Panthera onca*) tienen a los distintos disturbios tanto ambientales como antrópicos y la respuesta de las poblaciones a estas a través del tiempo es de suma importancia para los tomadores de decisiones priorizando esfuerzos de conservación y manejo para proteger a la especie en cuestión. Los estudios a largo plazo también son importantes para evaluar los cambios en la estructura poblacional y así comprender procesos fundamentales de la especie estudiada como la supervivencia, la reproducción y la emigración e inmigración temporales. Estas estimaciones de historia de vida son difíciles de obtener para los mamíferos inconspicuos y longevos con densidades poblacionales bajas, como los jaguares. El objetivo de este trabajo es determinar la tolerancia de los jaguares a las perturbaciones humanas, incluyendo las modificaciones de hábitat y a diversos grados de disponibilidad de presas en un paisaje heterogéneo de la selva Maya en México. Hipotetizamos que los jaguares tendrán poca tolerancia por la degradación del hábitat y la falta de presas naturales. Usamos la probabilidad de ocupación de sitio y la estabilidad de la población a largo plazo como indicadores de esta tolerancia. Evaluamos también la probabilidad de ocupación de sitio de cinco de sus presas más comunes en la región para conocer su estado actual: armadillo (*Dasypus novemcinctus*), coatí (*Nasua narica),* paca (*Cuniculus paca*), venado cola blanca (*Odocoileus virginianus*) y pecarí de collar (*Dicotiles tajacu*). Además, para conocer el estado de conservación de estas especies a mayor escala, proyectamos las ocupaciones de presas y jaguares en un paisaje de 5993 km^2 según el tipo de hábitat. Encontramos que la probabilidad de ocupación promedio para los jaguares fue de 35% ± 0.07 y el predictor más fuerte de la ocupación del jaguar fue un efecto positivo de la ocupación del pecarí de collar. Estos hallazgos respaldan estudios previos que muestran que la distribución de los depredadores está influenciada en gran medida por la disponibilidad de sus presas, incluso en hábitats degradados, y subyace la necesidad esencial de incorporar planes de protección para las especies presa en las estrategias de conservación del jaguar. En cuanto al seguimiento a largo plazo de esta población de jaguares, estimamos el número de individuos, las tasas de detección, la proporción de sexos y las residencias individuales. Utilizando las herramientas de Global Forest Watch, encontramos que los machos perdieron un total de 10.41 % de la cubierta forestal de su hábitat en el área de estudio, mientras que las hembras perdieron un 1.99 % de la cubierta forestal de su hábitat en el área de estudio área entre 2010 y 2020. El inicio de la deforestación aguda en el área coincide con el establecimiento de comunidades menonitas. Durante este tiempo también observamos frecuencias de detección erráticas entre los jaguares machos estudiados, lo que sugiere un repentina inestabilidad en esta población de jaguares. Mediante estos dos estudios, confirmamos nuestra hipótesis de que la ausencia de presas y de hábitat propicio ejerce una limitante en la presencia del jaguar dentro de nuestra área de estudio, demostrándonos así su baja tolerancia a estas disrupciones. El continúo deterioro y fragmentación del hábitat, así como la disminución de la presencia de presas naturales en el área de estudio pone en riesgo la supervivencia de esta pequeña pero estable población de jaguares en el sureste de México.

Abstract

In order to prioritize the conservation and management efforts to protect jaguars (*Panthera onca*), it is of utmost importance to determine their tolerance in face of anthropogenic and environmental disturbances and how these populations respond to these disruptions over time. Long term studies that assess changes in the structure of populations are also important because they help us understand fundamental processes of the species in question such as survival, reproduction and temporary emigration and immigration. These life history estimates are difficult to obtain for secretive, long-lived mammals that occur at low densities such as jaguars. The objective of this work is to determine the tolerance that jaguars have for human disturbances, habitat modifications and varying degrees of prey availability in a heterogeneous landscape in the Selva Maya of Mexico.We hypothesize that jaguars will have little tolerance for degraded habitats and a lack of prey. We use site occupancy probability and the long-term stability of the population studies as indicators for this tolerance. We also assessed the occupancy probability of five of their most common prey species in the region: armadillo (*Dasypus novemcinctus*), coati (*Nasua narica*), paca (*Cuniculus paca*), white-tailed deer (*Odocoileus virginianus*), and collared peccary (*Dicotyles tajacu).* Additionally, we projected prey and jaguar occupancies onto a 5,993 km2 landscape based on the habitat type in the area. We found that the average occupancy probability for jaguars was 35% ± 0.07 and the strongest predictor of jaguar occupancy was a positive effect of collared peccary occupancy. These findings support previous studies that show that predator distribution is largely influenced by their prey availability, even in the midst of degraded habitats, and underlies the essential need to incorporate protection plans for prey species in jaguar conservation strategies. We also followed this fragment of the jaguar population over 9 years and estimated number of individuals, detection rates, sex ratios and individual residencies. Using Global Forest Watch tools, we found that males lost a total of 10.41% forest cover from the habitat of their home range in the area while females lost 1.99% forest cover from the habitat of their home range from 2010 to 2020. The onset of acute deforestation in the area coincides with the establishment of Mennonite communities and erratic detection frequencies among the male jaguars studied, suggesting a sudden instability in the population. Through these two studies we confirm our hypothesis that the absence of prey and adequeate habitat is a limiting factor for the presence of jaguars in our study area, showing us their low tolerance for these disruptions. The ongoing habitat degradation and fragmentation surrounding the study area puts at risk the survival of this small but stable jaguar population in southeast Mexico.

Dedicatoria

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INTRODUCCIÓN GENERAL

The order *Carnivora* can generally be distinguished from other mammals by their carnassial dentition and, in general, a high proportion of vertebrates in their diets. The word Carnivora is derived from the Latin *caro: carnis* meaning "flesh" and *voro*, "to devour". Besides their dentition and diet, other poignant traits belonging to this order include: a jaw joint that is a transverse hinge which facilitates biting and cutting; a vertebral column that is strong and flexible and a long tail; a brain that is relatively large; well-developed anal and forehead scent glands used in marking, social recognition, and defense; a walking gait that ranges from plantigrade to digitigrade; and in numerous species, soft fur covered by longer guard hairs. (Bekoff et al. 1984).

Even though carnivores are characterized by a wide range of behavioral, ecological, and morphological adaptations, as well as substantial intraspecific variability, comparative analyses indicate that there also considerable convergence in the manner in which they adapt to their habitats (Gittleman et al. 1986). Therefore, it is possible to identify trends in the phylogeny of behavior and life history characteristics by gathering data from numerous disciplines, including anatomy, physiology, taxonomy, behavior, and ecology (Bekoff et al. 1984). Because of the great variation within the order, carnivores are an excellent group for studying the adaptive patterns of life history traits. Although some variables such as weaning age are difficult to measure and some taxa are overrepresented in the available data (e.g. Canidae), certain variables such as gestation length, birth weight, litter size, age at sexual maturity, longevity and interbirth interval have been amply measured in both captive and natural populations.

Though a multitude of environmental factors have been associated with mammalian life histories, the availability and quality of food resources are considered the main ecological variables as they have a direct influence on multiple traits such as growth rates, litter size and reproduction frequency (Gittleman et al. 1986). Comparative analysis of carnivores have found that life history variables such as inter-birth interval, gestation length, birth weight, litter weight, weaning age and longevity are similar to other mammalian orders and across eutherians as a whole, when scaled to size (Gittleman et al. 1986). Interestingly, studies suggested that birth weight, litter weight, and age of independence are more closely correlated with brain weight, whereas gestation length, weaning age, age of sexual maturity and inter-birth interval are more closely correlated with body weight (Gittleman et al. 1986).

Systematics

The order *Carnivora* is divided into two superfamilies, *Canoidea* and *Feloidea*, and seven polytypic families: *Canidae, Ursidae, Procyonidae, Mustelidae, Viverridae, Hyaenidae*, and *Felidae.* Modern taxonomy recognizes 40 wild felid species distributed across the globe, organized into 14 genera, eight lineages, and two sub-families (Kitchener et al. 2017). Recent molecular investigations suggest that all modern cats are descended from one of several *Pseudaelurus* species that lived in Asia approximately 11 million years ago (Werdelin et al. 2010). Johnson et al. (2006) proposed a biogeographic hypothesis of felid evolution based on geological events where major felid lineages were established during a short evolutionary time period (10.8 to 6.2 MA). Today, four major *Felidae* lineages occur within the zoogeographical regions where they were established: the bay cat and leopard cat lineages (Oriental), the caracal lineage (Ethiopian), and the ocelot lineage (Neotropical). The other lineages include species inhabiting different continents, supporting the premise of additional Pliocene/ Pleistocene migrations including Asian –derived *Panthera* species like the jaguar which spread into America (O'Brien and Johnson, 2005).

Reproduction

Although basic information regarding the reproductive behavior of jaguars is of extreme importance for the development of assisted reproduction and conservation actions, the data on the subject is scarce. We know that although ovulation in this species is usually induced through coitus (Wildt et al. 1979), recent studies on captive females (Gonzalez et al. 2017) reported luteal activity in non-pregnant females in individual enclosures, suggesting that spontaneous ovulation occurs occasionally. Additionally, Barnes et al. (2016) reported spontaneous ovulation in females housed with males whereas females housed without males did not have this effect, demonstrating that the Jaguar is a polyestrous species with induced ovulation.

Interbirth interval has been documented both in captivity and in the wild (Quigley 1987). Carrillo et al. (2009) published reproduction-related observations made on a radio collared adult female jaguar in Corcovado National Park, Costa Rica during 1996–1999. The 22- to 24-month birth interval was similar to the one calculated from observations by Quigley (1987) and Crawshaw and Quigley (2002). Also, the gestation interval of 2.5 to 3 months was similar to the ones observed in captive animals (Lopez-Perez et al. 2021) and the age at which subadults disperse was 18- 24 months, similar to the ages reported by Crawshaw and Quigley (2002).

Survival Rates

Estimates of survival rates are needed to assess the viability of carnivore populations and to develop conservation and recovery strategies (Sharma et al. 2014). This information allows us to identify major sources of species mortality and model populations under different management scenarios to predict the individuals’ response. However, these estimates are difficult to obtain for secretive, long-lived mammals that occur at low densities such as jaguars. Gutierrez- Gonzalez et al. (2012) determined the jaguar density in the Northern Jaguar Reserve in Sonora using an open population model and the best model explaining the capture record included a constant survival rate throughout the sampling period. Harmsen et al. (2017) estimated life history parameters and abundance using camera-trap data from a 14-year monitoring program in Belize. Using robust design open population models, they estimated a high and constant survival rate for both sexes, found the oldest individual to be 14 years of age and varying possible ages based on detection rates among sexes, years and individuals.

Sex Ratio

Studies on jaguars have generally found a higher proportion of male versus female individuals in any given site. Schaller and Crawshaw (1980) reported the presence of 2–3 female jaguars in the home range of one male in the Pantanal, Brazil. Palomares et al. (2012) presented estimates of the sex ratio of jaguars, pumas, ocelots and margays and found that in total, 72.6% of samples of all species were from males and the proportion from males was consistently higher for jaguars than for the other species. However, the reported male skewed sex ratios are likely due, at least in part, to a general higher male detectability and because males prefer to travel and mark along the paths where the sample faeces are being collected for analysis or camera traps are located. Nevertheless, the hypothesis that there are effectively more males than females in jaguar populations cannot be discarded , which could be due to female territoriality or a tendency for males to disperse into suboptimal areas and die more frequently (Palomares et al. 2012).

Habitat

Jaguar habitats range from rainforest to seasonally flooded swamp areas, pampas grassland, thorn scrub woodland, and dry deciduous forest, they are also strongly associated with the presence of water (Caso et al. 2008). Shaller and Crawhaw (1980) and Crawshaw and Quigley (1991) showed that jaguars prefer forest cover over pastures in Brazil. Cullen et al. (2013) found that jaguars prefer dense marshes and primary forests and avoided areas with significant human presence such as productive pastures in the upper Paraná River, Brazil. There is evidence for the role of unprotected areas for carnivore conservation and it has been found that species such as cheetahs, wolves, pumas, leopards, and jaguars are able to live in landscapes with anthropogenic influences (Thompson et al. 2022; Gonzalez-Gallina et al. 2018; Bouyer et al. 2015). However, many studies have shown that large carnivores are negatively affected by anthropogenic pressure in its various forms such as infrastructure and human settlements (Michalski et al. 2005; Schuette et al. 2013). In South America jaguar densities have been found to be affected by the degree of anthropogenic disturbance (Sanderson et al. 2002). Although densities can be high in some productive areas such as cattle ranches in the Pantanal, Brazil (Soisalo et al. 2006) and forest concessions in the Cerrado, they decrease sharply in highly degraded areas such as the Atlantic Forest (Quiroga et al. 2014). Boron et al. (2016) conducted a camera trap survey in the Magdalena River Valley and the Llanos of Colombia and concluded that both unprotected and productive areas can sustain jaguar populations or at least provide important biological corridors as long as remnants of natural habitat are still present. Spatial requirements of large carnivores imply that most protected areas alone are not viable for their survival and that they have to be integrated with increasing human modified areas into wider interconnected landscapes. Studies in Belize have also found a negative effect of human activity on the presence of jaguars and pumas (Harmsen, 2011).

It is important to note that examining habitat preferences in obligate carnivores such as jaguars only makes sense if prey presence and quality are also considered as a main factor driving carnivore densities (Fuller and Sievert 2001; Carbone and Gittleman 2002). Studies on other large carnivores provide insight on this matter. For example, vegetation communities and glacial features explained little about use of space by wolves in the Canadian arctic (McLoughlin et al. 2004), or by wolves in the Canadian Rockies (Hebblewhite et al. 2005). Quantifying the availability or abundance of prey across large spatial scales is difficult and probably the main reason why surrogates, such as vegetation type or land-cover classifications are often utilized instead to estimate prey densities. Numerous recent studies however have attempted to integrate availability of prey resources into habitat-selection models for carnivores, including jaguars (Santos et al. 2019). Not including a biotic definition of habitat is often the cause of the “empty forest syndrome” which exemplifies the conservation costs of using vegetation-only definitions of habitat for obligate carnivores. Because many carnivores are threatened or limited by human activity, many studies include the biotic interaction with humans as an important influence on carnivore habitat.

Often anthropogenic pressure is measured as presence of roads. Gray wolves, cougars, jaguars, Amur tigers, Tasmanian devils, grizzly bears, and black bears all show that roads may be important limiting factors in their environments (Thurber et al. 1994; Jones 2000; Gibeau et al. 2002; Hebblewhite et al. 2005; De Azevedo and Murray 2007). In Mexico, and throughout jaguar range roads have been found to negatively affect their mobility and dispersal (Colchero et al. 2011; Pallares et al. 2015; Gonzalez-Gallina and Hidalgo-Mihart 2018)

Prey Use and Feeding Habits

Jaguars are known to have up to 85 prey species (Seymour 1989). Although they have been traditionally considered to be opportunistic predators because they consume prey relative to its abundance (Rabinowitz & Nottingham, 1986), recent studies point to the possibility that they do in fact employ foraging strategies (Weckel et al. 2006). A preference for prey is said to occur when a particular prey is targeted and comprises a larger proportion of the predator's diet than expected by its relative abundance (Hayward and Kerley, 2005). There is substantial evidence that jaguars prefer medium and large prey (Schaller and Vasconcelos 1978; Rabinowitz and Nottingham 1986, Emmons 1987). Also, a clinal latitudinal pattern has been found where jaguars living further from the equator use larger prey more frequently than those living nearer to the equator which depend more heavily on medium-sized prey (Gonzalez and Miller, 2002). Jaguars have been found to have the most robust canines relative to size of all felids, possibly because they use these teeth to pierce the braincase of some prey and pierce tortoises' shells which requires reinforcement and support in order to avoid fracturing the canines. (Roemer et al. 2009). A preference for medium prey, smaller than expected for their size, could be due to an evolutionary adaptation to expand their prey base as a result of a strong competition for larger prey from other, now extinct predators. Even though presently, the jaguar is the most dominant predator in the Americas, during the end of the Pleistocene it was sympatric with at least 10 other larger carnivores (Cione 2009), suggesting the jaguar was more of a mesopredator and possibly survived the Pleistocene extinction due to its greater prey base which included smaller animals (Hayward 2016). Hayward et al. (2016), through a literature review found that jaguars mostly prefer their prey for ecological and behavioral reasons such as herd size rather than physical characteristics such as body size. However, they found a preferred prey weight range of 45-85 kg and a mean mass of 32+/- 13 kg throughout the species' distribution They also found a predator-prey ratio of 1:.53 which is much less than that of other solitary felids.

Current Population Status and Threats

Carnivores are some of the worlds most revered and iconic species but ironically they are also some of the most threatened. During the previous two centuries, many carnivores have experienced substantial population declines, geographic range contractions, and fragmentation of their habitat (Ceballos et al. 2020). The underlying cause of the carnivore population decline is the increase in the human population and the consequent impacts associated with hunting, habitat loss, fragmentation, and the proliferation of invasive species (Woodroffe et al. 2000). Large carnivores are particularly at risk of extinction in fragmented landscapes given their extensive home ranges, low population densities, low population growth rates, and direct persecution by humans (Woodroffe and Ginsberg 1998).

In the case of jaguars, despite the fact that their current distribution includes several types of viable habitats, under future scenarios of climate change, the climatic and fluvial conditions in these regions could change considerably limiting their distribution (Blair et al. 2012). As Latin America is one of the regions with the highest population growth rates (Leeson 2018), we can expect that the current anthropogenic pressure will continue to exert a strong constriction on jaguar's range and limit their dispersal possibilities.

Prior to the widespread use of genetic analysis to infer the phylogeny of species it was believed that given *Panthera onca's* ample geographic distribution, the fragmentation of its populations and the physical differences between populations of different regions, the species might be divided into several subspecies (Seymour 1989). When Eizrik et al. (2001) performed genetic analysis using mitochondrial DNA and microsatellites to determine the genetic diversity, population structure and demographic history, they found 4 large phylogeographic groups (Mexico and Guatemala, southern Central America, northern South America (north of the Amazon River) and southern South America. However, the differences were not enough to be considered subspecies and given the medium and high heterozygosity, the gene flow has been considerable and the structures are recent.

Sanderson et al. (2002) estimated that jaguars presently occupy approximately 46% of their historic distribution. Currently, with the incorporation of previously unmonitored sites, the estimation has gone up to 51% of their historic range, an area equivalent to 9.02 million km^2 with the Amazon forest being their stronghold consisting of 57% of their current occupation. In the last hundred years, jaguars have been eradicated from the south of the USA, some areas of the north of Mexico, the north of Brazil and the pampas in Argentina and Uruguay (Paviolo et al. 2016). The main threats that they currently face are the loss and fragmentation of their habitats (Harmsen et al. 2011; Bernal-Escobar et al. 2015), their illegal hunting for trophies, for the black market of their body parts or in revenge for the real or imaginary livestock predation (Hoogesteijn and Hoogesteijn 2008).

Sanderson et al. (2002) estimated the survival probability of jaguars in the long term in different areas varying in size, connectivity, habitat quality, hunting pressure and population status. The analysis found that 70% of the current distribution range (in 2002) represented areas had high probabilities of jaguar survival including the regions of the Amazon, Chaco and Pantanal. In 18% of the distribution range was found to have medium survival probability, including the Cerrado, the Colombian and Venezuelan plains and some areas in Costa Rica, Panama and southern of Mexico. The rest of the distribution range was deemed to have low probabilities of survival. Due to their wide continental distributions, jaguars are not listed as threatened according to the IUCN Red List (IUCN 2021). However, a revision of the IUCN status has been solicited given that regional studies have diagnosed habitat loss and fragmentation as significant threats for the species which could lead to unviable populations (de la Torre et al. 2018).

BACKGROUND

The Importance of Studying Jaguars

Jaguars, as many carnivores are top predators and regulate the population of their prey and, in turn, their prey’s prey. This ecological role has enormous implications for the conservation of ecosystems as large carnivores play key roles in controlling ecosystem function through top-downtrophic effects (Ripple et al. 2014). Furthermore, large carnivores play an important role as umbrella species for biodiversity conservation, with their occurrence associated with greater biodiversity (Ray et al. 2013).

Large carnivores provide economic and ecosystem services in a variety of both direct and indirect ways. Because of their iconic and charismatic nature, large carnivores provide direct economic benefits associated with tourism. In Yellowstone Park, wolf-related tourism expenditures range from $22 million to $48 million USD per year (Meyer et al. 2008) and in the Pantanal jaguar tourism yields an annual income of over $6 million USD (Tortato et al. 2017). Large carnivores also have strong potential to indirectly provide ecosystem services that can mitigate climate change such as carbon storage, biodiversity enhancement, and reestablishment of native plant diversity, riparian restoration, and disease regulation. In some ecosystems, large carnivores may enhance carbon storage by limiting the numbers of their herbivore prey, thus allowing plants to flourish. Carnivore conservation might also reverse declines in forests, especially in the highly productive tropics, where declines in plant biomass often occur after predator extirpation (Linell et al. 2005).

Objectives of this study

The general objective of this work is to evaluate the tolerance that jaguars have for degraded habitats, loss of prey and human presence using a small jaguar population in the Lagua de Terminos natural protected area region as a model. We use site occupancy probability and the long term stability of the population as indicators for this tolerance. It is common practice in large mammalian studies, to use the occupancy and habitat use (jaguars, Figel et al. 2019), abundance rates (giant ant eater, lowland tapir, giant armadillo and white lipped peccary, Teixeira-Santos et al. 2020) or activity patterns (jaguars, pumas, Foster et al. 2010) as indicators of species' tolerance for disruptions. Even though many of these novel habitats can be considered ecological traps (Robertosn et al. 2013) as their conditions are not optimal, animals still have the choice to stay or leave these habitats and their presence points to some level of tolerance. It is unknown however if this is a short or long term tolerance. The occupancy probabilities can also be viewed as a range of tolerance from low, where low occupancy probabilities were found (<50%) to high, where higher occupancy probabilities were found (>50%). I hypothesize that the presence of prey will be the main limitant on the presence of jaguars within our study site and that the acute deforestration the area has been subjected to will have meaningful impacts on the population's long term stability. The reasons I believe this are several, although ideally jaguars require large swaths of well conserved habitat to meet their basic needs for resources and space, recent studies have found that they can also use degraded environments like palm oil plantations (Boron et al. 2016), agricultural fields and pastures (Thompson et al. 2022) and even garbage dumps (Gonzalez-Gallina et al. 2018), albeit existing at lower densities or using these areas as biological corridors. Therefore I do not expect the population to be severely limited in the short term by the less than ideal patches of habitat found throughout our study site which would mean that in single season occupancy analysis habitat type will not be the most influential covariate. However, the effects of habitat degradation will become apparent in long term studies where we follow the population over time and witness the turnover of residents, new individuals arriving in the study area and cubs reach maturity and disperse to find their own territory. On the other hand, the presence of prey is absolutely esencial for individuals to stay for any length of time in a particular area as they cannot survive without food. If jaguars are not able to successfully hunt in an area, they will undoubltly move to another one in search for food in order to survive.

In the first chapter I follow a fragment of a small but stable population in the southeast of Mexico over 10 years with the objective of describing the dynamics they experience as their surroundings change with human encroachment and consequent habitat loss. I intend to publish this study in a peer reiewed journal in 2023. In the second chapter I use a larger study area which encompasses various types of habitat including secondary forests and agro livestock landscapes, various degrees of prey presence and human preassure to estimate the tolerance that jaguars have to these disruptions using occupancy probability. This study was published in the journal *Mammalia* in 2022. In my discussion I go over the general hypotheses planted and whether thse were proven to be true. Finally, in my general conclusion I elaborate on the threats that jaguars face in a rapidly changing environment and discuss the factors that might influence the long term survival of this population.

I hope that this work will contribute to our knowledge of the tolerance that jaguars have for anthropogenic and environmental disruptions and thus help design more realistic and efficient management plans. Most jaguars studies take place in well conserved areas which obilerates our ability to understand their tolerance for disruption and these inferences may not be representative of populations outside well conserved or protected areas (Thompson et al. 2022),. Given that many of the population estimates obtained from these areas are used to infer the general status of populations at regional and range-wide levels we might tot see the whole picture and make misinformed decisions on conservation and management plans. Additionally, I hope this work underlines the importance of protecting jaguar habitat and the need for government enforced land use regulations in areas that are essential for endangered species such as jaguars.

CAPITULO 1

A decade long survey of an isolated jaguar population in a region subjected to acute deforestation in southeastern Mexico

A decade long survey of an isolated jaguar population in a region subjected to acute deforestation in southeastern Mexico

Abstract

Long-term studies of wild carnivore populations are rare (Hayes et al. 2017) yet extremely necessary to adequately assess changes in the populations' structure and make well informed decisions regarding their conservation and management. Besides identifying trends in the dynamics of the population's structure, population monitoring programs can help understand fundamental processes of the species in question such as survival, reproduction and temporary emigration and immigration (Sharma et al. 2014). These life history estimates are difficult to obtain for stealthy, long-lived mammals that occur at low densities such as jaguars. Just as valuable but rare are long term studies that assess population trends throughout the process of the deterioration of their habitat. Here, we follow a jaguar population in the Area de Proteccion de Flora y Fauna Laguna de Terminos (APFFLT) over 10 years with the objective of describing basic traits of the population and identifying ways in which its stability is being disrupted by the ongoing and deforestation in the area. We estimate number of individuals, detection rates, sex proportions, resident and transient proportions and individual residencies. We identified a total of 7 females and 19 males which we grouped into residents and transients depending on the consecutive years we observed them. Using Global Forest Watch tools, we found that from 2010 to 2020 there was a forest cover loss of 1,586 ha from potential male habitat and 165 ha from potential female habitat. The onset of acute deforestation in the area coincides with the establishment of Mennonite communities. The ongoing habitat deterioration and fragmentation surrounding the study area puts at risk the stability of this jaguar population in southeast Mexico.

Resumen— Los estudios a largo plazo de poblaciones de carnívoros silvestres no son muy comunes (Hayes et al. 2017) pero extremadamente necesarios para evaluar los cambios en la estructura de las poblaciones adecuadamente y tomar decisiones bien informadas sobre su conservación y manejo. Además de identificar las tendencias de la población, los programas de monitoreo de poblaciones silvestres pueden ayudar a comprender los procesos fundamentales de la especie en cuestión, como la supervivencia, la reproducción y la emigración e inmigración temporal (Sharma et al. 2014). Estas estimaciones de la historia de vida son difíciles de obtener para mamíferos longevos que viven a densidades poblacionales bajas, como los jaguares. Igual de valiosos y escasos son los estudios a largo plazo que identifican tendencias poblacionales a través del proceso de deterioro de su hábitat. En este estudio, seguimos una población de jaguares en el Área de Protección de Flora y Fauna Laguna de Términos (APFFLT) durante 10 años con el objetivo de describir aspectos básicos de la población e identificar como la deforestación del area esta afectando su estabilidad. Estimamos número de individuos, tasas de detección, proporción de sexos, proporción de residentes y transeuntes y longitud de residencias de los individuos. Identificamos un total de 7 hembras y 19 machos que agrupamos en residentes y transeúntes dependiendo de los años consecutivos en que los observamos. Utilizando herramientas de SIG y Global Forest Watch, encontramos que del 2010 al 2020 hubo una perdida de cobertura forestal de1,586 ha de hábitat potencial de jaguares machos y 165 ha de hábitat potencial de jaguares hembras. El inicio de la deforestación aguda en la zona coincide con el establecimiento de comunidades menonitas. El continúo deterioro y fragmentación del hábitat que rodea el área de estudio pone en riesgo la estabilidad de esta población de jaguares en el sureste de México.

Key words: jaguars, long–term study, carnivores, Mexico, population ecology, population structure, deforestation, habitat loss

Introduction

Long-term studies of wildlife carnivore populations are rare (Hayes et al. 2017) yet extremely necessary to adequately assess changes in the populations' structure and make well informed decisions regarding their conservation and management. Long term studies provide a wealth of information regarding the physiological mediation of life-history traits such as survival, reproduction and temporary emigration and immigration (Sharma et al. 2014; Pallemaerts et al. 2020) as well as the roles of both bottom-up and top-down processes regulating populations (Smith et al. 2017), how animals cope with a changing environment and how pathogen transmission interacts with various social structures shaping disease ecology (Munson et al. 2008; Craft et al. 2009). They can uncover the effects of developmental, physiological, and demographic processes influencing socioecological and evolutionary traits to an extent that short-term investigations could never do so (Clutton-Brock and Sheldon 2010). Finally, long-term data can provide unique opportunities to ask questions that were perhaps not thought of at the beginning of the study and we have yet to take full advantage of these repositories (Smith et al. 2017). In the case of large carnivores such as jaguars, monitoring populations through time is relevant given their role as umbrella and keystone species (Bond et al. 1994; Olsoy et al. 2016) and their current near threatened status (Caso et al. 2015). Recent studies have followed felid populations for over 10 years (Harmsen et al. 2017; Gutierrez-Gonzalez et al. 2015), but these studies have taken place in well conserved areas and thus fail to measure how anthropogenic pressure in its varying forms can affect these populations over time. Other studies that do incorporate degraded habitats have been limited to making ‘‘snapshot’’ assessments, rather than tracking change over time (Johnsingh and Negi 2003; Boron et al. 2019). Given that changes in population numbers or detections may be a product of anthropogenic factors or natural temporal fluctuations in the population, appropriate monitoring strategies are necessary to take into account the scale and range of these fluctuations (Gibbs et al. 1998; Smith et al. 2017).

Jaguar habitats range from rainforest to seasonally flooded swamp areas, wetlands, pampas grassland, thorn scrub woodland and dry deciduous forest (Caso et al. 2008). Though jaguars typically favor tropical lowland habitats with sufficient natural cover and access to water and prey, they also been found in coastal mangroves and might especially use these habitats in fragmented landscapes (Figel et al. 2019). The Terminos Lagoon Flora and Fauna Protected Area (APFFLT for its initials in Spanish, herein) was created fundamentally to protect the wetlands in the region of the Gulf of Mexico. Together with the Centla Biosphere Reserve, it forms the most important coastal ecological unit in Mesoamerica (Rivera-Arriaga and

Villalobos-Zapata 2005). Nevertheless, this region has suffered considerable destruction in the last 50 years. From 1974 to 2001, the Terminos Lagoon lost 12% of its mangroves and 31% of its forests (Soto-Galera et al. 2010; Hidalgo et al. 2017) mainly due to the expansion of cattle ranching, wetland drainage, deforestation for agricultural development, oil drilling, and recent tourism developments (Guerra-Martínez and Ochoa-Gaona 2008; Macías et al. 2014). Hidalgo et al. (2017) identified medium and large sized mammals from the wetland complex and recorded 30 native and 1 introduced species, representing 9 orders, 14 families, and 27 genera. Out of the species identified, 4 are listed as Threatened, 9 as Endangered and 1 is under special protection under Mexican legislation. Jaguar densities calculated in 2016 were 1.934 ± 0.529 individuals per 100 km^2 (Hidalgo et al. 2019) and the average jaguar occupancy in the region was 35 +/- .07 % with collared peccary occupancy being the strongest positive predictor for their presence which was limited to better conserved habitat in a heterogeneous landscape (Friedeberg et al. 2022). Compared to other sites of southeastern Mexico, the area of the Terminos-Centla wetlands is extremely rich in biodiversity (Hidalgo et al. 2017). Wetlands are also indispensable for many ecosystem services ranging from freshwater supply, food and building materials, flood control, groundwater recharge, and climate change mitigation (Gocke, 2019).

Beginning in 2009 several families purchased land in the buffer area of TLFFPA and destined it to conservation or sustainable agricultural and cattle ranching practices. We began our yearly monitoring program in 2010 and in 2015 and 2016, witnessed the neighboring property suffer from severe deforestation when a group of approximately 120 Mennonites bought the property and developed it rapidly. The extreme deforestation that these human settlements provoke has been reported recently in the region (Ellis et al. 2017) and across other tropical regions such as lowland Bolivia (Tejada et al. 2016) the Paraguayan Chaco (Mereles and Rodas, 2014) and Belize (le Polain de Waroux et al. 2021).

In this study, using camera trap data from 2010 to 2020, we describe life history parameters of a fragment of jaguar population in APFFLT and relate the changes in the population's structure identified to the habitat loss observed in the area using Global Forest Watch resources. Our objectives were to estimate detection frequencies, sex proportions, resident and transient proportions and describe how they change over time in the context of deforestation. We intend to identify how human-caused habitat loss is affecting the jaguar population we study. We hypothesize that we will identify clear indications of instability in the jaguar population studied. This could be in the form of less individuals identified over time or changes in sex proportions and resident- transient proportions.

Study area

The study area is located in the buffer zone of the Laguna de Terminos Natural Protected Area, located in the municipalities of Carmen and Palizada in the state of Campeche, Mexico. It is situated almost at sea level (between 2 and 3 meters) in the coastal plains of the Gulf of Mexico within the physiographic sub-province of Pantanos and the Plains of Tabasco (INEGI 2015). The climate is warm and humid with an average temperature of 27 °C and up to 2,000 mm of annual precipitation (INEGI 2013). The area is subject to seasonal floods, which can range from 2 to 8 months (June-February), followed by a relatively dry season where the highest areas are partially or completely dry (March to May). Depending on the flooding regime, different types of vegetation flourish: hydrophilic vegetation, flooded grasslands, mangroves, evergreen riparian forests and medium and low tropical forests (Ocaña and Lot, 1996). The human activities in the region include fishing, hunting, irrigated agriculture and cattle ranching (Soto-Galera, 2010). The land tenure of the study site is private and 3 UMAs, similar to wildlife management units have been established, one for the hunting of white tailed deer and 2 solely for conservation purposes.

Materials and methods

We performed camera trap surveys yearly from 2010 to 2020, excluding 2015. Each survey lasted at least 3 months (between February and July). The yearly camera setup varied from 20 to 40 camera trap stations, most years we had 24 stations. From 2010 to 2012 we used Wildview Xtreme cameras, from 2013 to 2014 we used Cuddeback Attack IR, AcornLtl and

Moultrie M80XT cameras and after 2016 we used Pantheracams® model IV, V or VI and Cuddeback E2 Long Range IR. Before 2016 roughly half of the stations were double, after 2016 most stations were double (Table 1). The decision to install one or two cameras per camera station was based on trying to decrease the probability of equipment theft and availability at the time. The cameras were placed on trails or waterholes to increase our capture probabilities (Noss et al. 2013) at intervals of approximately 1.5 to 2 km and attached to trees at an approximate height of 50 cm. The cameras were programed to run 24 hours during the duration of the study, each motion- triggered event was programmed to take 3 pictures every minute and all images were identified to species.

Table 1. Camera trap types and stations used in APFFLT from 2010- 2020, excluding 2015.

Year	Single Stations	Double Stations	Camera trap models		
2010	30		WildView Xtreme		
2011	21		WildView Xtreme		
2012	9	22	WildView Xtreme	Cuddeback Attack IR	
2013	16	9	Cuddeback Attack IR	Acorn Ltl	Moultrie M80XT
2014	17	4	Cuddeback Attack IR	Acorn Ltl	Moultrie M80XT
2016	56	10	Cuddeback E2 Long Range IR	Panthera IV,V, VI	Moultrie M80XT
2017	20	22	Panthera VI	Cuddeback E2 Long Range IR	
2018	14	19	Panthera VI	Cuddeback E2 Long Range IR	

2019	30	10	Panthera VI	Cuddeback E2 Long Range IR
2020	30	10	Panthera VI	Cuddeback E2 Long Range IR

Once the cameras were removed, the photographs were stored and processed using *Camera Base* (Tobler, 2014). To calculate the sampling effort per site, we obtained the number of camera days that each individual camera functioned on the field by counting the number of days from when the camera was activated to the date of the last photograph taken. We considered a camera day to be a period of 24 hours during which the camera was operating. The total sampling effort for each study period was obtained by adding the number of camera days that each camera operated on each site. We considered a detection as a capture of an individual within a 24 hr period, whether that meant a single photograph or several. We identified jaguars individually on the basis of their spot pattern (Karanth, 1995; Silver et al. 2004) and gender by secondary sexual traits (e.g testicles) (Silver et al. 2004). If a photo could not be clearly assigned to an individual it was removed from the analysis. We performed the analysis including all the individuals identified by both sides. In the cases where we did not have both sides of the individual as occurred in the single camera stations, we used the side where we had more identified individuals to estimate the minimum number of individuals present in the area (Paviolo et al. 2008).

Following Barlow et al. (2009) and Hidalgo-Mihart et al. (2018), we classified a jaguar as a resident of our study area if it was photographed 2 or more consecutive years. We considered residency as the length of years that an individual, including transients were detected in our study site, excluding gap years. We considered animals to be at least 2 years of age when first sighted given that cubs leave their mothers at this time and are in the process of reaching sexual maturity (Hope and Deem 2006; Viau et al. 2020). We calculated the yearly sex proportions of all individuals detected and of the resident cohort. We estimated these traits (number of individual residents and transients, residency, minimum lifespan and sex proportions) every year from 2010 to 2020, excluding 2015 and compared the yearly values to identify tendencies in the population cohort. All calculations were done using excel spreadsheets.

To evaluate the habitat loss over the years of the jaguar population studied, we created a buffer in Arc GIS based on the area calculated with the scale parameter (σ) obtained from the best density model in the study area (Hidalgo-Mihart et al. 2019). This value describes how the jaguar encounter rate decreases with increasing distance from the home range center and is related to the home range radius (Tobler et al. 2013). Given that in the study by Hidalgo-Mihart et al. (2019), the best model included different σ values for males and females, we determined the areas of influence for each sex separately. Based on these parameters we estimated the buffer area around each camera trap to be 4,750 m for males and 2,050 for females. The buffer area was traced from the location of the cameras used in 2016 because these were the locations that Hidalgo-Mihart et al. (2019) used to calculate the scale parameters. We overlapped all the resulting buffers from each camera trap and joined them to produce a single buffer polygon that included all the camera traps. Finally, we subtracted the bodies of water from these polygons given that water is not considered a habitat for jaguars.

To calculate the yearly loss of forest cover in the male and female buffer areas, we transformed the final polygons for males and females to Google Earth kmz files in order to be able to insert them in the analysis tool of forest gain/loss utilized in the Global Forest Watch Web Site (https://mapbuilder.wri.org/mapbuilder-tutorial/ Hansen et al. 2013). Through this process we estimated the amount of forest area that both males and females lost from their respective habitats in the study area on a yearly basis from 2010 to 2020. It is important to note that the Forest Global watch tool calculates the yearly annual forest cover loss that results from the accumulation of loss during the prior year. This means that the years presented here in reality represent the forest cover loss of the year before.

Results

The minimum number of active camera traps per site in one season was 20, and the minimum number of operating days was 90. From 2010 to 2020 we had a total trapping effort of approximately 24,952 camera days (we cannot know the exact number as some cameras used in 2010 and 2014 failed to register this data) in which we obtained 1,065 photographs of jaguars corresponding to 7 females 19 males and 7 individuals that we weren't able to identify and were removed from the analysis. One of the females was detected with 1 male in a year and spotted with a cub the following year. The number of individuals present within the study area each year varied from 1 to 11 (Fig. 1). On average, we detected 5.09 ± 3.47 individuals per year and each individual was detected an average of 2.38 ± 1.59 years. We performed a simple correlation analysis between the number of camera trap stations used each year and the number of individuals detected and found the data sets to be only moderately correlated |r|= .52 (supplementary table 1, Taylor 1990). The number of individual detections per year varied from 0 to 118 and 2012 and 2016 were the years with the highest number of individuals (11) and 2016 with the highest number of detections (214) (Figs. 1,2,3).We observed a total of 4 resident females (57% of all females), 3 transient females (43% of all females), 11 resident males (58% of all males) and 8 transient males (42% of all males) (Figs. 1, 4). The length of residency varied from 1 to 9 years and the average residency was 2.7 +/-2.4 years. The average residency of males was 2.5 ± 2.1 years and average residency of females was 3.3 ± 2.9 years. The average minimum lifespan calculated was of 3.7 ± 2.4 years, the longest lifespan for both males and females was 10 years (Fig. 4).

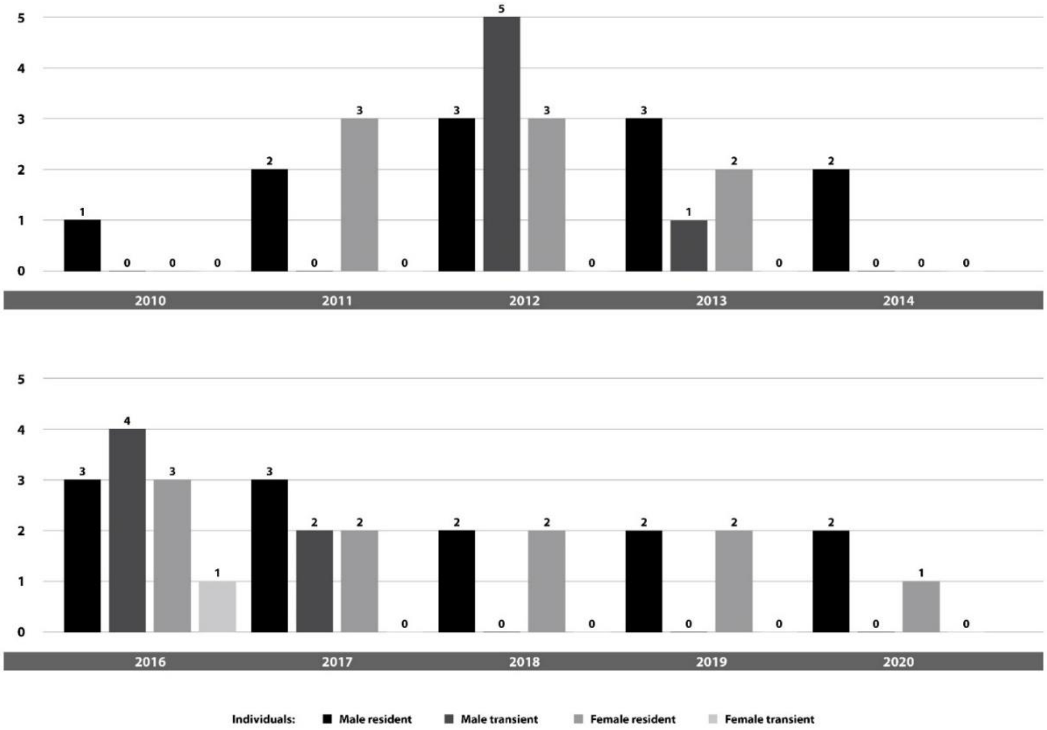


Fig. 1 Total Number of Individuals detected in APFFLT from 2010- 2020, excluding 2015

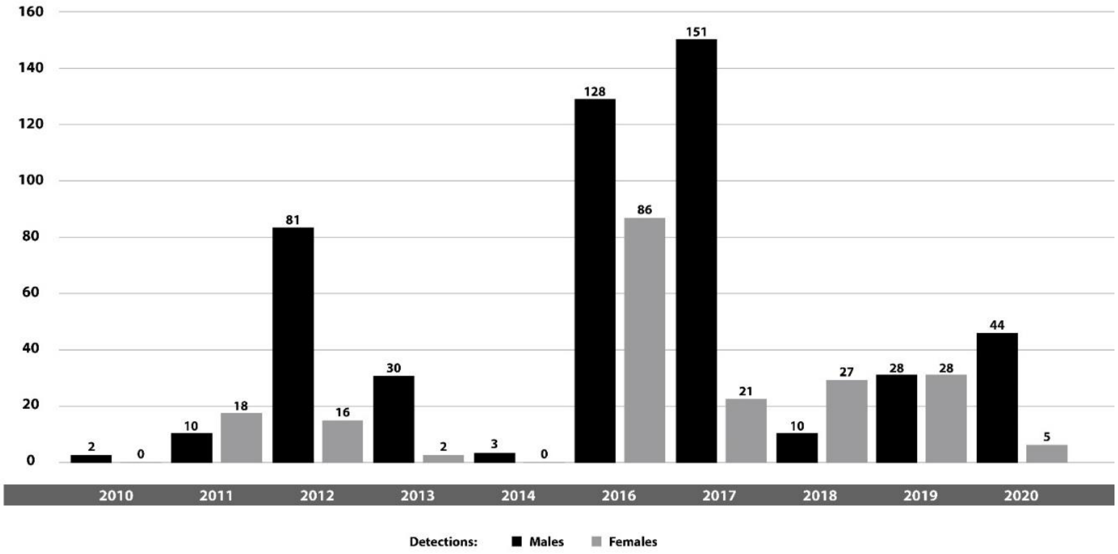


Fig. 2 Total Number of Male and Female Jaguar Detections in APFFLT from 2010- 2020, excluding 2015

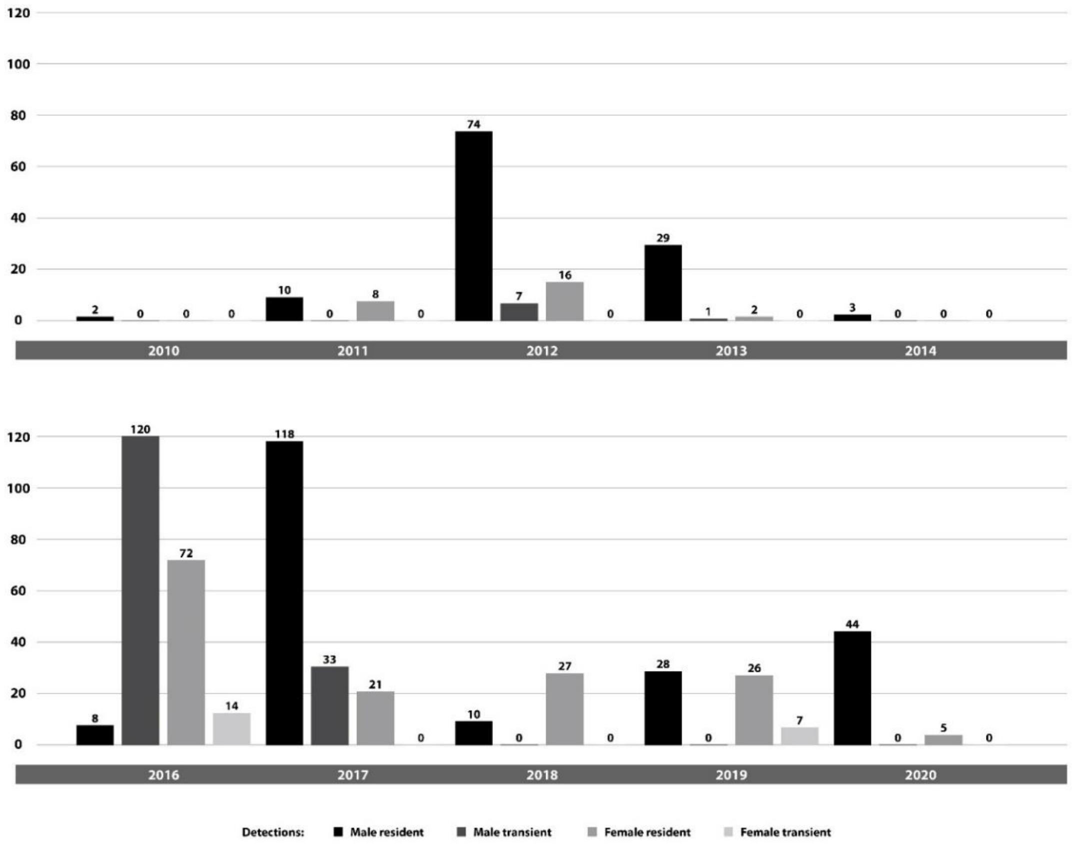
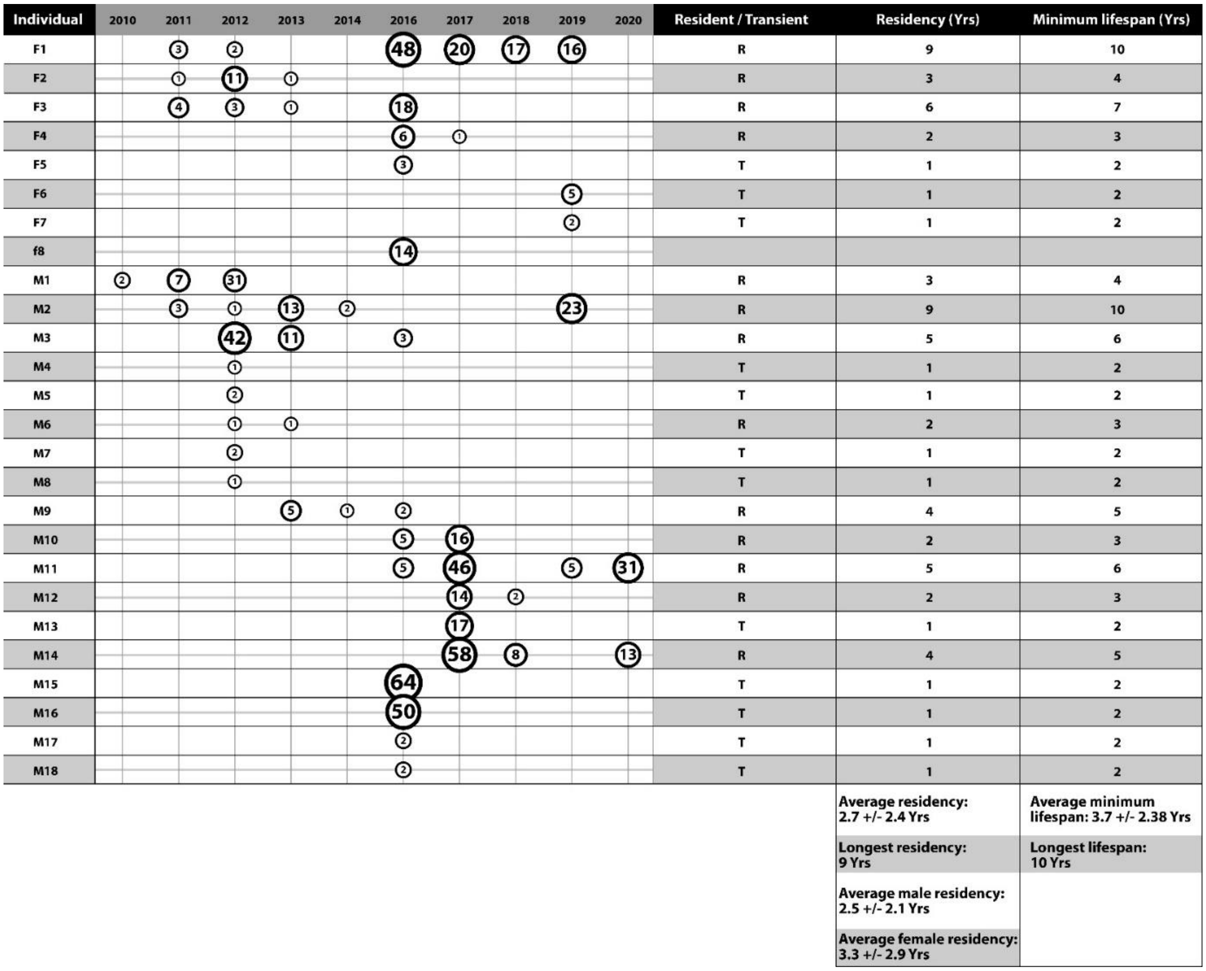


Fig. 3 Total Number of Male Resident, Male Transient, Female Resident and Female Transient Jaguar Detections in APFFLT from 2010- 2020, excluding 2015



Individual	2010	2011	2012	2013	2014	2016	2017	2018	2019	2020	Resident / Transient	Residency (Yrs)	Minimum lifespan (Yrs)
F1		3	2			48	20	17	16		R	9	10
F2		1	11	1							R	3	4
F3		4	3	1		18					R	6	7
F4						6	1				R	2	3
F5						3					T	1	2
F6									5		T	1	2
F7									2		T	1	2
f8						14							
M1	2	7	31								R	3	4
M2		3	1	13	2				23		R	9	10
M3			42	11		3					R	5	6
M4			1								T	1	2
M5			2								T	1	2
M6			1	1							R	2	3
M7			2								T	1	2
M8			1								T	1	2
M9				5	1	2					R	4	5
M10						5	16				R	2	3
M11						5	46		5	31	R	5	6
M12							14	2			R	2	3
M13							17				T	1	2
M14							58	8		13	R	4	5
M15						64					T	1	2
M16						50					T	1	2
M17						2					T	1	2
M18						2					T	1	2

Average residency: 2.7 +/- 2.4 Yrs	**Average minimum lifespan:** 3.7 +/- 2.38 Yrs
Longest residency: 9 Yrs	**Longest lifespan:** 10 Yrs
Average male residency: 2.5 +/- 2.1 Yrs	
Average female residency: 3.3 +/- 2.9 Yrs	

Fig. 4 Residency and Minimum Lifespan of all Jaguar Individuals in APFFLT from 2010-2020, excluding 2015

Our sex proportions calculations resulted in 7 years with a male bias sex ratio, 2 years with a female bias and 1 year with no bias. When looking at only the resident pool, we found a male bias in 5 years, a female bias in 1 year and no bias in 4 years (Figs 5, 6). From 2010 to 2020 there was forest cover loss in our area which translated into a total of 1,586 ha (10.41%) of buffer area loss for males and 165 ha (1.99%) loss for females (Table 2, Fig. 7). The years with no forest cover loss for either sex were 2011 and 2013, the years with the highest forest cover loss for both sexes were 2018 (454 ha) and 2019 (464).

Table 2. Yearly forest cover loss in male and female jaguar buffers in APFFLT from 2010 to 2020

	Year	Males	Females
Camera buffer area (ha)		24984	11460
Camera buffer area covered with water (ha)		1452	11460
Camera buffer area covered with forest (Percentage of forest)		15240 (60.6%)	8285 (72.3%)

Table 3. Yearly camera buffer forest area loss in hecatares in male and female jaguar buffers in APFFLT from 2010 to 2020

	Year	Males	Females
Camera buffer forest area lost per year (ha)	2010	1	0
	2011	0	0
	2012	12	2
	2013	0	0
	2014	3	2
	2015	1	0
	2016	21	9
	2017	361	37
	2018	445	9
	2019	422	42
	2020	320	64
Sum of camera buffer forest area lost durig the 2010-2020 period (ha)		1586	165

Camera buffer area (ha)	24984	11460	
Camera buffer area covered with water	1451.7	11460	
Camera buffer area covered with forest (Percentage of forest)	15240.79 (60.6%)	8285.62 (72.3%)	
Percentage of camera buffer forest area lost durig the 2010-2020 period	10.41	1.99	

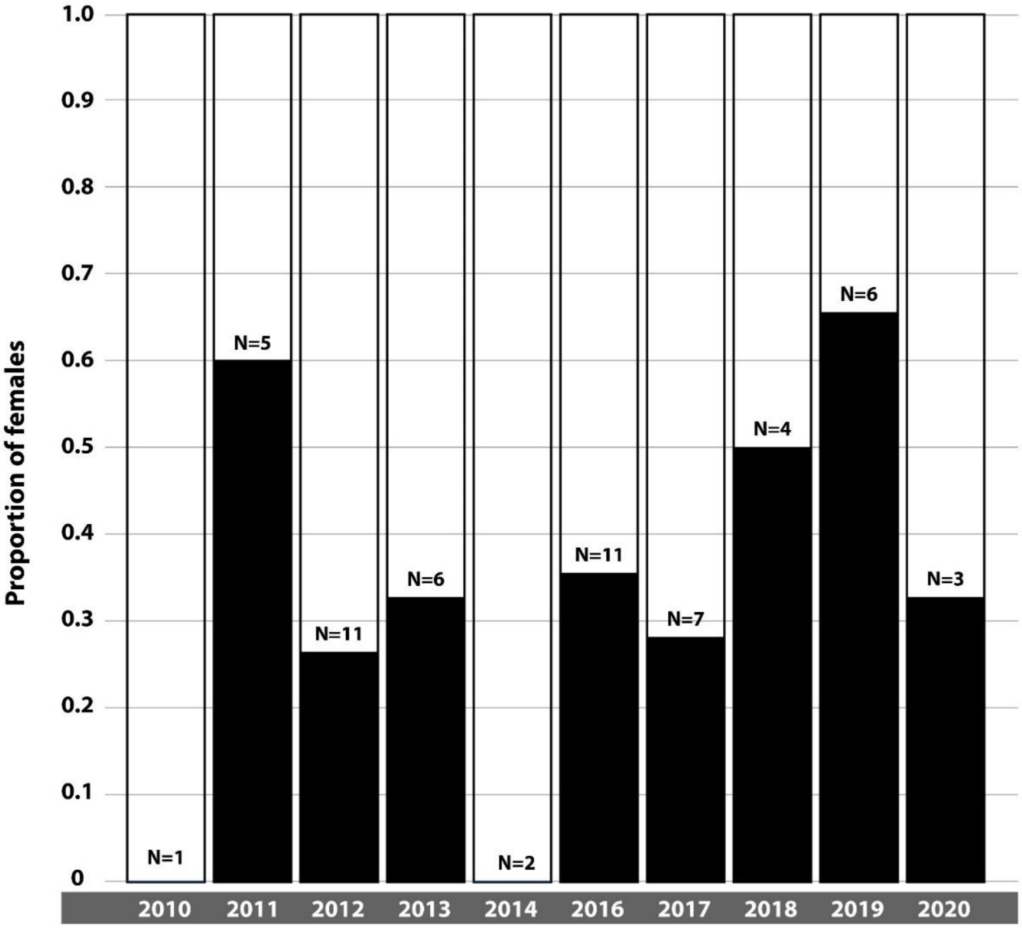


Fig. 5 Sex Proportions of all Jaguar Individuals in APFFLT from 2010- 2020, excluding 2015

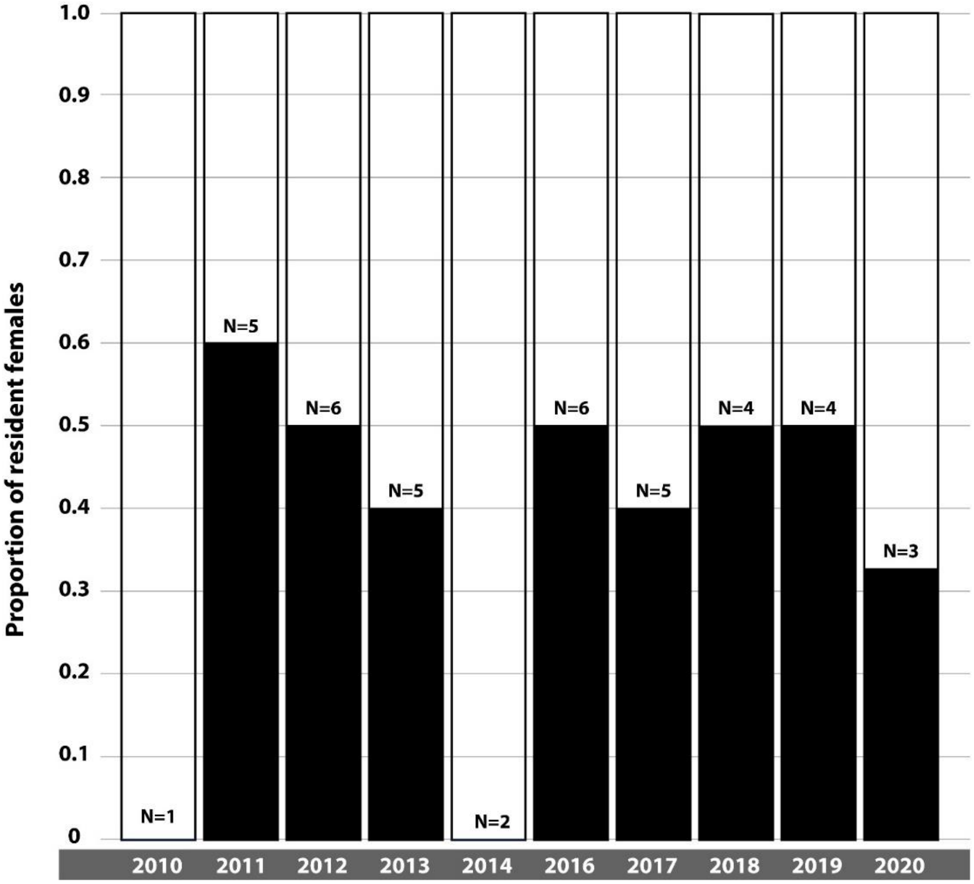


Fig. 6 Sex Proportions of Resident Jaguar Individuals in APFFLT from 2010- 2020, excluding 2015

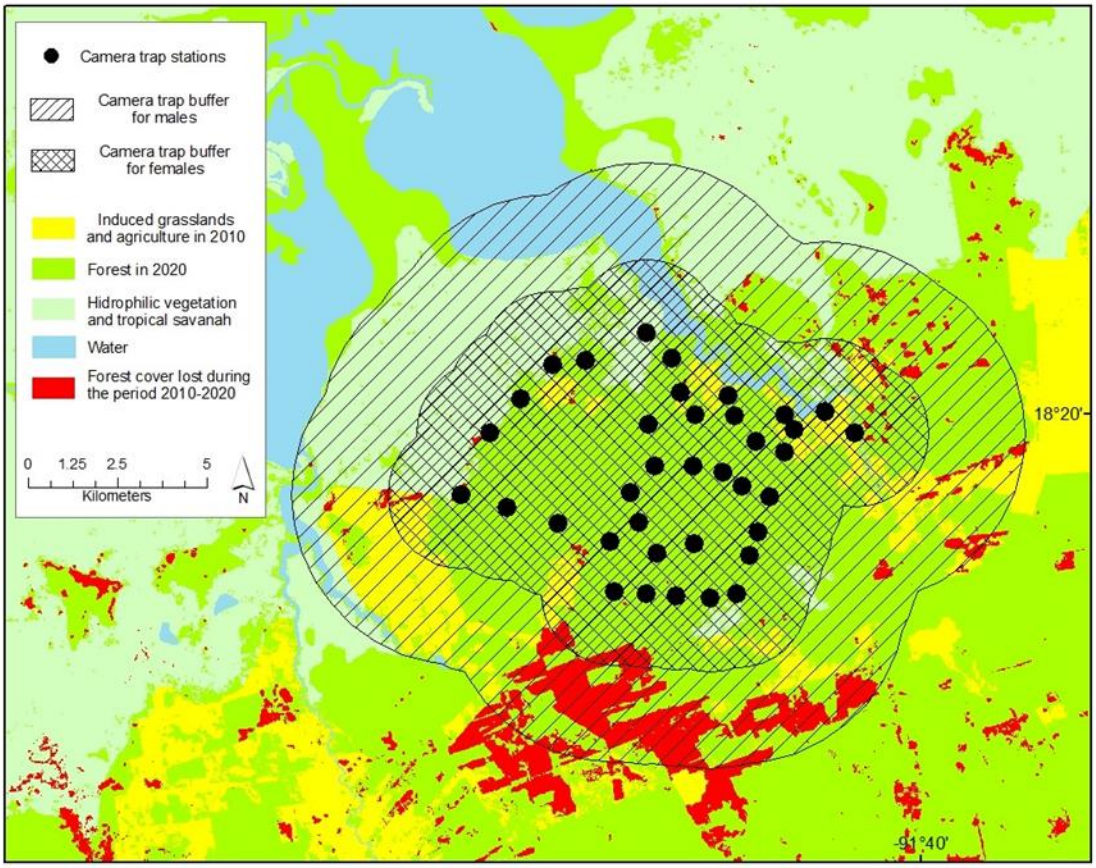


Fig. 7 Forest cover loss in the camera trap buffers of male and female jaguars in APFFLT from 2010 to 2020.

Discussion

Jaguar's lifespan in the wild is approximately 12- 15 years (Quigley et al. 2017) and in captivity can extend up to 20 years (Weigl et al. 2005). Given that our study did not run that long, we cannot relate our data to that recorded previously. However, because our study site has an abundant prey base and little poaching, we would expect the individuals detected to live long lives and die of natural causes (Friedeberg et al. 2022). Nevertheless, as the region as a whole is composed of a heterogeneous landscape which includes induced grasslands and degraded habitat, the population studied is at risk from the increasing human encroachment. The average residency found for males (2.5 ± 2.1 years) and for females (3.3 ± 2.9 years) in our study area are similar to those found by Gutierrez-Gonzalez et al. (2015) in northeastern

Sonora, Mexico (1.7 ± 0.25 years for males and 2.5 ± 0.50 years for females). The true residencies might be longer given that we excluded gap years in between detection years from our estimations. The short gap years, like the ones seen for F3 and M3 might be the result of the individuals remaining in the study area but not being detected or them meandering outside our camera grid and then returning. The longer gap years like those seen in M2 might be true absences from the population.

The sex proportions we identified over the years are generally male biased. However, when only looking at resident sex proportions there are more no-bias years than when looking at all individuals. These fluctuations in sex ratios can only be identified when using long term data (Sharma et al. 2014). Resident individuals can also be thought of as the breeding cohort given that they dominate resources, including access to mating opportunities and concentrating on counting breeding individuals in monitoring programs increases the power of such studies and consequent management programs because this sector of the population contributes more strongly to the long term viability of the population (Barlow et al. 2009). Single season studies in the Pantanal, Brazil have found a male: female ratio of 1.5:1.0 and 1.2:1.0 during 2003 and 2004 (Soisalo and Cavalcanti 2006) and 0.6:1 during 2007 (Azevedo and Murray 2007) pointing at either methodological differences or population fluctuations. 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). In addition, some species show clear sexual differences in their response to roads (Mace et al. 1996; Kerley et al. 2002; Gaines et al. 2005). Likewise, studies on livestock predation show that males are the primary culprits for most predation attacks given their higher mobility and possible differences in diet preferences which translates into a higher number of males killed by local people in retaliation for livestock predation (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 mate-seeking behaviors and the distribution of females (Morato et al. 2016). Female jaguars often have lower capture probabilities than males in camera trap studies, a behavior attributed to females having smaller territories and moving less in order to protect their cubs (Salom-Pérez et al. 2007).

Additionally, females may be less likely than males to use human-made trails and roads (Salom-Pérez et al. 2007; Conde et al. 2010; Sollmann et al. 2011) which can also lower their detection rates.

Our study site is composed of well conserved habitat with an ample prey base for jaguars consisting of armadillo (*Dasypus novemcintus*), coati (*Nasua narica*), paca (*Cuniculus paca),* white- tailed deer (*Odocoileus virginianus),* and peccary (*Pecari tajacu*) (Hidalgo et al. 2017; Friedeberg et al. 2022) and artificial waterholes managed by the landowners. Given its relatively small extension of 90 km^2 when compared to jaguar home ranges in the region (average of 296 km^2 for males and 148 for females km^2, Cruz et al. 2021) this patch of habitat can only support a small population yet the continuous presence of resident females and indications of reproductions suggest it is stable. Jaguar detection rates had been fairly constant over the years until 2016 when we see spikes in the detection frequency of male individuals. These events coincide with the loss of forest cover we found using Global Forest Watch resources which goes from almost null to rapidly increasing during this time. This deterioration is taking place precisely in the areas where Mennonites have been establishing communities which leads us to infer at least a correlation between the events. Given that male jaguars have larger home ranges than females (Cruz et al. 2021) the loss of their habitat is more severe (Table 2, Fig. 7). Furthermore, given that males tend to move more than females (Morato et al. 2016) they have a higher probability of human encounters which could lead to their hunting. At least 2 jaguars were killed during the time of the initial Mennonite colonization (personal anecdote). Additionally, 8 new individuals (2 females and 6 males) appear in our cameras for the first time in 2016 but only 2 of these individuals become residents; and 3 resident individuals (2 males and 1 female) that had been consistently spotted in the study area disappear at this time. This turnover could reflect a high rate of immigration and emigration at this time and/or low survival probabilities or a deterioration of habitat suitability (Rosas-Rosas et al. 2008; Rosas-Rosas et al. 2012). The newly identified individuals are probably displaced from the neighboring ranch. Male biased dispersal is common in solitary carnivores, possibly as a mechanism to avoid inbreeding or reduce competition for mates or resources (Kantek et al. 2021). Several male jaguars appear to overlap over the years, notably during 2012 (M1, M2, M3 and M8) and 2017 (M10, M11, M12, M13 and M14). Given that we did not find signs of confrontations, this suggests some sort of intraspecific temporal portioning and tolerance between residents which has been seen before in jaguars (Harmsen et al. 2009; Guilder et al. 2015) as well as other felines (e.g. leopard cat: Grassman et al. 2005). Though home range overlap between males is possible and has been documented (Cavalcanti and Gese 2009) especially when resources are plentiful, we are unsure if the increased amount of transients will establish their territory in our study area or its surroundings. There are several biological corridors connecting this area with larger jaguar populations (Zeller et al. 2013; Ceballos et al. 2021). However, the Laguna de Terminos- Calakmul corridor is the only one that has been verified as functional (Hidalgo et al. 2018). The corridor traverses an increasingly fragmented landscape, fraught with cattle ranches and agricultural land which greatly hamper the dispersing jaguars' probabilities of survival. It is worth noting that even though in our analysis we created the buffers evenly around the camera trap stations, part of the study area contains hydrophilic vegetation and it is possible that jaguars avoid this type of habitat, thus their home ranges might actually overlap more on the forested areas of our study site (Fig. 7). This means that the deleterious effects of habitat loss on jaguars' habitat might actually be worse than we estimated.

We had initially hypothesized that we would be able to see clear indices of instability in the jaguar population studied. We believe that although this study did not include formal statistical analysis, our descriptions of basic trends in number of detections, number of individuals and sex and resident- transient proportions is enough to see how the population's stability is being affected. Given that deforestation is the main threat that jaguars face in the region (Hidalgo et al. 2017) and we have witnessed acute deforestation in recent years, we infer that it is precisely this factor what is causing the instability.

Conclusion

Given that 32% of the world's 234 carnivore species are threatened (Sechrest et al. 2002) and human land use and habitat conversion are largely responsible for these extinction rates

(Zanin et al. 2015), long-term carnivore population monitoring programs that enable managers to assess changes in their structures and that of their prey are particularly important for the conservation of these species. Additionally, many basic life history traits are only apparent when following a population over long periods of time. Long-term research has significantly enhanced our understanding of cooperation, dispersal, grouping, and reproductive success in carnivores (Smith et al. 2017). Fragmentation and loss of habitat are major threats to the viability of endangered species and by 2008 the International Union for Conservation of Nature (IUCN) had determined that habitat fragmentation threatened 40% of endangered species (Schipper et al. 2008). The negative effects of fragmentation go beyond the initial loss of habitat. Natural flows of matter and energy are interrupted and altered, and populations become isolated, which reduces the genetic flow between them, promoting processes of genetic drift which decrease genetic variability and increase inbreeding (Templeton et al. 1990). Our findings show a stable but increasingly susceptible jaguar population in in the southeast of APFFLT and underlies the importance of protecting their habitat and the need for government enforced land use regulations in areas that are essential for endangered species such as jaguars. We have documented how anthropogenic pressure, in the form of habitat fragmentation is affecting this population over time. We identified indicators such as number of resident individuals, number of detections and sex ratios that are changing in response to alterations in the populations’ habitat and forsee that these indicators will increasingly vary if the protection in our study area is not more strongly regulated.

CAPITULO 2

Landscape patterns in the occupancy of jaguars (*Panthera onca)* and their primary prey species in a disturbed region of the Selva Maya in Mexico

Landscape patterns in the occupancy of jaguars (*Panthera onca)* and their primary prey species in a disturbed region of the Selva Maya in Mexico

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Abstract

In order to prioritize the conservation and management efforts to protect jaguars (*Panthera onca)*, it is of utmost importance to determine their tolerance in face of human disturbances, habitat modifications and varying degrees of prey availability. We assessed the occupancy probability of jaguars and five of their most common prey species throughout a heterogeneous landscape in the Selva Maya in southern Mexico: armadillo (*Dasypus novemcinctus*), coati (*Nasua narica*), paca (*Cuniculus paca*), white-tailed deer *(Odocoileus virginianus)*, and collared peccary (*Dicotyles tajacu*). Additionally, we projected prey and jaguar occupancies onto a 5,993 km^2 landscape based on the habitat type in the area. We averaged the best prey models ranked by QAICc and found that white-tailed deer had the highest average occupancy probability of 0.72 ± 0.06 and paca the lowest with 0.14 ± 0.04.

The average occupancy probability for jaguars was 0.35 ± 0.07 and the strongest predictor of jaguar occupancy was a positive effect of collared peccary occupancy. These findings support previous studies that show that predator distribution is largely influenced by their prey availability, even in the midst of degraded habitats, and underlies the essential need to incorporate protection plans for prey species in jaguar conservation strategies.

Keywords Jaguar, Site Occupancy, Selva Maya, Conservation, Carnivore Ecology

Introduction

The Jaguar *Panthera onca* (Linnaeus 1758) is a large New World carnivore that has exhibited population declines and range contractions across the Americas (Paviolo et al. 2016) and is categorized as Near Threatened in the IUCN red list (Caso et al. 2008) and considered in danger of extinction in Mexico listed under the NOM-059-SEMARNAT-2010 (SEMARNAT, 2010). The Selva Maya is the largest block of tropical forest in Mesoamerica and it is home to the largest jaguar population in the northern hemisphere (Zeller 2007; Medellin 2011; de la Torre et al. 2018); Though these tropical moist lowland forests are believed to be areas of high probability of survival for jaguars in the long-term (Caso et al. 2015), more recent analyses point to the increasing fragmentation of jaguar populations in this region (Quigley et al. 2017) likely caused by the expansion of agriculture, livestock herding and road development (Tovar and Villanueva 2009). The Mexican states of Tabasco, West Campeche and Chiapas are some of the regions where habitat loss and consequent fragmentation has been more profound in Mesoamerica (Hidalgo et al. 2015). Nevertheless, there are peripheral jaguar populations in the *Area de Proteccion de Flora y Fauna Laguna de Terminos* (Terminos herein) and its surroundings in the southwest portion of the state of Campeche (Figure 1) (Rabinowitz and Zeller 2010; Hidalgo et al. 2019). Terminos has an estimated jaguar density of 1.93 ± 0.52 individuals/100 km^2 and there is a great risk of it becoming an isolated population from others in southern Mexico due to habitat transformation in the form of agriculture, cattle ranching, urban growth and road development (Hidalgo et al. 2018; de la Torre et al. 2018; Hidalgo et al. 2019).

Environmental and anthropogenic factors limit the distribution of jaguars (Arias et al. 2020). In South America, jaguar densities are affected by the degree of anthropogenic disturbance and although densities can be high in some productive areas (Polisar et al. 2017), they decrease sharply in highly degraded areas (Paviolo et al. 2016). However, recent studies in agro-landscapes have concluded that unprotected and productive areas can sustain jaguar populations or at least provide important biological corridors as long as remnants of natural habitat are still present (Boron et al. 2016). Jaguar presence and occupancy are negatively affected by the proximity of human settlements and/or roads (Arroyo-Arce et al. 2014); and human activities such as cattle ranching (Rosas-Rosas 2010). Habitat fragmentation is one of the major threats to felid conservation (Zanin et al. 2015) as it affects potential landscape connectivity (Olsoy et al. 2016) and increases the risk of encounters with humans or vehicles (Colchero et al. 2011; Duenas-Lopez et al. 2015;) hinders gene flow, promotes drift-induced differentiation and increases the risk of extinction in the long run (Yumnam et al. 2014).

The distribution and abundance of prey species is a fundamental factor in the distribution of jaguars (Greenspan et al. 2020). Common jaguar prey species in the Selva Maya region such as collared and white–lipped peccaries *Dicotyles tajacu* (Linnaeus 1758), *Tayassu pecari* (Link 1795), Central American red brocket deer *Mazama temama* (Kerr 1792), white–tailed deer *Odoicoleus virginianus* (Zimmermann 1780), nine banded armadillo *Dasypus novemcinctus* (Linnaeus 1758), paca *Agouti paca* (Linnaeus 1766) and coati *Nasua narica* (Linnaeus 1766) (Weckel et al. 2006; Petracca 2010) are also preferred game species for local hunters (Reyna-Hurtado et al. 2010) and are found in the Laguna de Teminos- Pantanos de Centla wetland complex (Hidalgo et al. 2017). The combination of severe habitat fragmentation with increased hunting pressure threatens the integrity of wildlife prey populations (Urquiza-Haas et al. 2009), exacerbating the already precarious situation of large predators such as jaguars.

White lipped peccary and white- tailed deer sport hunting is permitted in Campeche under the official scheme of Conservation and Management Units (UMA for its Spanish initials) (Reyna-Hurtado 2010). Peccaries in anthropogenic landscapes exhibit smaller group sizes as compared to those in wilderness areas (Reyna-Hurtado 2010).

Various attempts to estimate jaguar population densities in regions of the Selva Maya have taken place over the years. However, most of these studies have focused on well-conserved, intact habitats (Chavez et al. 2010; Avila Najera et al. 2015; Harmsen et al. 2017), precluding the evaluation of jaguar tolerance of degraded or prey-depleted habitats. These studies can be useful to compare to those done in nearby regions and contribute important information regarding jaguar population status, their dynamics and the conservation efficiency in well-preserved areas. However, in order to make better- informed decisions concerning conservation strategies we must first understand jaguars' tolerance for disturbance. Previous investigations have incorporated disturbed areas into their analysis, yet they have constituted only a small proportion (de la Torre et al. 2011) or have used areas subject to well- managed natural resource extraction (Tobler at al. 2018).

In this study we estimate the detection and occupancy probabilities of jaguars and five common prey species with the objective of measuring the effect of habitat type, prey availability and human presence on the occurrence of jaguars in a severely fragmented area within the Selva Maya.

Methods

Study Area

The study area is 5,993 km^2 in the western portion of the Selva Maya, along the Terminos JCU (Jaguar Conservation Unit), located in the municipalities of Carmen and Palizada in the state of Campeche, Mexico (Figure 8). It is situated between 2 and 3 meters above sea level in the coastal plains of the Gulf of Mexico within the physiographic sub-province of Pantanos and the Plains of Tabasco (INEGI 2015). The climate is warm and humid with an average temperature of 27 °C and up to 2,000 mm of annual precipitation (INEGI 2013). Most of the area is subject to seasonal floods, which can last from June to February, followed by a relatively dry season from March to May where the highest areas are partially or completely dry (Ocaña and Lot 1996). Depending on the flooding regime, different types of vegetation flourish: hydrophilic vegetation, flooded grasslands, mangroves, evergreen riparian forests and medium and low tropical forests (Ocaña and Lot 1996). The human activities in the region include fishing, hunting, irrigated agriculture and cattle ranching (Soto-Galera 2010). The land tenure is mostly private, with few *ejidos* (a form of communal land property) and approximately 100 km^2 that have been assigned for conservation and sustainable wildlife management by the owners in the form of a wildlife management unit of legal white-tailed deer hunting. This private land is composed of well conserved seasonally flooded forest.

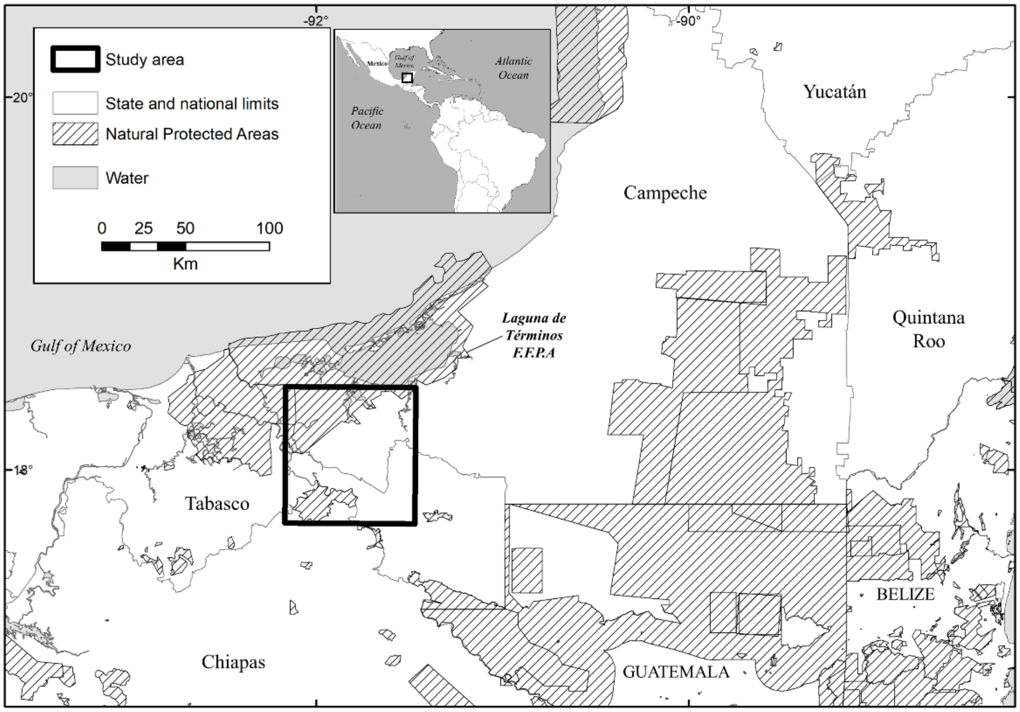

Fig. 8 Study Area. The figure shows the study area in the west of Campeche, Mexico on the edge of the Laguna de Términos and Panatanos de Centla Natural Protected Areas.

The photographic captures used to determine the presence of all species were obtained from 2 yearly camera trap surveys performed during the dry seasons between February and July

2015 and between February and July 2016 in Terminos and the adjacent areas (Figure 9). Each survey in each quadrant demonstrated in Figure 8 lasted at least 3 months (between February and July). The camera setup consisted of 143 camera stations out of which 7 were double and 136 were single (125 Pantheracams® model IV or V, and 18 Cuddebacks) and was performed following recommendations by Tobler and Powell (2013) where the cameras were placed on trails or waterholes to increase capture probabilities at intervals of approximately 1.5 to 2.0 km and attached to trees at an approximate height of 50 cm (Noss et al. 2013). At approximately 5 m in front of the camera, we placed a partially open sardine can to function as a lure. Placing lures has been shown not to bias density estimates in large carnivores but may improve individual identifications or detectability (du Preez et al. 2014). The cameras were programed to run 24 hours during the duration of the study, each motion-triggered event was programmed to take 3 pictures every minute followed by a standby of 1 minute, all images were identified to species (Aranda et al. 1994; Ceballos et al. 2002).

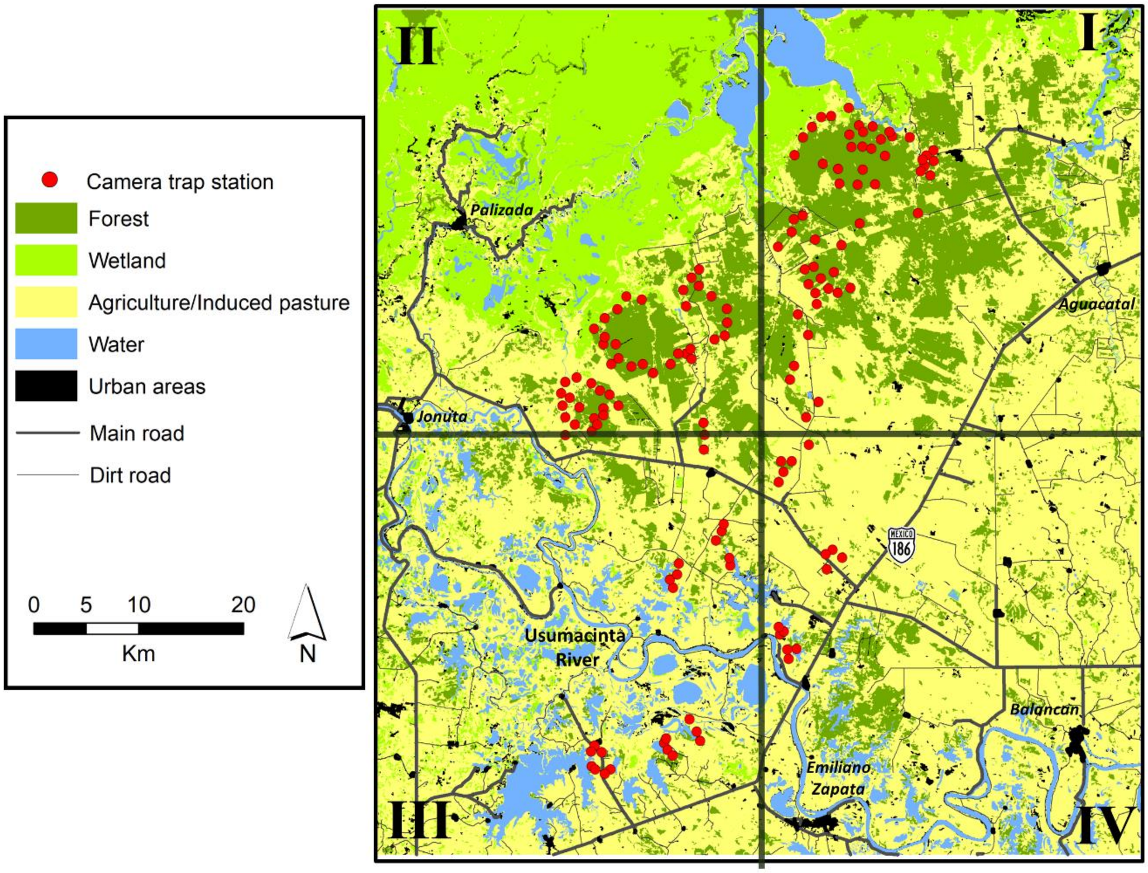

Fig. 9 Camera Trap Locations. The figure shows the camera trap locations throughout different habitat types in a disturbed area in the Selva Maya during 2015 and 2016 divided into four quadrants for easy identification: Quadrant I: fragmented forests, Quadrant II: Palizada wetlands, Quadrant III: Usumacinta wetlands and Quadrant IV Balancan agrolivestock landscape.

The ability to measure the influence of covariates on the species' occurrence and detection provided by site occupancy methodology is extremely valuable when attempting to elucidate the distributional behavior and preferences of endangered and low density-occurring species. Additionally, the incorporation of measurements of imperfect detection provide studies with more robust estimates (Guillera-Arroita et al. 2014) and represent a viable alternative for large scale single or multi-species studies that can improve the estimations provided by relative abundance indices (MacKenzie and Nichols 2004).

For our occupancy and detection analyses, we chose covariates that have been found to affect the presence and abundance of jaguars and the elected prey species: prey abundance (for jaguars) (Rabelo et al. 2019), habitat type (Ceballos et al. 2002; De Perno et al. 2003; Desbiez et al. 2009; Greenspan et al. 2020), distance to human settlements and roads (Garcia Marmolejo et al. 2015; Carrillo-Reyna et al. 2015; Hernandez-Perez et al 2020) and human abundance (Urquiza-Haas et al. 2011; Ramos-Robles et al. 2013; Arroyo-Arce et al. 2014). Season and year were not included as variables as we don't consider there to be significant changes in species abundance or distribution over short periods of time given that most of our study area is composed of private land and there is little illegal hunting. Both our surveys were done during the dry season because flooding makes it impossible to survey during the wet season.

Habitat type analysis

We used a mosaic of two LANDSAT 8 images of the study area obtained on the 8th of January 2017 and performed a supervised classification of the habitat types using the Maximum Likelihood method from the software ENVI 5.3. We classified the images according to their reflectivity in seven habitat types: forests (tropical dry forest, tropical deciduous forest and secondary growth forests), mangroves, grasslands, wetlands, and agro-livestock (agricultural land and induced grasslands), water and urban areas. Once classified, we extracted the habitat type around each of the camera stations using circular buffers with 1.0 km diameters and obtained the proportion of each one. Because the occurrence of water, urban areas and mangroves was very small in the buffers, we removed these categories from the analysis. The resulting values of each habitat type were used as proportions of total buffer area in the analysis. For easier identification, we divided the study area into a quadrant of distinct geographic regions: Quadrant I: fragmented forests, Quadrant II: Palizada wetlands, Quadrant III: Usumacinta wetlands and Quadrant IV Balancan agro livestock landscape (Figure 9).

Distance to roads and human settlements

Using maps of the study area (INEGI 2013), we calculated the Euclidian distances in meters from the location of each camera trap station to the nearest paved road and the nearest human settlement of at least 50 people.

Human abundance index

Similar to measures of Relative Abundance Index (RAI) based on capture frequencies, we obtained a human abundance index (HAI) by dividing the number of photographs of people that were taken by the number of days the camera trap was active in each of the camera trap stations. Though we know this estimate is not without errors as it does not incorporate imperfect detection, we believe that for our purposes it is sufficient as a general measure of human presence.

Site Occupancy Estimations for Prey Species

For the purposes of our study the two survey periods (2015 and 2016) were considered a single season consisting of 100 days, as it was assumed there were no changes in which sites were used by jaguars or prey species in consecutive years. Not all camera traps were active at the same time during the entire survey season, hence detection data was considered 'missing' for sites on the days when the cameras were not operating. We elaborated individual detection histories based on presence (1) or absence (0) for five of the most common jaguar prey species in the region and used habitat type, distance to roads and distance to settlements as covariates for occupancy and number of active camera trap days, absence or presence of forest and HAI as covariates for detection probability. We examined pair-wise correlations between variables and eliminated grassland from habitat type as it was found to be highly (|r| >0.70; Taylor 1990) negatively correlated to forest (Supplements Table 1). The detection probability and site occupancy were calculated from the capture histories using the methods suggested by Mackenzie et al. (2003) with the equation: $\text{logit}(\psi i) = \ln(\frac{\psi i}{1-\psi i}) = \alpha 0 + \alpha 1 x 1, i + \alpha 2 x 2, i$ utilizing the Unmarked package (Fiske and

Chandler 2015) in R (R Development Core Team 2019). However, we did not use a stepwise approach and instead combined all detection and occupancy models using the dredge function given that we had a manageable amount of covariate combinations and wanted to see all covariate interactions. Following the recommendations of MacKenzie and Bailey (2004) we assessed the goodness of fit of our global models using a Pearson chi-square analysis and parametric bootstrap procedure prior to running the occupancy analyses. Given that several species' models had over dispersion (Supplements Table 3), we calculated a QAICc (quasi Akaike Information Criterion) and used this metric to select the best fitting models for each prey species. Then, we averaged the models with delta ≤ 2 following the recommendations of Richards (2005) who states that the models with these values can be considered to be as good as the best one (Supplements Tables 4-15).

Site Occupancy Estimations for Jaguars

Similar to prey species, number of active camera trap days, absence or presence of forest and human abundance index were used as covariates for detection probability. The resulting occupancy probabilities from the prey species and human influence (expressed as distance to roads and settlements) were used as covariates to estimate the occupancy probability of jaguars. Given that the correlation analyses revealed that coati, white- tailed deer and paca were correlated with each other, we removed them from the analysis (Supplements Table 2). As with prey species, we calculated the models' QAIc and averaged those with delta ≤ 2.0.

Occupancy Projections

We constructed a grid with 1 km² cells in an area of 5,993 km² surrounding our study area and stretching out to the west of Campeche, the east of Tabasco and a small northern region of Chiapas. We then projected the occupancy probabilities of each species onto these cells based on the betas of each covariate using ArcMap 10.3 (ESRI 2012). The values projected on the maps represent the occupancy probabilities of the various species.

Results

During the 100 days of survey, 11 cameras were active from 20 to 40 days, 34 were active from 40 to 60 days, 50 were active from 60 to 80 days, 41 were active from 80-99 days and 7 were active all 100 days. This averaged 71 active camera trap days and a survey effort of 10,147 days. Our coati detections represented 41.50% of total detections from all species, white-tailed deer detections were 35.60%, collared peccary detections were 9.80% , armadillo detections were 4.60%, paca detections were 3.30%, , and jaguar detections were 5.20% (Table 3).

Table 4. Number of detections of prey species gathered from a survey in a disturbed area in the Selva Maya during 2015 and 2016, percent of total detections corresponding to that species, number of sites with species detections and mean detections per site.

Species	**Detections**	**% of total detections**	**Number of sites with detections**	**Mean detections per site**
Armadillo	194	4.60%	44	1.35 ±4
Coati	1,757	41.50%	101	12.2 ±38
Paca	141	3.30%	19	0.98 ±4
White-tailed deer	1,508	35.60%	100	10.5 ±30
Collared peccary	413	9.80%	72	2.9 ±7
Jaguar	222	5.20%	38	1.5 ±3.8
Total	4,235	100%	374	

The results from the Mackenzie Bailey test showed that armadillo (Č = 1.28) and paca (Č =1.22) resulted in over dispersion and did not pass the test (Supplements Table 3). Thus, we used a quasi-likelihood version of AIC (QAIC) to find the best fitting models and averaged those with delta ≤ 2 (Table 4 Supplements Tables 5, 7, 9, 11, 13). The species with the highest occupancy probabilities were coati (β 0.71% ± .05) with a negative effect of agro-livestock (β -5.62 ± 1.60) and positive effect of forest (β 0.17 ± .50) habitat and white- tailed deer (β 0.72% ± .06) with a negative effect of agro-livestock (β -5.9 ± 2.0) and positive effect of forest (β 0.79 ± ± 0.95) and wetland (β 12.64 ± 7.30) (Table 5 and Figure 10). Human abundance and forest cover were the detection covariates that were present in most of the best models from the prey species (Supplements Tables 4, 6, 8, 10, 12).

Table 5. Best model explaining the occupancy of each species in a disturbed area in the Selva Maya during 2015 and 2016. p=detection probability, psi=occupancy probability, df= number of parameters in the model $QAIC_c$= calculated c-hat from the Quasi Akaike Information Criterion, delta: difference in QAIC values relative to the top model, weight= AIC_c weight

Species	**Best model**	**df**	**loglik**	**QAICc**	**Delta**	**Weight**
Armadillo	p(capturedays+forest)	4	-588.92	925.62	0	0.08
Coati	psi(agrolivestock) p(capturedays+forest+ humanabundance)	6	-1708.57	3429.75	0	0.40
Paca	psi(agrolivestock)+ p(humanabundance)	4	-374.17	618.85	0	0.10
White-tailed deer	psi(forest+wetland+ agrolivestock) p(capturedays+forest+ humanabundance)	8	-1788.45	3593.99	0	0.48

Collared peccary	psi(forest) p(forest+humanabundance)	5	-975.28	1961.01	0	0.07
Jaguar	psi(collared peccary+armadillo) p(capturedays+forest+ humanabundance)	7	-430.79	876.41	0	0.48

Table 6 Averaged occupancy probabilities of each species in a disturbed area in the Selva Maya during 2015 and 2016 and their covariate effects using QAIC and averaging those with delta ≤ 2.

Species	**Goodness of Fit Result Ĉ**	**Number of averaged models with delta <2**	**Average occupancy probability**	**Covariate effects**
Armadillo	1.287 overdispersion	13	33 ±0.07	β 1.39 ±1.8 agrolivestock β 0.34 ±0.67 forest β -2.28 ±3.43 wetland
Coati	0.97	2	71 ±0.05	β -5.62 ±1.6 agrolivestock β 0.17 ±0.5 forest
Paca	1.22 overdispersion	5	14 ±0.04	β 2.37 ±1.8 agrolivestock β 0.64 ±0.38 forest
White-tailed deer	0.90	2	72 ±0.06	β -5.9 ± 2.0 agrolivestock β 0.79 ±0.95 forest β 12.64 ±7.3 wetland
Collared peccary	0.96	15	49 ±0.07	β -1.79 ±1.9 agrolivestock β 0.87 ±0.81 forest

Jaguar	0.78	2	35 ±0.07	β 15.56 ±4.5 collared peccary occupancy β -12.04 ±11.2 armadillo occupancy

The occupancy landscapes for the smaller species (armadillo, coati and paca) had mixed results. The armadillo landscape projection displayed general low probabilities in the fragmented forest (quadrant I) and Balancan agro livestock landscape (quadrant IV) regions with patches of medium probabilities in the fragmented forests (quadrant I) and Usumacinta wetlands (quadrant III) (Figure 12). The projection for coati showed a clear low occupancy probability in the Usumacinta wetlands (quadrant III) and very high probabilities in the remaining 3 quadrants (Figure 12). The paca projection showed generally low occupancy probabilities throughout the region and medium probabilities in the Usumacinta wetlands (quadrant III) and some patches in the fragmented forests (quadrant I) and Palizada wetlands (quadrant II) (Figure 12). The occupancy landscapes of the larger species (white- tailed deer and collared peccary) generally showed higher occupancy probabilities in the patches of well-preserved forests that constitute private ranches in the west of Campeche (quadrant I) and areas of low probabilities in the Usumacinta wetlands (quadrant III) though the white-tailed deer showed high occupancy in a larger part of the projected area (Figure 12). We examined pair-wise correlations between the covariates used for jaguar occupancy and eliminated coati, white- tailed deer and paca as they were found to be highly ($|r| > 0.70$; Taylor, 1990) correlated with each other (Supplements Table 2).We used QAIC to find the best fitting models and averaged those with delta ≤ 2 (Supplements Table 14). The best model for jaguars had a QAICc of 876.4 and a weight of 48.0% and had an effect of capture days, forest and human abundance on detection and collared peccary and armadillo occupancies on occupancy (Table 4). Their average occupancy was 35.0% ± 0.07, and had a positive effect of collared peccary occupancy (β 15.56 ± 4.50) and a negative effect of armadillo occupancy (β -12.04 ± 11.20) (Table 5, Figure 11). The occupancy landscape projection for jaguars showed high occupancy probability patches in the fragmented forests (quadrant I) and Palizada wetlands (quadrant II) and generally low occupancy probabilities in the

Usumacinta wetlands (quadrant III) and Balancan agrolivestock landscape (quadrant IV) (Figure 13).

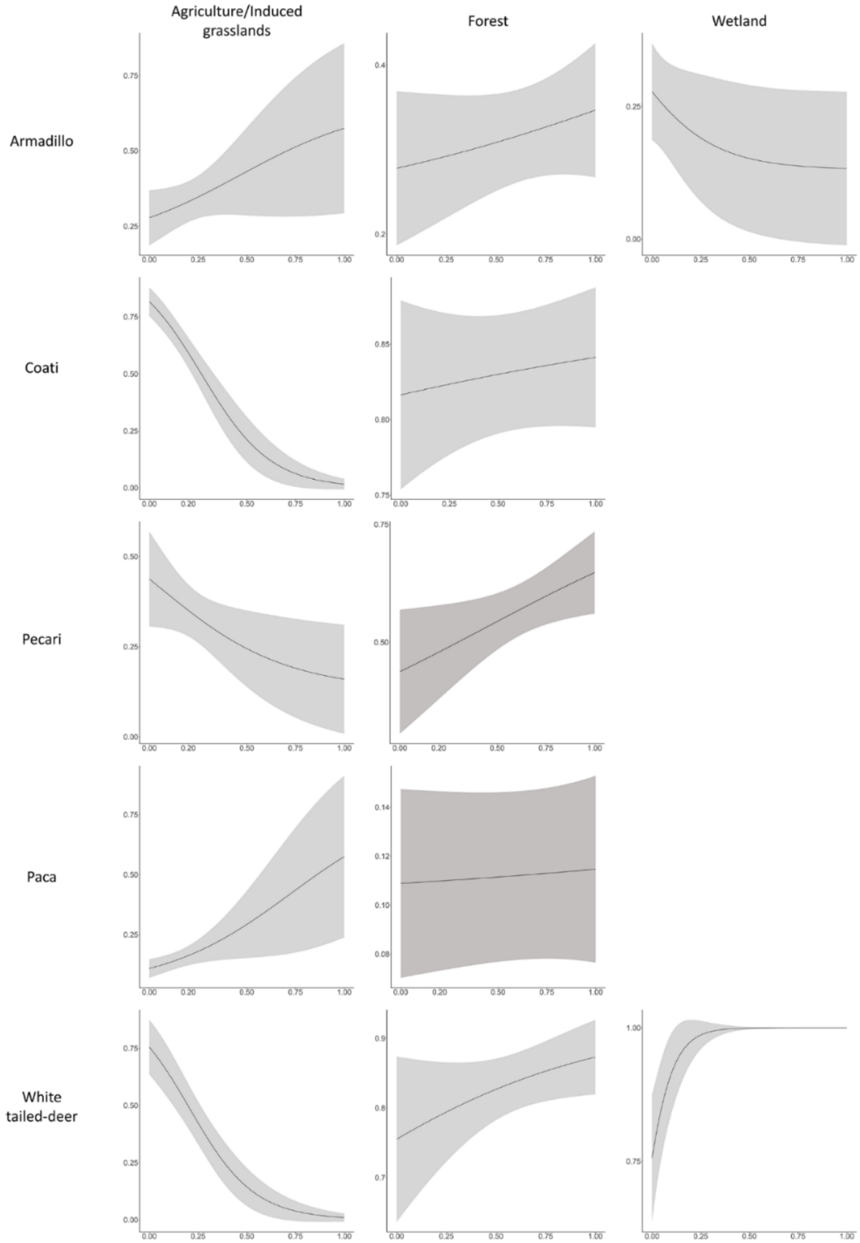

Fig. 10 Occupancy Graphs for Prey Species. The figure shows the occupancy graphs for all prey species studied in a disturbed area in the Selva Maya during 2015 and 2016 as a function of habitat types: agrolivestock, forest, and wetland.

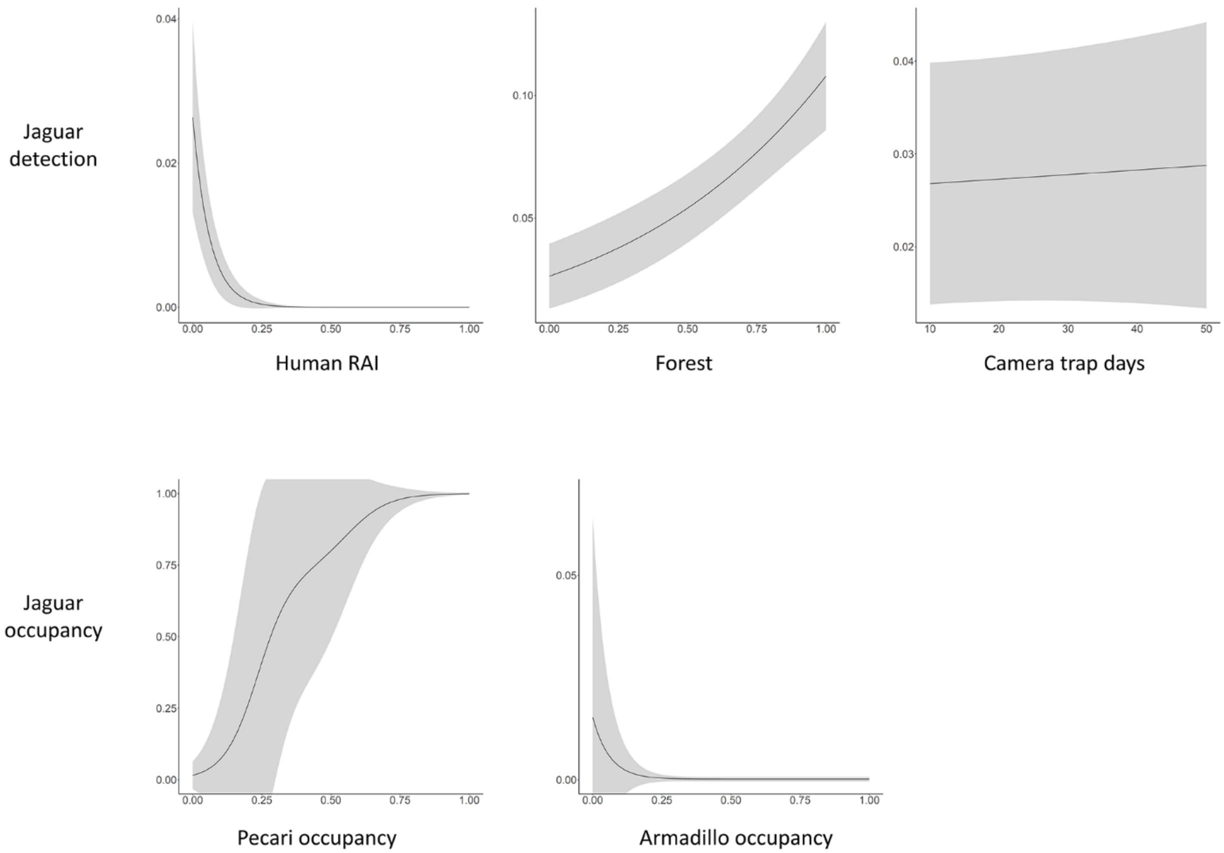

Fig. 11 Occupancy Graphs for Jaguars. The figure shows the jaguar's occupancy probability as a function of peccary and armadillo occupancy and the jaguar's detection probability as a function of human relative abundance index RAI, forest and camera trap days.

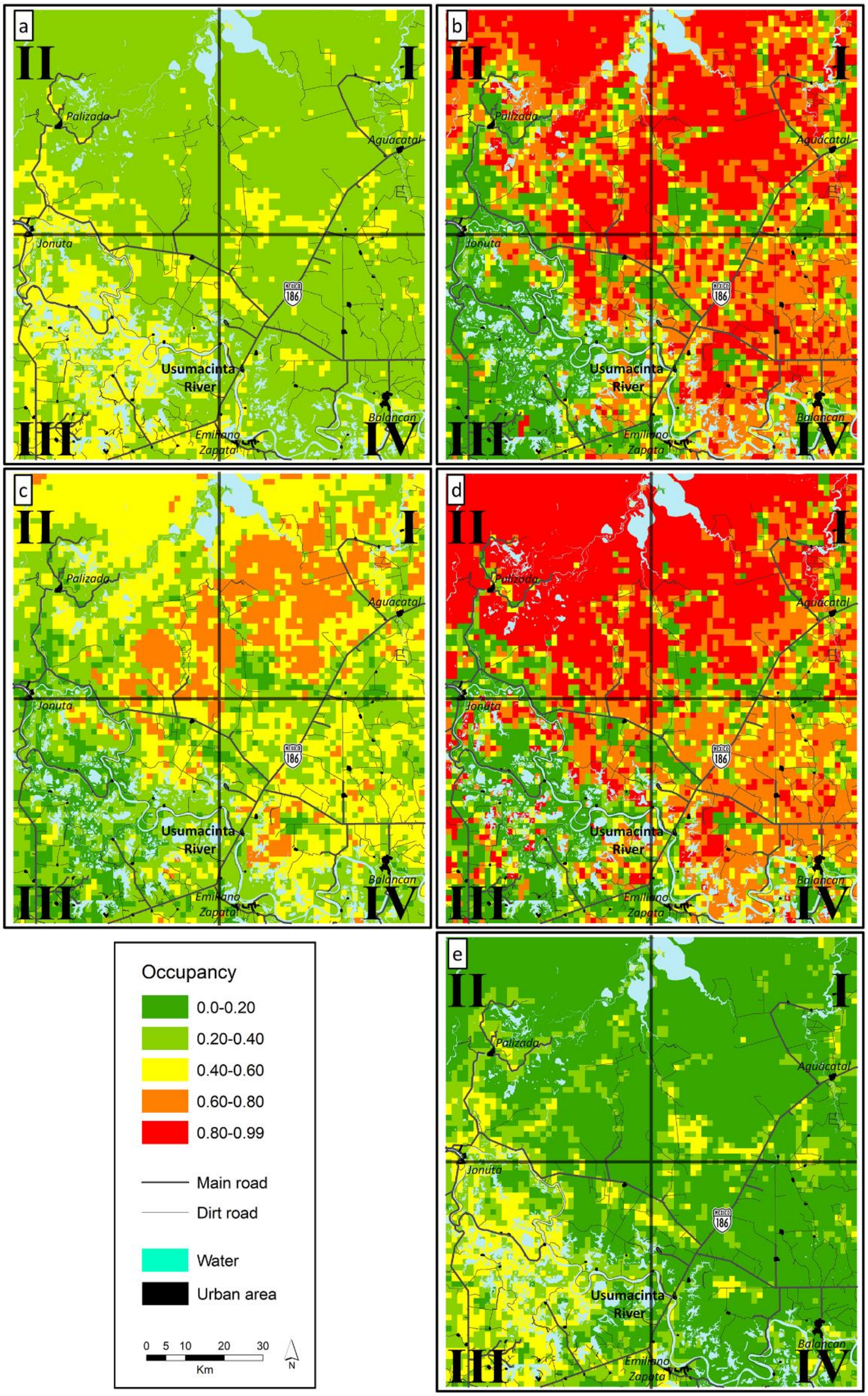
a
b
c
d
e
I
II
III
IV
Palizada
Aguacatal
Jonuta
186
Usumacinta River
Balancan
Emiliano Zapata
Occupancy
0.0-0.20
0.20-0.40
0.40-0.60
0.60-0.80
0.80-0.99
Main road
Dirt road
Water
Urban area
0 5 10 20 30
Km
N

Fig. 12 Prey Species Projections. The figure shows the prey species occupancy probability projected onto an area of 5,993 km² surrounding our study area during 2015 and 2016 and stretching out to the west of Campeche, the east of Tabasco and a small northern region of Chiapas in Mexico.

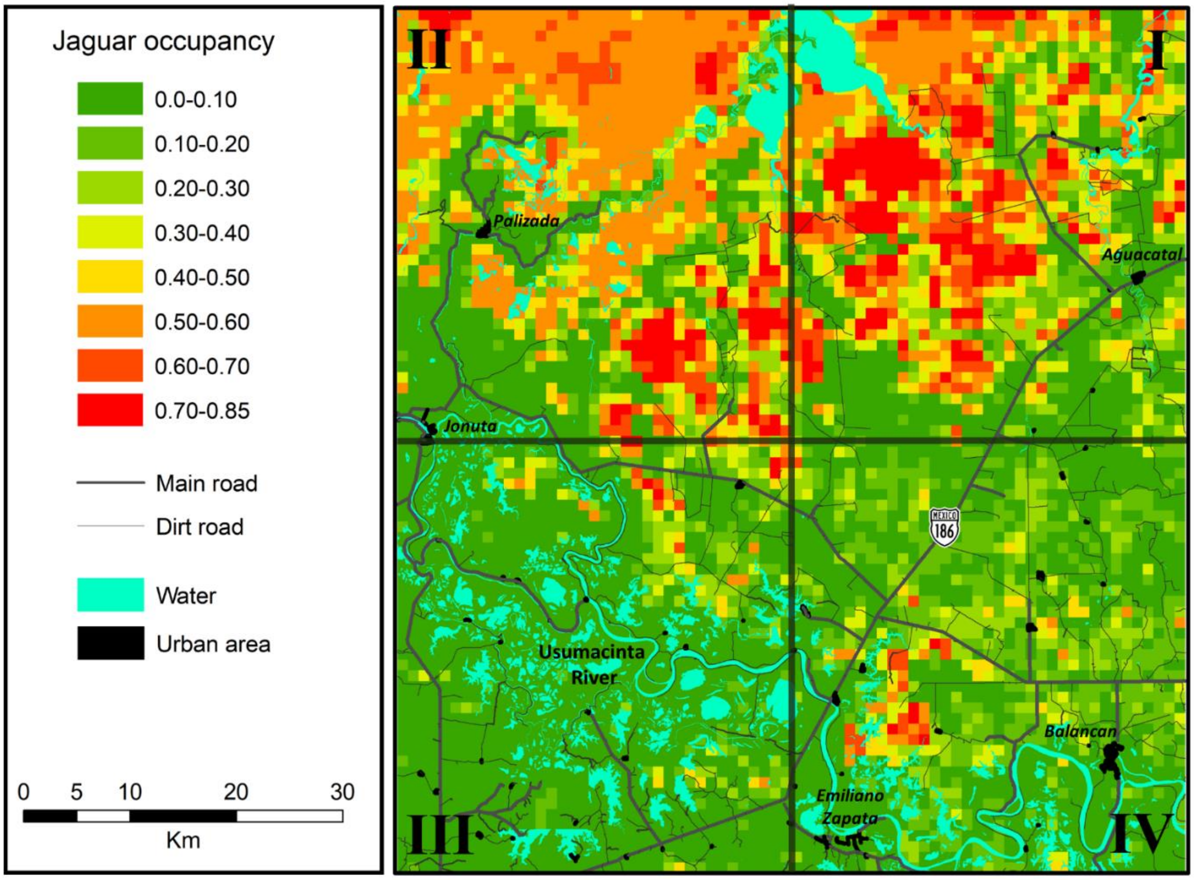

Fig. 13 Jaguar Occupancy Projection. The figure shows the jaguar occupancy probability projections onto an area of 5,993 km² surrounding our study area during 2015 and 2016 and stretching out to the west of Campeche, the east of Tabasco and a small northern region of Chiapas in Mexico.

Discussion

Despite having limitations in the occupancy estimations of small prey, we believe that our analysis adequately modeled the influence that the presence of peccary exerts on jaguar occupancy, even when other prey species are available and more abundant. This is unsurprising given that throughout jaguar range several studies have found peccary to be an important prey species (Harmsen et al. 2010; Miranda et al. 2018). Even though habitat type was not present in the best fitting model of jaguar occupancy, it is important to note that it still poses a strong limiting factor on their conservation as most preferred prey species rely on well conserved habitat (Reyna-Hurtado et al. 2010; Ramos-Robles et al. 2013; Petracca et al. 2014; Contreras-Moreno et al. 2015).

Site Occupancy Estimations and Projections for Prey Species

The Usumacinta basin region identified as quadrant IV in our study holds the lowest species' occupancy probabilities. This is unsurprising given the history of extensive deforestation that the area has been subjected to since the 1940's to give way to pastures (Kolb et al. 2012) through government credits and by a high demand for bovine meat (Manjarrez et al. 2007). Given that our survey was designed to increase the capture probability of jaguars, the separation between camera stations was likely too large to effectively capture small mammals such as armadillo, coati or paca. This was probably reflected in that two of these species did not pass the Mackenzie- Bailey goodness of fit test and thus the results should be taken with measure. However, the lack of strong habitat selection for armadillos found in our study (Figure 9) could be a result of the rapid evolutionary radiation from the tropics that they have experienced, their extraordinary ecological potential and that now they face many diversified ecological situations (Gammons et al. 2009). Though coatis are known to adapt well to anthropogenic disturbances (Novack et al. 2005), the negative effect of agro-livestock habitat and positive effect of forest that we observed suggests a preference for wooded habitats (Figure 10) or a result of hunting in the region (Escamilla et al. 2000). The low occupancy probability that we found for paca (β 14.0% ± 0.04) might also reflect a strong hunting pressure (Escamilla et al. 2000) (Figure 10). Our results on collared peccary occupancy (Figure 9) coincide with those found by Thornton et al. (2020) where human footprint exerted a negative effect on the occupancy of collared peccary and with Petracca et al. (2014) where agricultural encroachment was the limiting factor for collared peccary presence in a Central American corridor. It is unsurprising that white-tailed deer had the highest occupancy probability of β 72% ± .06 as it is known that this species has a high tolerance for degraded and open habitats (Bello-Gutierrez et al. 2010) (Figure 9). In accordance with the Landscape of Fear (Laundre et al. 2010), white-tailed deer might be using wetlands to conceal themselves from hunters who do not regularly use this habitat type (Contreras Moreno et al. 2015). Recent studies (Contreras-Moreno et al. 2021) found that white-tailed deer in our study area do not move to drier areas during the wet season and have a strong site fidelity suggesting these results would be consistent across seasons.

Site Occupancy Estimations and Projections for Jaguars

Several studies have estimated jaguar site occupancy across the species' range (Zeller et al. 2011; Sollmann et al. 2012; Tobler et al. 2015). Given that our study area is composed of a mosaic of preserved and disturbed habitat patches, it is unsurprising that our estimation is in the lower range (β 35.0% ± .07) when compared to studies carried out in better conserved areas. Our results are closer to the estimates made in Rio Magdalena (β 24-77% and 03-33%) where patches of palm tree plantations are ubiquitous (Boron et al. 2019). Felid distribution is influenced largely by prey availability (Fueller and Sievert 2001; Bled et al. 2015) and though this has been evaluated using indices of presence/absence (Petracca et al. 2014) or prey species richness (Zanin et al. 2015), to our knowledge it has not been assessed, as prey occupancy, with other anthropogenic and environmental factors to determine which variables exert the strongest influence on jaguar occupancy. The prey- abundance hypothesis (Palomares et al. 2001; Spong 2002) states that the distribution of obligate carnivores such as jaguars should be correlated to that of their primary prey. Additionally, the ecology of Felidae, is driven largely by prey availability and some studies (Santos et al. 2019) have found that it is more determinant in their habitat use than both landscape variables and interaction with other species. However, more recent studies (Kohl et al. 2018; Coon et al. 2020) suggest that at finer scales, the habitat selection of predators and prey is more varied than previously thought. It is possible that jaguars are not only preferring habitats where their preferred prey, such as collared peccary (Scognamillo et al. 2003; Azevedo and Murray 2007) are found, but also those in which they can hunt more easily. This would support optimal foraging theory, where predators are believed to select prey species that maximize the resources gained and minimize their foraging costs (Griffith 1975). Even though the large group associations and aggressive behavior of peccaries can represent a risk for jaguars, these same characteristics increase their detectability (Sollmann 2011).

Conclusion

The occupancy projections presented herein were especially insightful in determine jaguar occurrence in the region. Because some of our sites in conserved forests have had constant jaguar captures over the years, without projecting the probabilities onto a larger regional landscape, we could have erroneously concluded that the occupancy in this type of habitat, as a whole, was high and missed other variables that influence jaguar occurrence. Given that other areas in our study site also have conserved forests but are owned by *ejidos* or communities that practice subsistence and illegal hunting, it is likely that hunting activity of both jaguars and their prey is the limiting factor for their occupancy. Given that the landscape in our study area is completely flat, species cannot migrate to higher altitudes during the wet season but can move further inland which would also increase the interactions with human populations and potentially foster more conflict. Furthermore, this behavior is important given increased flooding projected under climate change scenarios (Morita and Robinson 2000; Marquez- Garcia et al. 2010) and should be taken into consideration when planning the location of new conservation areas along with conflict mitigation strategies.

Some of the private ranches we monitored have established wildlife management units (WMUs) for white- tailed deer hunting and thus take the necessary measures to secure a viable population required to have permits, including not hunting other protected species like jaguars. Given the threatened state of jaguars in Mexico, despite both private and governmental continuous efforts and the difficulty in properly securing natural protected areas given their communal and private land tenure, establishing more WMUs for legal hunting could increase the protection of jaguars and other large carnivores by securing an ample prey base as well as effective hunting regulations. Given that jaguars exist at low population densities, the conservation of large landscapes and corridors of adequate habitat are needed to ensure their long term survival.

Several attempts have been made to project jaguar density estimations to regional scales based solely on the habitat type of small surveyed areas (Ceballos et al. 2007). Government conservation strategies largely rely on the data provided by these studies. Given that there is an inherent high risk of overestimation in these extrapolations (Gros 1996), we believe that occupancy landscape projections could be a viable alternative to assess the possible occurrence of species throughout a wider landscape. The information gathered in this study will help make better informed and realistic decisions on the management and conservation of jaguars and some of their most common prey species in the region.

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DISCUSIÓN GENERAL

The general objective of this work was to assess the threshold that jaguars have for degraded habitats, loss of prey and human presence using a jaguar population in the NPA Laguna de Terminos region as a model. We used site occupancy probability and the long-term trend of the population as indicators for this human dominated landscape tolerance.

Although the long term study's descriptions of basic trends in number of detections, number of individuals and sex and resident-transient proportions characterizes how the population's growth is affected. Average jaguar detection rates had been constant over the years until 2016 when we see spikes in the detection frequency with male bias individuals. These events coincide with the loss of forest cover estimated using Global Forest Watch resources, which goes from almost null to rapidly increasing during this time. This deterioration is taking place precisely in the areas where large-scale farming (Mennonites acquired land) communities. Given that male jaguars have larger home ranges than females (Cruz et al. 2021) the loss of their habitat is more severe (Table 2). Furthermore, given that males tend to move more than females (Morato et al. 2016) they have a higher probability of human encounters which could lead to their killing. A population turnover event occurred in 2016, 8 new individuals (2 females and 6 males) appeared in our cameras for the first time but only 2 of these became residents; and 3 resident individuals (2 males and 1 female) disappear at this time. This event could reflect a high rate of immigration and emigration at this time and/or low survival probabilities or a deterioration of habitat suitability (Rosas-Rosas et al. 2008; Rosas-Rosas et al. 2012). The newly identified individuals were probably displaced from the neighboring ranch. Male biased dispersal is common in solitary carnivores, possibly as a mechanism to avoid inbreeding or reduce competition for mates or resources (Kantek et al. 2021). Several male jaguars appear to overlap over the years, notably during 2012 (M1, M2, M3 and M8) and 2017 (M10, M11, M12, M13 and M14). Given that we did not find signs of confrontations (i.e. scars, dead jagaurs), this suggests some sort of intraspecific temporal portioning between residents previously documented in jaguars (Harmsen et al. 2009; Guilder et al. 2015).

Our occupancy analysis had limitations in the occupancy estimations of small prey, we believe that our analysis adequately modeled the influence that the presence of peccary exerts on jaguar occupancy, even when other prey species are available and more abundant. This is unsurprising given that throughout jaguar range several studies have found peccary to be an important prey species (Harmsen et al. 2010; Miranda et al. 2018). Even though habitat type was not present in the best fitting model of jaguar occupancy, it is important to note that it still poses a strong limiting factor on their conservation as most preferred prey species rely on well conserved habitat (Reyna-Hurtado et al. 2010; Ramos-Robles et al. 2013; Petracca et al. 2014; Contreras-Moreno et al. 2015). Our results on collared peccary occupancy (Figure 9) coincide with those found by Thornton et al. (2020) where human footprint exerted a negative effect on the occupancy of collared peccary and with Petracca et al. (2014) where agricultural encroachment was the limiting factor for collared peccary presence in a Central American corridor. It is unsurprising that white-tailed deer had the highest occupancy probability of β 72% ± .06 as it is known that this species has a high tolerance for degraded and open habitats (Bello-Gutierrez et al. 2010) (Figure 9).

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Through these two studies we confirm our hypothesis that the absence of prey and adequeate habitat is a limiting factor for the presence of jaguars in our study area, showing us their low tolerance for these disruptions. The ongoing habitat degradation and fragmentation surrounding the study area puts at risk the survival of this small but stable jaguar population in southeast Mexico.

CONCLUSIÓN GENERAL

In the studies presented here we describe how a jaguar population in the northern portion of the Selva Maya has been greatly affected by anthropogenic pressure. We can clearly see that individuals avoid areas with human presence and degraded habitats and choose those patches with the presence of prey and forest cover. We witness considerable forest cover loss within a decade and translate it into jaguar habitat loss within the home ranges of the population we follow. Additionally, we observe changes in the behavior of individuals during the peaks of forest loss and identify considerable shifts in the population structure.

Anthropogenic Preassure and Climate Change Threats

Although human activities have influenced the distribution of species and their population trends since ancient times, the impacts have increased considerably since the 1970s (Di Marco et al. 2014). Numerous cases of shrinkage of mammalian ranges have been reported worldwide (Laliberte and Ripple 2004; Wolf et al. 2017), and the external variables of anthropogenic pressure and climate change are those that exert the greatest influence on the range contractions of mammals (Di Marco et al. 2014). Compunded to the direct anthropogenic preassure that we observe on this jaguar population are the effects of climate change that this region has already begun experiencing. Our study area is in the vicinity of Laguna de Terminos which is projected to experience severe flooding and become a bay if the sea level rises only 40 cm (Marquez Garcia et al. 2010). If the extensive mangroves in the study area are lost, the natural barriers they form will cease to protect the forest from hurricanes and tropical storms. The state of Campeche is projected to have an increase in temperature in all climate change scenarios (Secretaria del medio ambiente y Aprovechamiento Sustentables, Gobierno del Estado de Campeche 2015), and this will undoubtly have an effect on all the habitat types that are within our study area. Importantly, the increased temperature and consecutive lower humidity levels in the soil could gradually transform tropical forests into savannahs (Salazar et al. 2007) and hinder their photosynthetic capacities (Huang et al. 2019). The increased burning of fossil fuels together with deforestation to give way to cattle ranches, agriculture and urbanization are creating a synergy that is severely threatening. The large ecological changes projected such as floods, more frequent and intense tropical storms, severe droughts and higher temperatures will exert a strong pressure on wildlife which will have to adapt if they are to survive. Climate change is expected to cause some areas to become less suitable for species survival, while other areas become more suitable, resulting in shifts in species distributions (Velasquez-Tibata et al. 2013), and increasing the likelihood of local and global extinctions (Franco et al. 2006). The impact of range shifts on species depends on the velocity of change and the species dispersion rates (Schloss et al. 2012). During historical glaciation periods, many of the species that managed to survive did so because they migrated to more suitable areas (Root et al. 2002). This will be more complicated presently because this will signify migrating across cities, roads and other such modified landscapes. In general, a reduction in the total number of individuals is expected in the face of contractions in the distributions of populations.

Will Jaguars Adapt Fast Enough?

Evolutionarily, jaguars have exhibited extraordinary plasticity and although thought of as a characteristic predator in wet tropical forests, they have also adapted to living in very hot and dry regions such as Sonora, Mexico or the southwestern United States. We could expect that this species, having such a large distribution area has a high tolerance to a marked climatic range. However, it is difficult to determine if particular populations will be able to adapt sufficiently quickly to face the environmental and physical changes that are predicted to occur (Gittleman 2013). Current land cover changes are the main threat to felids (IUCN 2015) and have increased the extinction risk of jaguars (Zanin et al. 2015) by reducing and isolating populations. Agricultural lands are often expanded to compensate for losses in agricultural production caused by climate change, which reduces native vegetation and creates a positive feedback loop that accelerates deterioration (Feddema et al. 2005). Therefore, the current critical conservation status of felids caused by land cover changes will probably worsen in a non-linear manner due to climate change (Zanin et al. 2021). Additionally, as agricultural lands increase so will the conflict between humans and jaguars. An increase in temperature could also cause greater stress to individuals and affect their reproductive or hunting capacity, which would have long-term repercussions on populations. Prey species could also be affected by changes in temperature and precipitation and alter their normal activity patterns, which would affect the behavior of their predators. Additionally, it is believed that changes in temperature, rainfall patterns or changes in land use can lead to a higher incidence and transmission of pathogens. Many of the animal vectored diseases involve arthropod hosts at some point in their life cycle, these arthropods can multiply with the presence of stagnant water bodies or acute precipitation events which could be very common within the situations that are anticipated with climate change, additionally the spread of pathogens through hosts such as migratory birds could increase as these hosts expand to new territories given changing climatic conditions (Fueller et al. 2012). Diseases are a current threat to wild cats as there is a greater presence of feral fauna in their habitats. The abundance of this feral fauna may increase under climate change as human population increases and agricultural lands are abandoned. Little is known about the vulnerability of the jaguar to pathogens. Of the micro-parasites (viruses, bacteria, protozoa and fungi), viruses have been the most studied. Canine distemper has been found to be fatal in felines and reported to have 30% of the lions in the Serengeti (Roelke-Parker et al. 1996) and infected jaguars have been found in Brazil (Silva et al. 2016). Although the virus is sensitive to ultraviolet light, heat and dehydration and usually does not tolerate very hot climates, viruses can evolve extremely quickly and therefore adapt to new conditions. Feline Immunodeficiency Virus and lentiviruses have also been detected in free-living and captive jaguars (Barr 1989). From the protozoan family, Toxoplasma gondii can infect and kill felines (Patton et al. 1986) and parasites such as the Dirofilaria immitis nematode have also been observed in free-living jaguars.

Given the projection of these unfavorable scenarios, we must dedicate gargantuan efforts to conserve large felids such as jaguars and give them at least an opportunity to adapt to the new conditions brought on by climate change. Space and funds are often limiting factors in the protection of large mammals and we must prioritize them for actions that we know will give us the biggest payoffs and be efficient and successful. In order to strategically plan protocols and conservation actions, we must better understand jaguars' tolerance for degraded habitat, human presence and a less than optimal prey base. We must also simultaneously understand the changes that their prey species will undergo and what their habitat will look like. The studies presented here are an attempt to contribute to our research efforts in this direction and foster new long term studies and management plans that will help protect America's largest feline.

REFERENCIAS

Aranda, M. (1994). Diferenciación entre las huellas de jaguar y puma: Un análisis de criterios. *Acta Zoológica Mexicana* (ns), (63), 73-78.

Arias, M., Hinsley, A., & Milner-Gulland, E. J. (2020). Characteristics of, and uncertainties about, illegal jaguar trade in Belize and Guatemala. *Biological Conservation*, *250*, 108765.

Arroyo-Arce, S., Guilder, J., & Salom-Pérez, R. (2014). Habitat features influencing jaguar Panthera onca (Carnivora: *Felidae*) occupancy in Tortuguero National Park, Costa Rica. In *Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN* (Vol. 62, Issue 4).

Ávila-Nájera, D. M. (2015). Selección de recursos y coexistencia del jaguar y puma en la reserva ecológica El Edén, Quintana Roo, México. *Tesis de Doctorado, Colegio de Postgraduados*, 120.

Baldwin, R. A., & Bender, L. C. (2008). Distribution, occupancy, and habitat correlates of American martens (*Martes americana*) in Rocky Mountain National Park, Colorado. *Journal of Mammalogy*, *89*(2), 419–427.

Barlow, A. C., McDougal, C., Smith, J. L., Gurung, B., Bhatta, S. R., Kumal, & Tamang, D. B. (2009). Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. *Journal of Mammalogy*, 90(2), 472-478.

Barnes, S. A., Teare, J. A., Staaden, S., Metrione, L., & Penfold, L. M. (2016). Characterization and manipulation of reproductive cycles in the jaguar (*Panthera onca*). *General and Comparative Endocrinology*, *225*, 95-103.

Barr, M. C., Calle, P. P., Roelke, M. E., & Scott, F. W. (1989). Feline immunodeficiency virus infection in nondomestic felids. *Journal of Zoo and Wildlife Medicine*, 265-272.

Bekoff, M., Daniels, T. J., & Gittleman, J. L. (1984). Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics. Vol. 15*, 191–232.

Bello-Gutiérrez, J., Reyna-Hurtado, R., & Wilham, J. (2010). Central American red brocket deer *Mazama temama* (Kerr, 1992). Neotropical cervidology: biology and medicine of Latin American deer (JM Barbanti-Duarte and S. Gonzalez, eds.). International Union for the Conservation of Nature, Gland, Switzerland, 166-172.

Bernal-Escobar, A., Payan, E., & Cordovez, J. M. (2015). Sex dependent spatially explicit stochastic dispersal modeling as a framework for the study of jaguar conservation and management in South America. *Ecological Modelling*, *299*(May 2016), 40–50.

Blair, M. E., Rose, R. A., Ersts, P. J., Sanderson, E. W., Redford, K. H., Didier, K., ... & Pearson, R. G. (2012). Incorporating climate change into conservation planning: identifying priority areas across a species' range. *Frontiers of Biogeography*, *4*(4).

Bled, F., Summers, S., Martell, D., Petroelje, T. R., Beyer, D. E., & Belant, J. L. (2015). Effects of prey presence and scale on bobcat resource selection during winter. *PLoS ONE*, *10*(11).

Bond, W. J. (1994). Keystone species. In *Biodiversity and ecosystem function* (pp. 237-253). Springer, Berlin, Heidelberg.

Boron, V., Deere, N. J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., & Tzanopoulos, J. (2019). Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological conservation*, *232*, 108-116.

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long term conservation. *PLoS ONE*, *11*(5), 1–14.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. C. (2015). Tolerance to anthropogenic disturbance by a large carnivore: The case of Eurasian lynx in south-eastern Norway. *Animal Conservation*, *18*(3), 271–278.

Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, *295*(5563), 2273-2276.

Carrillo-Reyna, N., Reyna-Hurtado, R., & Schmook, B. (2015). Abundancia relativa y selección de hábitat de Tapirus bairdii en las reservas de Calakmul y Balam Kú, Campeche, México. *Revista Mexicana de Biodiversidad*, *86*(1), 202–207.

Carrillo, E., Saenz, J., & Fuller, T. (2009). Interbirth interval of a free-ranging jaguar. *Mammalian Biology*, *74*(4), 319-320.

Caso, A., Lopez-Gonzalez, C. A., Payan, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R., Kelly, M., & Valderrama, C. (2015). *Panthera onca*. The IUCN Red List of Threatened Species 2008. *2307-8235*, *8235*, 1–14.

Cavalcanti, S. M., & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (Panthera onca) in the southern Pantanal, Brazil. *Journal of Mammalogy*, *90*(4), 935-945.

Ceballos, G., Chávez, C., List, R., & Zarza, H. (2007). Conservación y manejo del jaguar en México: estudios de caso y perspectivas. In *Conabio-alianza WWF/telcel- universidad Nacional autónoma de México, México.* (Issue May 2015).

Ceballos, G., Chavez, C., Rivera, A., & Manterola, C. (2002). Tamaño poblacional y conservacion del Jaguar en la Reserva de la Biosfera de Calakmul, Campeche, Mexico. In *El jaguar en el nuevo milenio* (pp. 403–418).

Ceballos, G., de la Torre, J. A., Zarza, H., Huerta, M., Lazcano-Barrero, M. A., Barcenas, H & Torres-Romero, E. J. (2021). Jaguar distribution, biological corridors and protected areas in Mexico: from science to public policies. *Landscape Ecology*, *36*(11), 3287-3309.

Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences*, *117*(24), 13596-13602.

Chávez, C. (2010). Ecología y conservación del jaguar *(panthera onca)* y puma *(puma concolor)* en la región de calakmul y sus implicaciones para la conservación de la península yucatán (Doctoral dissertation, Universidad de Granada).

Cione, A. L., Tonni, E. P., & Soibelzon, L. (2009). Did Humans Cause the Late Pleistocene-Early Holocene Mammalian Extinctions in South America in a Context of Shrinking Open Areas? *Vertebrate Paleobiology and Paleoanthropology*, *9781402087929*, 125–144.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in ecology & evolution*, *25*(10), 562-573.

Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., & Ceballos, G. (2011). Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. *Animal Conservation*, *14*(2), 158-166.

Conde, D. A., Colchero, F., Zarza, H., Christensen Jr, N. L., Sexton, J. O., Manterola, C., ... & Ceballos, G. (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, *143*(9), 1980-1988.

Contreras-Moreno, F. M., Hidalgo-Mihart, M. G., Reyna-Hurtado, R., López-González, C. A., & Cruz, A. J. D. L. (2021). Seasonal home-range size of the white-tailed deer, *Odocoileus virginianus thomasi*, in a tropical wetland of southeastern Mexico. *Revista mexicana de biodiversidad*, *92*.

Contreras-Moreno, F. M., Zúñiga-Sánchez, J. S., & Bello-Gutiérrez, J. (2015). Parámetros poblacionales de *Odocoileus virginianus* (*Cervidae*) en dos comunidades de Tabasco, México. *Revista Latinoamericana de Conservación*, *4*, 7-13.

Coon, C. A. C., Mahoney, P. J., Edelblutte, E., McDonald, Z., & Stoner, D. C. (2020). Predictors of puma occupancy indicate prey vulnerability is more important than prey availability in a highly fragmented landscape. *Wildlife Biology*, *2020*(1).

Craft, M. E., Volz, E., Packer, C., & Meyers, L. A. (2009). Distinguishing epidemic waves from disease spillover in a wildlife population. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1777-1785.

Crawshaw Jr, P. G., & Quigley, H. B. (2002). Hábitos Alimenticios Del Jaguar Y El Puma En El Pantanal , Brasil. *El Jaguar En El Nuevo Milenio.*, *January 2002*, 215–227.

Crawshaw Jr, P. G., & Quigley, H. B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology*, *223*(3), 357-370.

Crook, J. H., Ellis, J. E., & Goss-Custard, J. D. (1976). Mammalian social systems: structure and function. *Animal Behaviour*, *24*(2), 261-274.

Cruz, C., Zarza, H., Vidal-Mateo, J., Urios, V., & Ceballos, G. (2021). Top predator ecology and conservation: Lesson from jaguars in southeastern Mexico. *Conservation Science and Practice*, *3*(2), e328.

Cullen, L., Sana, D. A., Lima, F., de Abreu, K. C., & Uezu, A. (2013). Selection of habitat by the jaguar, Panthera onca (Carnivora: Felidae), in the upper Paraná River, Brazil. *Zoologia*, *30*(4), 379–387.

De Azevedo, F. C. C., & Murray, D. L. (2007). Evaluation of potential factors predisposing livestock to predation by jaguars. *The journal of wildlife management*, *71*(7), 2379-2386.

De Azevedo, F. C. C., & Murray, D. L. (2007). Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological conservation*, *137*(3), 391-402.

De La Torre, J. A., & Medellín, R. A. (2011). Jaguars *Panthera onca* in the greater lacandona ecosystem, Chiapas, Mexico: Population estimates and future prospects. *Oryx*, *45*(4), 546–553.

De La Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*. *Oryx*, *52*(2), 300-315.

DePerno, C. S., Jenks, J. A., & Griffin, S. L. (2003). Multidimensional cover characteristics: Is variation in habitat selection related to white-tailed deer sexual segregation? *Journal of Mammalogy*, *84*(4), 1316–1329.

Desbiez, A. L., Bodmer, R. E., & Aparecida, S. (2009). Wildlife habitat selection and sustainable resources management in a Neotropical wetland. *International Journal of Biodiversity and Conservation*, *1*(1), 11–20.

Di Marco, M., Boitani, L., Mallon, D., Hoffmann, M., Iacucci, A., Meijaard, E., & Rondinini, C. (2014). A retrospective evaluation of the global decline of carnivores and ungulates. *Conservation Biology*, *28*(4), 1109-1118.

Du Preez, B. D., Loveridge, A. J., & Macdonald, D. W. (2014). To bait or not to bait: A comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation*, *176*(August 2016), 153–161.

Dueñas-López, G., Rosas Rosas, O. C., Chapa-Vargas, L., Bender, L. C., Tarango-Arámbula, L. A., Martínez-Montoya, J. F., & Alcántara-Carbajal, J. L. (2015). Connectivity among jaguar populations in the Sierra Madre Oriental, México. *Therya*, *6*(2), 449–468.

Efford, M. G., & Fewster, R. M. (2013). Estimating population size by spatially explicit capture-recapture. *Oikos*, *122*(6), 918–928. https://doi.org/10.1111/j.1600-0706.2012.20440.x

Eizirik, E., Kim, J. H., Menotti-Raymond, M., Crawshaw, P. G., O'Brien, S. J., & Johnson, W. E. (2001). Phylogeography, population history and conservation genetics of jaguars (*Panthera onca,* Mammalia, Felidae). *Molecular Ecology*, *10*(1), 65–79.

Ellis, E. A., Montero, J. A. R., Gómez, I. U. H., Porter-Bolland, L., & Ellis, P. W. (2017). Private property and Mennonites are major drivers of forest cover loss in central Yucatan Peninsula, Mexico. *Land Use Policy*, *69*, 474-484.

Emmons, L. H. (1987). Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology*, *20*(4), 271–283.

Escamilla, A., Sanvicente, M., Sosa, M., & Galindo-Leal, C. (2000). Habitat Mosaic, Wildlife Availability, and Hunting in the Tropical Forest of Calakmul, Mexico. *Conservation Biology*, *14*(6), 1592–1601.

Everatt, K. T., Andresen, L., & Somers, M. J. (2014). Trophic scaling and occupancy analysis reveals a lion population limited by top-down anthropogenic pressure in the Limpopo National Park, Mozambique. *PloS one*, *9*(6), e99389.

Feddema, J. J., Oleson, K. W., Bonan, G. B., Mearns, L. O., Buja, L. E., Meehl, G. A., & Washington, W. M. (2005). Atmospheric science: The importance of land-cover change in simulating future climates. *Science*, *310*(5754), 1674–1678.

Figel, Joe J., et al. "Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot." PloS one 14.9 (2019): e0221705.

Fiske, I., & Chandler, R. (2015). Overview of Unmarked: An R Package for the Analysis of Data from Unmarked Animals. *R*, 1–5.

Foster, R. J., Harmsen, B. J., & Doncaster, C. P. (2010). Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*, *42*(6), 724-731.

Franco, A. M. A., Hill, J. K., Kitschke, C., Collingham, Y. C., Roy, D. B., Fox, R., Huntley, B., & Thomas, C. D. (2006). Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, *12*(8), 1545–1553.

Friedeberg-Gutiérrez, D. B., López-González, C. A., Lara-Díaz, N. E., MacKenzie, D., Jesús-de la Cruz, A., Juárez-Lopez, R., & Hidalgo-Mihart, M. (2022). Landscape patterns in the occupancy of jaguars (*Panthera onca*) and their primary prey species in a disturbed region of the Selva Maya in Mexico. *Mammalia*

Fuller, T., & Sievert, P. (2001). Carnivore demography and the consequences of changes in prey availability. *Carnivore Conservation*, *December*, 163–179.

Fuller, T., Bensch, S., Müller, I., Novembre, J., Pérez-Tris, J., Ricklefs, R. E., Smith, T. B., & Waldenström, J. (2012). The ecology of emerging infectious diseases in migratory birds: An assessment of the role of climate change and priorities for future research. *EcoHealth*, *9*(1), 80–88.

Gaines, W. L., Lyons, A. L., Lehmkuhl, J. F., & Raedeke, K. J. (2005). Landscape evaluation of female black bear habitat effectiveness and capability in the North Cascades, Washington. *Biological Conservation*, *125*(4), 411-425.

Gammons, D. A. J. G., & Resources, N. (2009). *Translocation of nine-banded armadillos*. *3*(1), 64–71.

Gammons, D. J., Mengak, M. T., & Conner, L. M. (2009). Armadillo habitat selection in southwestern Georgia. *Journal of Mammalogy*, *90*(2), 356-362.

García-Marmolejo, G., Chapa-Vargas, L., Weber, M., & Huber-Sannwald, E. (2015). Landscape composition influences abundance patterns and habitat use of three ungulate species in fragmented secondary deciduous tropical forests, Mexico. *Global Ecology and Conservation*, *3*, 744–755.

Gerber, B. D., Karpanty, S. M., & Randrianantenaina, J. (2012). The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx*, *46*(3), 414–422.

Gibbs, J. P., Droege, S., & Eagle, P. (1998). Monitoring populations of plants and animals. *BioScience*, *48*(11), 935-940.

Gibeau, M. L., Clevenger, A. P., Herrero, S., & Wierzchowski, J. (2002). Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological conservation*, *103*(2), 227-236.

Gittleman, J. L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammalogy*, *67*(1), 23-36.

Gittleman, J. L. (2013). *Carnivore behavior, ecology, and evolution*. Springer Science & Business Media.

Gokce, D. (2019). Introductory chapter: Wetland importance and management. *Wetlands management–Assessing risk and sustainable solutions*, 3-10.

González, C. A. L., & Miller, B. J. (2002). Do jaguars (*Panthera onca*) depend on large prey?. *Western North American Naturalist*, 218-222.

González-Gallina, A., Hidalgo-Mihart, M. G., & Castelazo-Calva, V. (2018). Conservation implications for jaguars and other neotropical mammals using highway underpasses. *PLoS ONE*, *13*(11), 1–20.

González-Gallina, A., Hidalgo-Mihart, M. G., Pérez-Garduza, F., Iglesias-Hernández, J. A., De Ita, A. O., Chacón-Hernández, A., & Vázquez-Zúñiga, O. (2018). Home range of a male jaguar spatially associated with the landfill of the city of Playa del Carmen, Mexico. *Mammalia*, *82*(1), 54–61.

Gonzalez, S. J., Howard, J. G., Brown, J., Grajales, H., Pinzón, J., Monsalve, H., & Escobar, C. J. (2017). Reproductive analysis of male and female captive jaguars (Panthera onca) in a Colombian zoological park. *Theriogenology, 89*, 192-200.

Greenspan, E., Anile, S., & Nielsen, C. K. (2020). Density of wild felids in Sonora, Mexico: a comparison of spatially explicit capture-recapture methods. *European Journal of Wildlife Research*, *66*(4), 1-12.

Griffiths, D. (1975). Prey Availability and the Food of Predators. *Ecology*, *56*(5), 1209–1214.

Gros, P. M., Kelly, M. J., Caro Gros P M, T. M., J, K. M., Gros, P. M., Kelly, M. J., & Caro, T. M. (1996). *Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data*.

Guerra-Martínez, V., & Ochoa-Gaona, S. (2008). Evaluation of the management program of the Pantanos de Centla Biosphere Reserve in Tabasco, Mexico. *Universidad y ciencia*, *24*(2), 135-146.

Guilder, J., Barca, B., Arroyo-Arce, S., Gramajo, R., & Salom-Pérez, R. (2015). Jaguars *(Panthera onca*) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle (*Chelonia mydas mydas*) abundance in Tortuguero National Park, Costa Rica. *Mammalian Biology*, *80*(2), 65-72.

Guillera-Arroita, G., Lahoz-Monfort, J. J., MacKenzie, D. I., Wintle, B. A., & McCarthy, M. A. (2014). Ignoring imperfect detection in biological surveys is dangerous: A response to “fitting and interpreting occupancy models.” *PLoS ONE*, *9*(7).

Gutiérrez-González, C. E., Gómez-Ramírez, M. Á., & López-González, C. A. (2012). Estimation of the density of the Near Threatened jaguar Panthera onca in Sonora, Mexico, using camera trapping and an open population model. *ORYX*, *46*(3), 431–437.

Gutiérrez-González, C. E., Gómez-Ramírez, M. A., López-González, C. A., & Doherty Jr, P. F. (2015). Are private reserves effective for jaguar conservation?. *PLoS one*, *10*(9), e0137541.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A. & Townshend, J. (2013). High-resolution global maps of 21st-century forest cover change. *science*, *342*(6160), 850-853.

Harmsen, B. J., Foster, R. J., Silver, S. C., Ostro, L. E., & Doncaster, C. P. (2009). Spatial and temporal interactions of sympatric jaguars (Panthera onca) and pumas (Puma concolor) in a neotropical forest. *Journal of mammalogy*, *90*(3), 612-620.

Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. *Biotropica*, *42*(1), 126–133.

Harmsen, B. J., Foster, R. J., Silver, S. C., Ostro, L. E. T., & Doncaster, C. P. (2011). Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology*, *76*(3), 320–324.

Harmsen, B. J., Foster, R. J., Sanchez, E., Gutierrez-González, C. E., Silver, S. C., Ostro, L. E. T., Kelly, M. J., Kay, E., & Quigley, H. (2017). Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of carnivores. *PLoS ONE*, *12*(6), 1–19.

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, *34*(4), 325–333.

Hartle, D. L., & Clark, A. G. (1997). Principles of population genetics. Sinauer Associations. *Inc. Sunderland*.

Hayes, L. D., & Schradin, C. (2017). Long-term field studies of mammals: what the short-term study cannot tell us. *Journal of Mammalogy*, *98*(3), 600-602.

Hayward, M. W., & Kerley, G. I. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of zoology*, *267*(3), 309-322.

Hayward, M. W., Kamler, J. F., Montgomery, R. A., Newlove, A., Rostro-García, S., Sales, L. P., & Van Valkenburgh, B. (2016). Prey preferences of the jaguar *Panthera onca* reflect the post-pleistocene demise of large prey. *Frontiers in Ecology and Evolution*, *3*(JAN).

Hernández-Pérez, E. L., Sosa, J. L., Friedeberg, D., Contreras-Moreno, F. M., & Hidalgo-Mihart, M. G. (2020). Jaguars and Roads in the Calakmul Region: Evidence of Road Crossing and Collisions with Vehicles. *Western North American Naturalist*, *80*(4), 556–562.

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., & Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, *86*(8), 2135-2144.

Hidalgo-Mihart, M. G., Contreras-Moreno, F. M., De La Cruz, A. J., Juárez-López, R., Valera-Aguilar, D., Pérez-Solano, L. A., & Hernández-Lara, C. (2015). Registros recientes de jaguar en Tabasco, norte de Chiapas y oeste de Campeche, México. *Revista Mexicana de Biodiversidad*, *86*(2), 469–477.

Hidalgo-Mihart, M. G., Contreras-Moreno, F. M., Jesús-De La Cruz, A., Juárez-López, R., Bravata De La Cruz, Y., Pérez-Solano, L. A., Hernández-Lara, C., Friedeberg, D., Thornton, D., & Koller-González, J. M. (2017). Inventory of medium-sized and large mammals in the wetlands of laguna de terminos and pantanos de centla, Mexico. *Check List*, *13*(6), 711–726.

Hidalgo-Mihart, M. G., Contreras-Moreno, F. M., Jesús De La Cruz, A., & Juárez-López, R. (2018). Validation of the Calakmul-Laguna de Terminos corridor for jaguars *Panthera onca* in south-eastern Mexico. *Oryx*, *52*(2), 292–299.

Hidalgo-Mihart, M. G., Jesus-de La Cruz, A., Contreras-Moreno, F. M., Juárez-López, R., Bravata-de La Cruz, Y., Friedeberg, D., & Bautista-Ramírez, P. (2019). Jaguar density in a mosaic of disturbed/preserved areas in southeastern Mexico. *Mammalian Biology*, *98*, 173-178.

Hoogesteijn, R., & Hoogesteijn, A. (2008). Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation?. *Oryx*, *42*(1), 132-138.

Hope, K., & Deem, S. L. (2006). Retrospective study of morbidity and mortality of captive jaguars (Panthera onca) in North America: 1982–2002. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *25*(6), 501-512.

Huang, M., Piao, S., Ciais, P., Peñuelas, J., Wang, X., Keenan, T. F., & Janssens, I. A. (2019). Air temperature optima of vegetation productivity across global biomes. *Nature ecology & evolution*, *3*(5), 772-779.

INEGI, C. E. (2009). Instituto Nacional de Estadística y Geografía. Censo Económico.

INEGI (2013) Instituto Nacional de Estadística y Geografía. Anuario estadístico de los Estados Unidos Mexicanos 2012. Instituto Nacional de Estadística y Geografía. Aguascalientes, México.

INEGI (2015) Instituto Nacional de Estadística y Geografía. Anuario estadístico y geográfico por entidad federativa 2015. Instituto Nacional de Estadística y Geografía. Aguascalientes, México.

Iriarte, J. A., Franklin, W. L., Johnson, W. E., & Redford, K. H. (1990). Biogeographic variation of food habits and body size of the American puma. *Oecologia*, *85*(2), 185-190.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-3.

Jennings, A. P., Naim, M., Advento, A. D., Aryawan, A. A. K., Ps, S., Caliman, J. P., Verwilghen, A., & Veron, G. (2015). Diversity and occupancy of small carnivores within oil palm plantations in central Sumatra, Indonesia. *Mammal Research*, *60*(2), 181–188.

Johnsingh, A. J. T., & Negi, A. S. (2003). Status of tiger and leopard in Rajaji–Corbett Conservation Unit, northern India. *Biological Conservation*, *111*(3), 385-393.

Johnson, W. E., Eizirik, E., Pecon-Slattery, J., Murphy, W. J., Antunes, A., Teeling, E., & O'Brien, S. J. (2006). The late Miocene radiation of modern Felidae: a genetic assessment. *Science*, *311*(5757), 73-77.

Jones, J. A., Swanson, F. J., Wemple, B. C., & Snyder, K. U. (2000). Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. *Conservation Biology*, *14*(1), 76-85.

Kantek, D. L. Z., Trinca, C. S., Tortato, F., Devlin, A. L., de Azevedo, F. C. C., Cavalcanti, S., & Eizirik, E. (2021). Jaguars from the Brazilian Pantanal: Low genetic structure, male-biased dispersal, and implications for long-term conservation. *Biological Conservation*, *259*, 109153.

Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture—recapture models. *Biological conservation*, *71*(3), 333-338.

Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology*, *87*(11), 2925-2937.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B., & Hornocker, M. G. (2002). Effects of roads and human disturbance on Amur tigers. *Conservation biology*, *16*(1), 97-108.

Kitchener, A. C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A. & Tobe, S. (2017). A revised taxonomy of the Felidae: The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. *Cat News*.

Klar, N., Herrmann, M., & Kramer-Schadt, Stephanie (2009). Effects and mitigation of road impacts on individual movement behavior of wildcats. *The journal of wildlife management*, *73*(5), 631-638.

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W., & MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, *88*(4), 638–652.

Kolb, M., & Galicia, L. (2012). Challenging the linear forestation narrative in the Neo-tropic: Regional patterns and processes of deforestation and regeneration in southern Mexico. *Geographical Journal*, *178*(2), 147–161.

Krebs, C. J. (1995). Two paradigms of population regulation. *Wildlife Research*, *22*(1), 1-10.

Laliberte, A. S., & Ripple, W. J. (2004). Range Contractions of North American Carnivores and Ungulates. *BioScience*, *54*(2), 123–138.

Laundre, J. W., Hernandez, L., & Ripple, W. J. (2010). The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! *The Open Ecology Journal*, *3*(3), 1–7.

Lazenby, B. T., & Dickman, C. R. (2013). Patterns of Detection and Capture Are Associated with Cohabiting Predators and Prey. *PLoS ONE*, *8*(4).

Leeson, G. W. (2018). The growth, ageing and urbanisation of our world. *Journal of Population Ageing*, *11*(2), 107-115.

le Polain de Waroux, Y., Neumann, J., O'Driscoll, A., & Schreiber, K. (2021). Pious pioneers: the expansion of Mennonite colonies in Latin America. *Journal of Land Use Science*, *16*(1), 1-17.

Linnaeus, C. (1758). *Systema naturae* (Vol. 1, No. part 1, p. 532). Laurentii Salvii: Stockholm.

Linnell, J. D., Odden, J., Smith, M. E., Aanes, R., & Swenson, J. E. (1999). Large carnivores that kill livestock: do" problem individuals" really exist?. *Wildlife Society Bulletin*, 698-705.

Linnell, J. D. C., Promberger, C., Boitani, L., Swenson, J. E., Breitenmoser, U., & Andersen, R. (2005). The Linkage between conservation strategies for large carnivores and biodiversity: the view from the "half-full" forests of Europe. *Large Carnivores and the Conservation of Biodiverstiy*, *Rosenzweig 2003*, 381–398.

López-Pérez, E., Avalos-Rodriguez, A., Gallegos-Sánchez, J., & Bautista-Ortega, J. (2021). Reproductive aspects of the female jaguar (Panthera onca L.). *AGROProductividad*, *14*(11), 89-99.

Lukacs, P. M., & Burnham, K. P. (2005). Review of capture–recapture methods applicable to noninvasive genetic sampling. Molecular ecology, 14(13), 3909-3919.

Mace, R. D., Waller, J. S., Manley, T. L., Lyon, L. J., & Zuuring, H. (1996). Relationships among grizzly bears, roads and habitat in the Swan Mountains Montana. *Journal of Applied ecology*, 1395-1404.

Macías, E. B., Cruz, F. V., Rendón, M. Á. P., & Rendón, M. J. P. (2014). Revisión de la problemática socioambiental de la Reserva de la Biósfera Pantanos de Centla, Tabasco. *Investigación y Ciencia*, *22*(60), 50-57.

Mackenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. In 2200 Ecology (Vol. 84, Issue 8).

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*(3), 300–318.

Maddox, T., Priatna, D., Gemita, E., & Salampessy, A. (2007). Jambi Province, Sumatra, Indonesia (October 2007).

Manjarrez Muñoz, B., Hernández Daumás, S., De Jong, B., Nahed Toral, J., Dios Vallejo, O. O. D., & Salvatierra Zaba, E. B. (2007). Configuración territorial y perspectivas de ordenamiento de la ganadería bovina en los municipios de Balancán y Tenosique, Tabasco. *Investigaciones geográficas*, (64), 90-115.

Márquez García, a. Z., Márquez García, E., Bolongo Crevenna Recaséns, a., & Torres Rodríguez, V. (2010). Cambio en la línea de costa en la Rivera Maya debido a fenómenos hidrometeorológicos extremos, ¿consecuencia del cambio global climático global? *Vulnerabilidad de Las Zonas Costeras Mexicanas Ante El Cambio Climático*, *March 2016*, 345–358.

McLoughlin, P. D., Walton, L. R., Cluff, H. D., Paquet, P. C., & Ramsay, M. A. (2004). Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy*, *85*(3), 576-580.

Mereles, M. F., & Rodas, O. (2014). Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. *Climatic change*, *127*(1), 55-71.

Meyer, J. L. (2008). Withstanding the test of time: Yellowstone and sustainable tourism. *Tourism, Recreation and Sustainability: Linking Culture & the Environment,*, 142-157.

Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, *124*(3), 383–396.

Miranda, E. B. P., Jácomo, A. T. D. A., Tôrres, N. M., Alves, G. B., & Silveira, L. (2018). What are jaguars eating in a half-empty forest? Insights from diet in an overhunted Caatinga reserve. *Journal of Mammalogy*, *99*(3), 724–731.

Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., De Paula, R. C., Ferraz, K. M., & Leimgruber, P. (2016). Space use and movement of a neotropical top predator: the endangered jaguar. *PloS one*, *11*(12), e0168176.

Morita, T., Nakićenović, N., & Robinson, J. (2000). Overview of mitigation scenarios for global climate stabilization based on new IPCC emission scenarios (SRES). Environmental Economics and Policy Studies, 3(2), 65-88.

Munson, L., Terio, K. A., Kock, R., Mlengeya, T., Roelke, M. E., Dubovi, E., & Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. *PloS one*, *3*(6), e2545.

Neilson, E. W., Avgar, T., Cole Burton, A., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*, *9*(1).

Nichols, J. D., O’Connell, A. F., & Karanth, K. U. (2011). Camera traps in animal ecology and conservation: What’s next?. In *Camera traps in animal ecology* (pp. 253-263). Springer, Tokyo.

Nogeire, T. M., Davis, F. W., Duggan, J. M., Crooks, K. R., & Boydston, E. E. (2013). Carnivore Use of Avocado Orchards across an Agricultural-Wildland Gradient. *PLoS ONE*, *8*(7), 1–6.

Noss, a., Polisar, J., Maffei, L., Garcia, R., & Silver, S. (2013). *Evaluating jaguar densities with camera traps*. *2004*, 78.

Novack, A. J., Main, M. B., Sunquist, M. E., & Labisky, R. F. (2005). Foraging ecology of jaguar (Panthera onca) and puma (Puma concolor) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology*, *267*(2), 167-178.

O'Brien, S. J., & Johnson, W. E. (2005). Big cat genomics. In *Annual Review of Genomics and Human Genetics* (Vol. 6, pp. 407–429).

O'Brien, S. J., Johnson, W., Driscoll, C., Pontius, J., Pecon-Slattery, J., & Menotti-Raymond, M. (2008). State of cat genomics. In *Trends in Genetics* (Vol. 24, Issue 6, pp. 268–279).

Olsoy, P. J., Zeller, K. A., Hicke, J. A., Quigley, H. B., Rabinowitz, A. R., & Thornton, D. H. (2016). Quantifying the effects of deforestation and fragmentation on a range-wide conservation plan for jaguars. *Biological Conservation*, *203*(March 2019), 8–16.

Ocaña, D., & Lot, A. (1996). Estudio de la vegetación acuática vascular del sistema fluvio-lagunar-deltaico del Río Palizada en Campeche, México. *Anales del Instituto de Biología Serie Botánica*, *67*(002).

Olsoy, P. J., Zeller, K. A., Hicke, J. A., Quigley, H. B., Rabinowitz, A. R., & Thornton, D. H. (2016). Quantifying the effects of deforestation and fragmentation on a range-wide conservation plan for jaguars. *Biological Conservation*, *203*, 8-16.

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*, (62), 3-135.

Pallares, E., Manterola, C., Conde, D. A., & Colchero, F. (2015). Case Study: Roads and Jaguars in the Mayan Forests. *Handbook of Road Ecology*, 313–316.

Pallemaerts, L., Kulu, I. P., Jeffers, K. A., Macdonald, D. W., & Cheyne, S. M. (2020). Male residency of Sunda Clouded Leopard Neofelis diardi (Cuvier, 1823)(Mammalia: Carnivora: Felidae) in a peat swamp forest, Indonesian Borneo. *Journal of Threatened Taxa*, *12*(16), 17222-17228.

Palomares, F. (2001). Vegetation structure and prey abundance requirements of the Iberian lynx: Implications for the design of reserves and corridors. *Journal of Applied Ecology*, *38*(1), 9–18.

Palomares, F., Roques, S., Chávez, C., Silveira, L., Keller, C., Sollmann, R., do Prado, D. M., Torres, P. C., Adrados, B., Godoy, J. A., de Almeida Jácomo, A. T., Tôrres, N. M., Furtado, M. M., & López-Bao, J. V. (2012). High Proportion of Male Faeces in Jaguar Populations. *PLoS ONE*, *7*(12).

Patton, S., Rabinowitz, A., Randolph, S., & Strawbridge Johnson, S. (1986). A coprological survey of parasites of wild neotropical felidae. *Journal of Parasitology*, *72*(4), 517–520.

Paviolo, A., De Angelo, C. D., Di Blanco, Y. E., & Di Bitetti, M. S. (2008). Jaguar Panthera onca population decline in the upper Paraná Atlantic forest of Argentina and Brazil. *Oryx*, *42*(4), 554-561.

Paviolo, A., De Angelo, C., Ferraz, K. M. P. M. B., Morato, R. G., Martinez Pardo, J., Srbek-Araujo, A. C., Beisiegel, B. D. M., Lima, F., Sana, D., Xavier Da Silva, M., Velázquez, M. C., Cullen, L., Crawshaw, P., Jorge, M. L. S. P., Galetti, P. M., Di Bitetti, M. S., De Paula, R. C., Eizirik, E., Aide, T. M.,Azevedo, F. (2016). A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. *Scientific Reports*, *6*(October), 1–16.

Perinchery, A., Jathanna, D., & Kumar, A. (2011). Factors determining occupancy and habitat use by Asian small-clawed otters in the Western Ghats, India. *Journal of Mammalogy*, *92*(4), 796–802.

Petracca, L. S. (2010). Use of site occupancy modeling to delineate a jaguar corridor in southern Belize.

Petracca, L. S., Ramírez-Bravo, O. E., & Hernández-Santín, L. (2014). Occupancy estimation of jaguar Panthera onca to assess the value of east-central Mexico as a jaguar corridor. *Oryx*, *48*(1), 133–140.

Pillay, R., Miller, D. A. W., Hines, J. E., Joshi, A. A., & Madhusudan, M. D. (2014). Accounting for false positives improves estimates of occupancy from key informant interviews. *Diversity and Distributions*, *20*(2), 223–235.

Polisar, J., de Thoisy, B., Rumiz, D. I., Santos, F. D., McNab, R. B., Garcia-Anleu, R., & Venegas, C. (2017). Using certified timber extraction to benefit jaguar and ecosystem conservation. *Ambio*, *46*(5), 588-603.

Quigley, H. B. (1987). Ecology and conservation of the jaguar in the Pantanal region, Mato Grosso do Sul, Brazil (Doctoral dissertation, University of Idaho).

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R., & Harmsen, B. (2017). Panthera onca. The IUCN red list of threatened species 2017: e. T15953A50658693.

Quiroga, V. A., Boaglio, G. I., Noss, A. J., & Di Bitetti, M. S. (2014). Critical population status of the jaguar Panthera onca in the Argentine Chaco: Camera-trap surveys suggest recent collapse and imminent regional extinction. *Oryx*, *48*(1), 141–148.

Rabelo, R. M., Aragón, S., & Bicca-Marques, J. C. (2019). Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. *Acta Oecologica*, *97*, 28–33.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological conservation*, *143*(4), 939-945.

Rabinowitz, A. R., & Jr2, B. N. (1986). Ecology and behaviour of the Jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology*, *210*(1), 149-159.

Ramos-Robles, M., Gallina, S., & Mandujano, S. (2013). Habitat and human factors associated with white-tailed deer density in the tropical dry forest of Tehuacán-Cuicatlán Biosphere Reserve, Mexico. *Tropical Conservation Science*, *6*(1), 70–86.

Ray, J., Redford, K. H., Steneck, R., & Berger, J. (Eds.). (2013). *Large carnivores and the conservation of biodiversity*. Island Press.

Reuter, A., Maffei, L., Polisar, J., Radachowsky, J., Montefiore, A., de la Torre, A., & Urbina, Y. (2018). Jaguar hunting and trafficking in Mesoamerica recent observations. *Wildlife Conservation Society, New York*.

Reyna-Hurtado, R., Naranjo, E., Chapman, C. A., & Tanner, G. W. (2010). Hunting and the conservation of a social ungulate: The white-lipped peccary *Tayassu pecari* in Calakmul, Mexico. *Oryx*, *44*(1), 89–96.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology*, *86*(10), 2805–2814.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. In *Science* (Vol. 343, Issue 6167). American Association for the Advancement of Science.

Rivera-Arriaga, E., & Villalobos-Zapata, G. J. (2005). The coastal zone of Campeche, Mexico: Opportunities for implementing an integrated coastal management framework. *Journal of coastal research*, 184-190.

Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in ecology & evolution*, *28*(9), 552-560.

Roelke-Parker, M. E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S. J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., Mwamengele, G. L. M., Mgasa, M. N., Machange, G. A., Summers, B. A., & Appel, M. J. G. (1996). A canine distemper virus epidemic in Serengeti lions (*Panthera leo). Nature*, *379*(6564), 441–445.

Roemer, G. W., Gompper, M. E., & Valkenburgh, B. Van. (2009). The ecological role of the mammalian mesocarnivore. *BioScience*, *59*(2), 165–173.

Root, T. L., & Schneider, S. H. (2002). Climate Change : Overview and Implications for Wildlife. *North*, 1–56.

Rosas-Rosas, O. C., Bender, L. C., & Valdez, R. (2008). Jaguar and puma predation on cattle calves in northeastern Sonora, Mexico. *Rangeland Ecology & Management*, *61*(5), 554-560.

Rosas-Rosas, O. C., & Valdez, R. (2010). El papel de propietarios de tierras en la conservacíon de jaguar en Sonora, México. *Conservation Biology*, *24*(2), 366–371.

Rosas-Rosas, O. C., & Bender, L. C. (2012). Population status of jaguars (Panthera onca) and pumas (Puma concolor) in northeastern Sonora, Mexico. *Acta zoológica mexicana*, *28*(1), 86-101.

Salazar, L. F., Nobre, C. A., & Oyama, M. D. (2007). Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters*, *34*(9).

Salom-Pérez, R., Carrillo, E., Sáenz, J. C., & Mora, J. M. (2007). Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx*, *41*(1), 51-56.

Sanderson, E. W., Redford, K. H., Chetkiewicz, C. L. B., Medellin, R. A., Rabinowitz, A. R., Robinson, J. G., & Taber, A. B. (2002). Planning to save a species: The jaguar as a model. *Conservation Biology*, *16*(1), 58–72.

Sanei, A., & Zakaria, M. (2010). Possible first jungle cat record from Malaysia. *Cat News*, *53*, 13-14.

Santos, F., Carbone, C., Wearn, O. R., Rowcliffe, J. M., Espinosa, S., Moreira, M. G., Ahumada, J. A., Gonçalves, A. L. S., Trevelin, L. C., Alvarez-Loayza, P., Spironello, W. R., Jansen, P. A., Juen, L., & Peres, C. A. (2019). Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. *PLoS ONE*, *14*(3).

Schaller, G. B., & Crawshaw Jr, P. G. (1980). Movement patterns of jaguar. *Biotropica*, 161-168.

Schaller, G. B., & Vasconcelos, J. M. C. (1978). Jaguar predation on capybara. *Z. Saeugetierk*, *43*(c), 296–301.

Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V. & Young, B. E. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, *322*(5899), 225-230.

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(22), 8606–8611.

Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, *158*(February), 301–312.

Scognamillo, D., Maxit, I. E., Sunquist, M., & Polisar, J. (2003). Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology*, *259*(3), 269–279.

Sechrest, W., Brooks, T. M., da Fonseca, G. A., Konstant, W. R., Mittermeier, R. A., Purvis, A., & Gittleman, J. L. (2002). Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences*, *99*(4), 2067-2071.

Seymour, K. L. (1989). Panthera onca. *Mammalian species*, (340), 1-9.

Scott, R., Easterbee, N., & Jefferies, D. (1993). A radio-tracking study of wildcats in western Scotland. In *Proc. Seminar on the biology and conservation of the wildcat*.

Seymour, K. L. (1989). *Panthera onca*. *Mammalian species*, (340), 1-9.

https://www.semabicce.campeche.gob.mx/cambio-climatico/

Sharma, K., Bayrakcismith, R., Tumursukh, L., Johansson, O., Sevger, P., McCarthy, T., & Mishra, C. (2014). Vigorous dynamics underlie a stable population of the endangered snow leopard Panthera uncia in Tost Mountains, South Gobi, Mongolia. *PLoS ONE*, *9*(7).

Silva, A. P., Rosalino, L. M., Johnson, P. J., Macdonald, D. W., Anderson, N., & Kilshaw, K. (2013). Local-level determinants of wildcat occupancy in Northeast Scotland. *European Journal of Wildlife Research*, *59*(3), 449–453.

Silva, C. P. A. e., Onuma, S. S. M., de Aguiar, D. M., Dutra, V., & Nakazato, L. (2016). Molecular detection of Feline Leukemia Virus in free-ranging jaguars (*Panthera onca*) in the Pantanal region of Mato Grosso, Brazil. *Brazilian Journal of Infectious Diseases*, *20*(3), 316–317.

Silver, S. C., Ostro, L. E., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., & Ayala, G. (2004). The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, *38*(2), 148-154.

Smith, J. E., Lehmann, K. D., Montgomery, T. M., Strauss, E. D., & Holekamp, K. E. (2017). Insights from long-term field studies of mammalian carnivores. *Journal of Mammalogy*, *98*(3), 631-641.

Soisalo, M. K., & Cavalcanti, S. M. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, *129*(4), 487–496.

Sollmann, R. (2010). Ecology and conservation of the jaguar (*Panthera onca*) in the Cerrado grasslands of central Brazil. *Pharmazie*, *November*, 1–120.

Sollmann, R. (2011). *Ecology and conservation of the jaguar (Panthera onca) in the Cerrado grasslands of central Brazil* (Doctoral dissertation).

Sollmann, R., Furtado, M. M., Hofer, H., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2012). Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology*, *77*(1), 41–46.

Soto-Galera, E., Piera, J., & López, P. (2010). Spatial and temporal land cover changes in Terminos Lagoon Reserve, Mexico. *Revista de Biologia Tropical*, *58*(2), 565–575.

Spong, G. (2002). Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology*, *52*(4), 303-307.

Taylor, R. (1990). Interpretation of the correlation coefficient: a basic review. *Journal of diagnostic medical sonography*, *6*(1), 35-39.

Teixeira-Santos, J., Ribeiro, A. C. D. C., Wiig, Ø., Pinto, N. S., Cantanhêde, L. G., Sena, L., & Mendes-Oliveira, A. C. (2020). Environmental factors influencing the abundance of four species of threatened mammals in degraded habitats in the eastern Brazilian Amazon. *PloS one*, *15*(2), e0229459.

Tejada, G., Dalla-Nora, E., Cordoba, D., Lafortezza, R., Ovando, A., Assis, T., & Aguiar, A. P. (2016). Deforestation scenarios for the Bolivian lowlands. *Environmental research*, *144*, 49-63.

Templeton, Alan R., et al. "The genetic consequences of habitat fragmentation." Annals of the Missouri Botanical Garden (1990): 13-27.

Thompson, S. K., Ramsey, F. L., & Seber, G. A. (1992). An adaptive procedure for sampling animal populations. *Biometrics*, 1195-1199.

Thompson, J. J., Velilla, M., Cabral, H., Cantero, N., Bonzi, V. R., Britez, E.,& Cartes, J. L. (2022). Jaguar (*Panthera onca*) population density and landscape connectivity in a deforestation hotspot: The Paraguayan Dry Chaco as a case study. *Perspectives in Ecology and Conservation*.

Thornton, D., Reyna, R., Perera-Romero, L., Radachowsky, J., Hidalgo-Mihart, M. G., Garcia, R., McNab, R., Mcloughlin, L., Foster, R., Harmsen, B., Moreira-Ramírez, J. F., Diaz-Santos, F., Jordan, C., Salom-Pérez, R., Meyer, N., Castañeda, F., Valle, F. A. E., Santizo, G. P., Amit, R.,Polisar, J. (2020). Precipitous decline of white-lipped peccary populations in Mesoamerica. *Biological Conservation*, *242*(October 2019).

Thurber, J. M., Peterson, R. O., Drummer, T. D., & Thomasma, S. A. (1994). Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin*, 61-68.

Tobler, M. W., Garcia Anleu, R., Carrillo-Percastegui, S. E., Ponce Santizo, G., Polisar, J., Zuñiga Hartley, A., & Goldstein, I. (2018). Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? Two case studies from Guatemala and Peru. *Biological Conservation*, *220*(September 2017), 245–253.

Tobler, M. W., Zúñiga Hartley, A., Carrillo-Percastegui, S. E., & Powell, G. V. N. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, *52*(2), 413–421.

Tobler, M. W., & Powell, G. V. N. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, *159*, 109–118.

Tobler, M. (2014). Camera base version 1.6. 1. *Botanical Research Institute of Texas, Fort Worth, TX*.Tortato, F. R., Izzo, T. J., Hoogesteijn, R., & Peres, C. A. (2017). The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global ecology and conservation*, *11*, 106-114.

Tortato, F. R., Izzo, T. J., Hoogesteijn, R., & Peres, C. A. (2017). The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global ecology and conservation*, *11*, 106-114.

Tovar, C. C., & Villanueva, H. Z. (2009). Distribución potencial del hábitat del jaguar y áreas de conflicto humano–jaguar en la Península de Yucatán. *Revista Mexicana de Mastozoología (Nueva Época)*, *13*(1), 46-62.

Urquiza-Haas, T., Peres, C. A., & Dolman, P. M. (2009). Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico. *Biological Conservation*, 142(1), 134–148.

Urquiza-Haas, T., Peres, C. A., & Dolman, P. M. (2011). Large vertebrate responses to forest cover and hunting pressure in communal landholdings and protected areas of the Yucatan Peninsula, Mexico. *Animal Conservation*, *14*(3), 271–282.

Velásquez-Tibatá, J., Salaman, P., & Graham, C. H. (2013). Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia. *Regional Environmental Change*, *13*(2), 235-248.

Viau, P., Rodini, D.C., Sobral, G., Martins, G.S., Morato, R.G. and de Oliveira, C.A., 2020. Puberty and oestral cycle length in captive female jaguars *Panthera onca*. Conservation Physiology, 8(1), p.coaa052.

Waples, R. S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, *15*(6), 1419–1439.

Weckel, M., Giuliano, W., & Silver, S. (2006). Jaguar (Panthera onca) feeding ecology: Distribution of predator and prey through time and space. *Journal of Zoology*, *270*(1), 25–30.

Weigl, R. (2005). Longevity of mammals in captivity; from the living collections of the world.

Werdelin, L., Yamaguchi, N., Johnson, W. E., & O'Brien, S. J. (2010). Phylogeny and evolution of cats (*Felidae*). Biology and conservation of wild felids, 59-82.

Wildt, D. E., Platz, C. C., Chakraborty, P. K., & Seager, S. W. J. (1979). Oestrous and ovarian activity in a female jaguar (*Panthera onca*). *Reproduction*, *56*(2), 555-558.

Wilson, E. O. (1975). Some central problems of sociobiology. *Social Science Information*, *14*(6), 5-18.

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society open science*, *4*(7), 170052.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science*, *280*(5372), 2126–2128.

Yoccoz, N. G., Nichols, J. D., & Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, *16*(8), 446–453.

Yumnam, B., Jhala, Y. V., Qureshi, Q., Maldonado, J. E., Gopal, R., Saini, S., Srinivas, Y., & Fleischer, R. C. (2014). Prioritizing tiger conservation through landscape genetics and habitat linkages. *PLoS ONE*, *9*(11).

Zanin, M., Palomares, F., & Mangabeira Albernaz, A. L. (2021). Effects of climate change on the distribution of felids: mapping biogeographic patterns and establishing conservation priorities. *Biodiversity and Conservation*, *30*(5), 1375–1394.

Zanin, M., Sollmann, R., Tôrres, N. M., Furtado, M. M., Jácomo, A. T., Silveira, L., & De Marco, P. (2015). Landscapes attributes and their consequences on jaguar *Panthera onca* and cattle depredation occurrence. European journal of wildlife research, 61(4), 529-537.

Zeller, K. A., Nijhawan, S., Salom-Pérez, R., Potosme, S. H., & Hines, J. E. (2011). Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation*, *144*(2), 892–901.

Zeller, K. (2007). Jaguars in the new millennium data set update: the state of the jaguar in 2006. Wildlife Conservation Society, Bronx, New York, 1-77.

Zeller, K. A., Rabinowitz, A., Salom-Perez, R., & Quigley, H. (2013). The jaguar corridor initiative: a range-wide conservation strategy. *Molecular Population Genetics, Evolutionary Biology and Biological Conservation of Neotropical Carnivores. New York, USA: Nova Science Publishers, Inc*, 629-57.

APENDICE

A Review of Site Occupancy Studies in Carnivores

A Review of Site Occupancy Studies in Carnivores

Abstract

A key aspect of population biology is population size, which refers to the number of individuals in a particular place at a specific point in time. This parameter is usually calculated as an estimate, as a complete count is in most cases impossible. Various statistical methodologies attempt to estimate population size of animals from capture histories obtained from camera trap surveys. Site occupancy estimations are superior to relative abundance indices as they take into account imperfect detection. Also, habitat and anthropogenic factors can be used as covariates to measure the influence that they have on the presence and/or detectability of the species studied. The objective of this review was to gather recent published studies of carnivores that use occupancy modelling in order to decide whether it would be an appropriate analysis to evaluate jaguar's tolerance to anthropogenic and environmental disturbances. We underline the robustness of this method and also identify constraints that are yet to be addressed.

Introduction

Wright's and Fisher's early work on defining a population has been expanded considerably in modern times given the central role that this concept plays in ecology, evolutionary biology and conservation. We now hold a breadth of definitions of what a population is; these definitions can be divided into ecological, evolutionary and statistical paradigms among others (Waples and Gaggiotti 2006). For the purposes of this review we will combine the concepts of Krebs and Hartle and Clark (Hartle and Clark 1997) and define population as a group of organisms of the same species occupying a particular space at a particular time and which form an aggregate from which we want to draw inferences by sampling (Krebs 1995). A key aspect of population biology is population size, which refers to the number of individuals in a particular place at a specific point in time, a parameter that is often determined indirectly as a complete count is in most cases impossible. Capture–recapture is the sampling method frequently used in animals which are marked and returned to mix with the population. Data for each captured individual may be summarized as a ‘capture history’ and statistical modelling of these histories leads to an estimate of the unsampled fraction of the population and hence the total number (Efford and Fewster 2013). New technology that makes use of natural markings, such as microsatellite DNA or individual coat patterns identified on camera traps has in many cases obliterated the need for physical capture (Lukacs et al. 2005).

Statistical methodologies for estimating population size from the capture histories of trapped animals were detailed by Otis et al. (1978) and implemented in the software CAPTURE. If the same sites are sampled over several periods in time, camera trap studies can also provide useful information regarding the temporal dynamics of the population in question; Karanth et al. (2006) for example, used this method to investigate a population of tigers in Nagarahole Park from 1991 to 2000. This long- term study yielded survival probabilities and growth rates and were used to infer the viability of the population, data that is of utmost importance to make well-infomed decisions regarding conservation strategies.

When attempting to estimate a species’ abundance in large study areas one should pay close attention to variations in spatial abundance. As it is nearly impossible to sample the whole study area, researchers should be mindful to sample representative areas and make the proper inferences (Thompson, 1992). Another important aspect that should be considered is imperfect detection as it is likely that not all individuals of the population in the study will be registered during the sampling season (Nichols and Karanth 2011).

Since the 1990s ecologists concentrated on estimating species abundance, survival rates and other demographic parameters, primarily using capture-recapture analyses. It became apparent though that it was impossible to determine the changes in the absolute abundance of species in large study areas. A group of researchers lead by Dr. Darryl Mackenzie working in the newly formed US Geological Survey’s Amphibian Research and Monitoring Initiative suggested repeatedly measuring the presence or absence of species at a number of sites, they coined this method ‘proportion of area occupied’ and thus the use of occupancy measurements as a surrogate for abundance began. Similar to the primary role that capture probability plays in capture-recapture models, it was quickly recognized that imperfect detection in the presence or absence of species needed to be accounted for.

Incorporating absence data

When estimating occupancy, a basic sampling method is often used in which the researcher samples various sites collecting information, whether direct observations or indirect indications that a species is present. The information is gathered by physically surveying an area or by placing remote methods such as camera traps. This sampling produces a list of surveyed sites that are either ‘occupied’ or ‘unoccupied’. The issue with this method is that a site can be surveyed and deemed unoccupied but actually the species is present and was simply not detected, this can have a significant impact on statistical estimations (Mazkenzie et al. 2005). When reliable absence data is available many authors suggest its incorporation into the analysis.

There have been several attempts of estimating site occupancy given unknown imperfect detection. These methods can be classified into two approaches: a two step method where the probability of detection is calculated first and then used to determine the probability of occupancy; and one where the sampling process is modelled estimating detectability and occupancy simultaneously (MacKenzie et al. 2005). Once the various models are formulated incorporating covariates which are thought to influence either the probability of detection, occupancy, or both; an Akaike Information Criterion (AIC) is made in order to choose the best fitting model.

Methods

Our objective was to gather recent published studies of carnivores that use occupancy modelling in order to decide whether it would be an appropriate analysis to evaluate jaguar’s tolerance to anthropogenic and environmental disturbances. To accomplish this objective, several retrieval strategies were used to identify relevant published and unpublished studies. Published studies were found using a thorough search strategy of the Google Scholar databases with no language or regional restrictions. The following search terms were used: site occupancy, detection probability and carnivore occupancy. References within the included articles were reviewed and the corresponding abstracts and full articles were accessed if useful for this review. Textbooks containing themes relevant to this review were also examined. Such textbooks include: Population Biology, Occupancy Estimation and Camera Trap Manuals.

Results and Discussion

Studies on Carnivores that Employ Site Occupancy Estimations

Single- Species Studies on Carnivores

Sanei and Zakaria (2010) conducted a study in the Ayer Hitam Forest Reserve in Selangor, Malaysia in which they sought out to determine the occupancy of the Malayan Leopard's (*Panthera pardus delacouri)* prey and its relation to the presence of anthropogenic pressures in the area. Data was collected through direct observations, photographs and animal signs (feces and footprints). The researchers found that macaques, lesser mouse deer and wild boar were abundant in the area, with occupancy rates close to 1. They also found that their detection probability was higher through direct observations and indirect signs compared to camera trap photographs. As for the effect of anthropogenic factors, they found that construction activities had a stronger effect on wild boar and macaque presence while deforestation activities had a stronger effect on the lesser mouse deer (Sanei and Zakaria, 2010).

Silva et al. (2013) studied the effect of prey abundance, land cover and disturbance on European Wildcats in northeast Scotland. A camera trapping survey performed from December 2010 to July 2011 found that vegetation type was the most influential factor for wildcat detection. Occupancy on the other hand was determined largely by rodent abundance and land cover. Previous studies in other parts of the wildcats' range had found that wildcats avoid roads (Klar et al. 2009) yet in Scotland they have been associated with these constructions (Scott et al. 1993). This study also found a positive effect, though not robust, of human settlements on wildcat occupancy and suggested that wildcats living in small density populations might be attracted to feral cats living near communities. The investigators advised that local conservation plans should encompass diverse habitats where rodent and rabbit abundances would be higher (Silva et al. 2013)

Several studies on small carnivores have also successfully utilized occupancy estimations to make inferences about the population status and its changes through time. For example, the Asian small clawed otter was found to have a high occupancy of stream segments in the Western Ghats in India prior to the rainy season which decreased after summer (Perinchery et al. 2011). Baldwin and Bender (2008) compared different modelling techniques used to estimate the distribution and habitat correlates of martens (*Martes americana)* in the Rocky Mountain National Park. A 25- camera grid was set up with attached baits to collect data for 2,608 days. Twenty two of these sites registered martens. Occurrence was modelled as a function of habitat and landscape covariates using binary response, binomial count, logistic regression and occupancy. The authors concluded that occupancy modelling was the most appropriate given that incorporation of detection probabilities (Baldwin and Bender 2008).

Multi-Species Interaction Studies on Carnivores

Occupancy estimations can also be used to gather information on the interactions and relationships between multiple species cohabiting a single area. Sollman et al. (2012) used this method to investigate whether jaguar and pumas were partitioning space in Emas

National Park, Brazil. Jaguars were found to occupy 54.1% and pumas 39.3% of the study sites. Additionally, distance to water proved to negatively influence both species while pumas were also negatively correlated with presence of jaguars; these findings supported the idea of a spatial portioning of these sympatric carnivores (Sollman et al. 2012). Another study that aimed to determine whether spatial segregation was taking place between large predators and incorporated a small mammal was the one performed by Lazenby and Dickman (2013); using camera traps they investigated the interactions between feral cats (*Felis catus*), the Tasmanian devil (*Sarcophilus harrisii),* and the swamp rat (*Rattus lutreolus*). Using occupancy models, the study found that the detectability of the native species (Tasmanian devil) could affect that of the introduced species (feral cat), supporting the hypothesis of the existence of a dominant predator-mesopredator relationship (Lazenby and Dickman, 2013).

Measurements of the Anthropogenic Effects on Carnivores

Studies that use trophic scaling to estimate population abundances assume that only bottom-up regulation takes place. In order to correct this bias and incorporate possible top- down anthropogenic effects, Everatt el al. (2014) compared direct density estimates of a lion (*Panthera leo*) population in Lompopo National Park, Mozambique to those derived from trophic scaling. They also applied a site occupancy estimation using prey abundance and anthropogenic factors as covariates. The study found a large difference between the direct density estimation and the one derived from trophic scaling which supports the hypothesis that lions are limited by anthropogenic pressures. The covariate with the strongest influence on lion presence in the occupancy estimation was the agro-pastoralist settlements, which negatively affected their occurrence (Everatt et al. 2014).

Deforestation is an ongoing issue in Madagascar, with only 16% of the original forests remaining (Harper et al. 2007). Consequently, forest dwelling animals are severely threatened yet little is known of the carnivores' situation and how deforestation directly impacts them. Gerber et al. (2012) attempted to quantify the composition of carnivore species and their occupancy across a gradient of disturbed rainforest. The analysis related the probability of the occupancy of eight different carnivores including fossa (*Cryptocprocta ferox*) and Malagasy civet *(Fossa fossana*) with various habitat characteristics and with the presence of exotic carnivores, incorporating imperfect detection. There was a significantly higher density of carnivores in the undisturbed fragments, yet the sensitivity to the disturbances varied by species. The fossa for example, seemed to be unaltered by the disturbance of the forest, yet the Malagasy civet proved to be intolerant to disturbances and was absent in all study sites (Gerber et al. 2012).

Other studies however have documented the presence of native carnivores in fruit orchards and plantations. Nogeire et al. (2013) studied the occupancy of carnivores in avocado orchards in California and found that there was actually a higher occurrence of carnivores in the orchards compared with the studied wildlands. Because many of species detected were omnivores rather than obligate carnivores, it is likely that the avocados presented another food source and thus they were attracted to them (Nogeire et al. 2013). Another study, conducted in oil palm plantations not adjacent to extensive areas of continuous forest in Sumatra revealed the presence of only three small carnivores: leopard cat (*Prionailurus begalensis*), common palm civet (*Paradoxurus hermaphroditus*) and Malay Civet *(Viverra tangalunga*) even after 3,164 camera nights. These results demonstrate a very low diversity of carnivores, especially when compared to other studies in central Sumatra where 17 carnivore species were detected (Maddox et al. 2007). The results also indicate that distance from the edge of the plantation affected the occupancy of the Malay civet but not those of the leopard cat or palm civet (Jennings et al. 2015).

Conclusion

Using site occupancy to measure the presence and distribution of carnivore populations has become an extremely common practice in ecology. The ability to measure the influence of covariates on the species occurrence and detection is extremely valuable when attempting to elucidate the distributional behavior and preference of endangered and low density-occurring species. Additionally, the incorporation of measurements of imperfect detection provide studies with more robust, realistic estimates. Given these results, we conclude that site occupancy analyss is the most appropriate analysis that we can use to evaluate jaguar's tolerance to anthropogenic and environmental disturbances. However, there still exist some issues with the methods that should be addressed. For example, Pillay et al. (2014) suggested the incorporation of the probability of encountering false positive errors when performing occupancy estimates using informant surveys. The researchers compared occupancy models that accounted for false negatives (species is present but undetected by interviewee) as well as false positives (species is not presented but interviewee claims it is) against models that only accounted for false negatives as is usually done. They found that models only accounting for false negatives tended to overestimate species occupancy (Pillay et al. 2014). As many studies nowadays rely on interviews, the artifact of human error should be accounted for.

Another constraint, brought up by Neilson et al. (2018) is that many of the studies employing camera traps and using occupancy analysis do not explicitly consider how the underlying patterns of movement and the population density of the species studied affects detection and occupation probabilities. In order to test whether the occupancy estimations would withstand the aforementioned variations, the researchers developed simulations of detection histories that varied in animal movements, population densities and home range areas. The occupancy estimations derived from these simulations were then compared to the asymptotic proportion of area occupied (POA) which is the sum of all simulated home ranges. Occupancy models were found to overestimate POA measurements when the simulations were made from animals coming from a population of low density moving quickly through large home ranges. On the other hand, POA was underestimated when animals were simulated to move slowly in large home ranges. These results underline the importance of considering the behavioral patterns and basic ecology of the species studies (Neilson et al. 2018).

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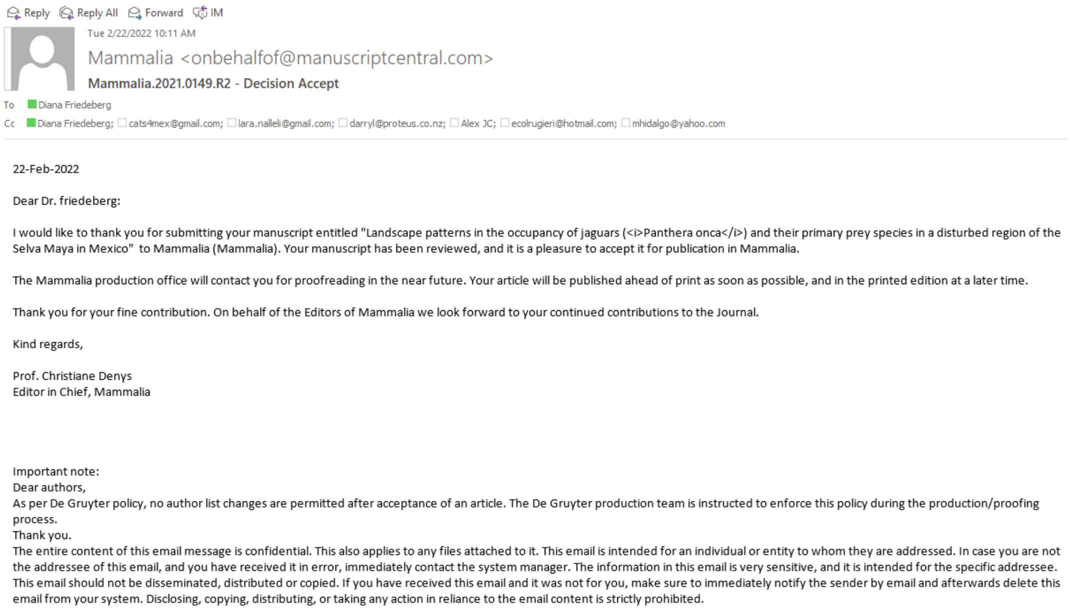

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To 🟩 Diana Friedeberg

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22-Feb-2022

Dear Dr. friedeberg:

I would like to thank you for submitting your manuscript entitled "Landscape patterns in the occupancy of jaguars (<i>Panthera onca</i>) and their primary prey species in a disturbed region of the Selva Maya in Mexico" to Mammalia (Mammalia). Your manuscript has been reviewed, and it is a pleasure to accept it for publication in Mammalia.

The Mammalia production office will contact you for proofreading in the near future. Your article will be published ahead of print as soon as possible, and in the printed edition at a later time.

Thank you for your fine contribution. On behalf of the Editors of Mammalia we look forward to your continued contributions to the Journal.

Kind regards,

Prof. Christiane Denys
Editor in Chief, Mammalia

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Thank you.

Supplementary Material to A decade long survey of an isolated jaguar population in a region subjected to acute deforestation in southeastern Mexico

Supplementary Table 1 Correlations between numbers of camera trap stations and number of individuals detected in our study site from 2010 to 2020, excluding 2015

year	number of camera stations	number of individuals detected
2010	30	1
2011	21	5
2012	31	11
2013	25	6
2014	21	2
2016	66	11
2017	42	7
2018	33	4
2019	40	4
2020	40	3
$\|r\|$= .52		

Supplementary Material to Landscape Patterns in the Occupancy of Jaguars (*Panthera onca)* and their Prey in the Selva Maya in Mexico

Supplementary Table 2 Pairwise Correlations between variables used to determine the site occupancy of prey species in a disturbed area in the Selva Maya. Highlighted is the correlation with $|r| > 0.70$ that was considered to be highly correlated. Grassland was removed from the analysis.

	Armadillo	White- tailed deer	Coati	Paca	collared peccary	Wetland	Agro-livestock	Conserved	Distance to nearest roads	
Armadillo	1.00									
White -tailed deer	-0.027	1.000								
Coati	0.005	0.112	1.000							
Paca	0.080	0.271	0.144	1.00						
Collared peccary	0.073	0.253	0.133	0.020	1.000					
Wetland	0.108	-0.082	-0.072	-0.017	-0.124	1.000				
Agro-livestock	0.048	-0.211	-0.016	0.121	-0.008	-0.096	1.000			
Conserved	-0.057	0.276	0.062	-0.062	-0.001	-0.226	-0.717	1.000		
Distance to nearest roads	-0.157	0.130	-0.119	-0.150	0.099	-0.169	-0.402	0.403	1.000	
Distance to nearest settlements	-0.036	0.475	0.026	0.052	0.221	-0.151	-0.264	0.453	0.215	1.0

Supplementary Table 3 Pairwise Correlations between variables used to determine the site occupancy of jaguars in a disturbed area in the Selva Maya, highlighted are those with |r| >0.70 that were considered to be highly correlated. Coati, deer and paca occupancy covariates were removed from the analysis.

	Log distance to nearest roads	Log distance to nearest settlements	Armadillo	Coati	White- tailed deer	Paca	Collared peccary
Log distance to nearest roads	1.000						
Log distance to nearest settlements	0.222	1.000					
Armadillo	-0.255	-0.154	1.000				
Coati	0.414	0.227	-0.546	1.000			
White- tailed deer	0.532	0.305	-0.716	0.879	1.000		
Paca	-0.372	-0.184	0.607	-0.973	-0.836	1.000	
Collared peccary	0.497	0.316	-0.203	0.874	0.797	-0.789	1.000

Supplementary Table 4 MacKenzie Bailey test used to assess the goodness of fit of our global models prior to running the occupancy models. Ĉ = overdispersion parameter   Estimate PAO= Occupancy Probability Estimate

Species	Number of simulations	Observed	Medium simulation	Deviation simulation	Test	Ĉ	Estimate PAO	2.5%	97.5%
Armadillo	1,000	6,398	4,970	247	>0.01	6398/4970= 1.287 overdispersion	0.300	0.300	0.657
Coati	1,000	4,940	5,042	171	>0.791	4940/5042 = 0.97	0.706	0.706	0.755
Paca	1,000	6,013	4,923	525	>0.016	6013/4923 = 1.22 overdispersion	0.139	0.139	0.146
Collared peccary	1,000	5,707	5,999	195	>0.94	5707/5999 = 0.905	0.475	0.475	0.629
White-tailed deer	1,000	4,835	5,029	271	>0.897	4835/5029 = 0.96	0.713	0.706	0.797
Jaguar		3,212	4,085	510	>0.55	3,212/4085 = 0.78	0.265	0.230	0.685

Supplementary Table 5 Armadillo Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	Loglik	QAICc	Delta	Weig
p(capturedays+forest)	4	-588.920	925.620	0	0.080
psi(wetland)p(capturedays+forest)	5	-587.576	925.712	0.091	0.076
psi(forest+agrolivestock)p(forest)	5	-587.687	925.885	0.264	0.070
psi(wetland+agrolivestock)p(capturedays+forest)	6	-586.518	926.280	0.659	0.057
psi(forest+wetland+agrolivestock)p(forest)	6	-586.534	926.305	0.684	0.057
psi(agrolivestock)p(capturedays+forest)	5	-588.056	926.457	0.836	0.053
psi(forest)p(forest)	4	-589.637	926.734	1.113	0.046
psi(forest+agrolivestock)p(forest+capturedays)	6	-586.884	926.848	1.227	0.043
p(forest+humanabundance)	4	-589.731	926.881	1.260	0.042
psi(wetland)p(forest+humanabundance)	5	-588.394	926.983	1.362	0.040
psi(forest+wetland)p(forest)	5	-588.401	926.993	1.372	0.040
psi(forest+wetland+agrolivestock)p(forest)	7	-585.723	927.289	1.668	0.035
psi(wetland+agrolivestock)p(humanabundance+forest)	6	-587.292	927.483	1.862	0.031
psi(forest)p(capturedays+forest)	5	-588.809	927.628	2.007	0.029
psi(agrolivestock)p(forest+humanabundance)	5	-588.832	927.664	2.043	0.029
p(capturedays+forest+humanabundance)	5	-588.906	927.778	2.157	0.027
psi(humedal)p(capturedays+forest+humanabundance)	6	-587.555	927.892	2.271	0.025
psi(forest+wetland)p(capturedays+forest)	6	-587.564	927.905	2.284	0.025
psi(forest+cattleranch)p(forest+humanabundance)	6	-587.660	928.055	2.434	0.023
psi(wetland+agrolivestock)p(capturedays+humanabundance)	7	-586.484	928.471	2.850	0.019
psi(forest+wetland+agrolivestock)p(forest+humanabundance)	7	-586.498	928.494	2.873	0.019
psi(agrolivestock)p(capturedays+forest+humanabundance)	6	-588.032	928.633	3.012	0.017

psi(forest)p(forest+humanabundance)	5	-589.626	928.898	3.277	0.015
psi(forest+agrolivestock)p(capturedays+forest+humanabundance)	7	-586.853	929.045	3.424	0.014
psi(forest+wetland)p(forest+humanabundance)	6	-588.384	929.180	3.559	0.013
psi(forest+wetland+agrolivestock)p(capturedays+forest+humanabundance)	8	-585.687	929.513	3.892	0.011
psi(forest)p(capturedays+forest+humanabundance)	6	-588.795	929.818	4.197	0.009
psi(forest+wetland)p(capturedays+forest+humanabundance)	7	-587.543	930.118	4.497	0.008
p(capturedays)	3	-594.113	931.542	5.921	0.004
psi(wetland+agrolivestock)p(capturedays)	5	-591.382	931.627	6.006	0.003
psi(agrolivestock)p(capturedays)	4	-592.854	931.734	6.113	0.003
psi(wetland)p(capturedays)	4	-592.891	931.792	6.171	0.003
psi(forest+agrolivestock)p(capturedays)	5	-592.099	932.740	7.119	0.002
psi(forest+wetland+agrolivestock)p(capturedays)	6	-590.929	933.135	7.514	0.001
p(days+humanabundance)	4	-593.889	933.342	7.721	0.001
psi(wetland+agrolivestock)p(capturedays+humanabundance)	6	-591.250	933.633	8.012	0.001
psi(wetland)p(capturedays+humanabundance)	5	-592.684	933.650	8.029	0.001
psi(agrolivestock)p(capturedays+humanabundance)	5	-592.698	933.671	8.050	0.001
psi(forest)p(capturedays)	4	-594.112	933.690	8.069	0.001
psi(forest+wetland)p(capturedays)	5	-592.848	933.905	8.284	0.001
psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-591.943	934.710	9.089	0.000
psi(forest+wetland+agrolivestock)p(capturedays+humanabundance)	7	-590.797	935.174	9.553	0.000
psi(forest)p(capturedays+humanabundance)	5	-593.888	935.521	9.900	0.000
psi(forest+wetland)p(capturedays+humanabundance)	6	-592.650	935.809	10.188	0.000
p(forest)	3	-680.161	1065.262	139.641	0
psi(wetland)p(forest)	4	-680.161	1067.410	141.789	0
psi(agrolivestock)p(forest)	4	-680.161	1067.410	141.789	0
psi(wetland+agrolivestock)p(forest)	5	-680.161	1069.590	143.969	0

	2	-685.929	1072.108	146.487	0
p(humanabundance)	3	-684.836	1072.527	146.906	0
psi(wetland)	3	-685.929	1074.226	148.605	0
psi(agrolivestock)	3	-685.930	1074.226	148.605	0
psi(forest)	3	-685.930	1074.227	148.606	0
psi(wetland)p(humanabundance)	4	-684.836	1074.675	149.054	0
psi(agrolivestock)p(humanabundance)	4	-684.836	1074.675	149.054	0
psi(forest)p(humanabundance)	4	-684.837	1074.676	149.055	0
psi(agrolivestock+wetland)	4	-685.930	1076.374	150.753	0
psi(forest+wetland)	4	-685.930	1076.375	150.754	0
psi(forest+agrolivestock)	4	-685.930	1076.375	150.754	0
psi(wetland)p(humanabundance)	5	-684.836	1076.855	151.234	0
psi(forest+wetland)p(humanabundance)	5	-684.837	1076.856	151.235	0
psi(forest+agrolivestock)p(humanabundance)	5	-684.837	1076.856	151.235	0
psi(forest+wetland+agrolivestock)	5	-685.930	1078.555	152.934	0
psi(forest+wetland+agrolivestock)p(humanabundance)	6	-684.837	1079.068	153.447	0

Supplementary Table 6. Armadillo Full Averaged Model Coefficients. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	-0.985	0.506	1.943	0.052	.
p(int)	-1.865	0.203	9.175	< 0	***
p(capture days)	-0.004	0.006	0.681	0.495	
p(forest)	-0.959	0.314	3.045	0.002	**
psi(wetland)	-2.286	3.434	0.666	0.505	
psi(forest)	0.347	0.675	0.514	0.607	
psi(agrolivestock)	1.395	1.833	0.761	0.446	
p(human abundance)	-0.023	0.313	0.074	0.940	

Supplementary Table. 7 Coati Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. Df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	Loglik	QAICc	Delta	Weig
psi(agrolivestock)p(capturedays+forest+humanabundance)	6	-1708.567	3429.752	0	0.402
psi(forest+agrolivestock)+p(capturedays+forest+humnabundance)	7	-1708.306	3431.441	1.689	0.172
psi(wetland+agrolivestock)p(capturedays+forest)	7	-1708.494	3431.819	2.067	0.143
psi(agrolivetsock)p(capturedays+humanabundance)	5	-1711.334	3433.106	3.354	0.075
psi(forest+wetland+agrolivestock)p(capturedays+forest+humanabundance)	8	-1708.277	3433.629	3.877	0.057
psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-1711.106	3434.830	5.0783	0.031
psi(agroliveestock)p(forest+humanabundance)	5	-1712.220	3434.879	5.127	0.030
psi(wetland+agrolivestock)p(capturedays+humanabundance)	6	-1711.269	3435.155	5.403	0.026
psi(forest+agrolivestock)p(forest+humanabundance)	6	-1711.936	3436.490	6.738	0.013
psi(wetland+agrolivestock)p(forest+humanabundance)	6	-1712.146	3436.910	7.158	0.011
psi(forest+wetland+agrolivestock)p(capturedays+humanabundance)	7	-1711.079	3436.989	7.237	0.010
psi(forest)p(capturedays+forest+humanabundance)	6	-1712.868	3438.354	8.602	0.005
psi(forest+wetland+agrolivestock)p(forest+humanabundance)	7	-1711.908	3438.645	8.893	0.004
psi(agrolivestock)p(humanabundance)	4	-1715.238	3438.767	9.015	0.004
psi(forest+agrolivestock)p(humanabundance)	5	-1714.995	3440.428	10.676	0.001
psi(forest+wetland)p(capturedays+forest+humanabundance)	7	-1712.867	3440.565	10.813	0.001

psi(wetland+agrolivestock)p(humanabundance)	5	-1715.173	3440.785	11.033	0.001
psi(forest)p(capturedays+humanabundance)	5	-1715.672	3441.783	12.031	0.000
psi(forest+wetland+agrolivestock)p(humanabundance)	6	-1714.969	3442.557	12.805	0.000
psi(forest)psi(forest+humanabundance)	5	-1716.468	3443.374	13.621	0
psi(capturedays+humanabundance)p(forest+wetland)	6	-1715.672	3443.962	14.210	0
psi(forest+wetland)p(forest+humanabundance)	6	-1716.467	3445.553	15.801	0
p(capturedays+forest+humanabundance)	5	-1717.829	3446.096	16.344	0
psi(forest)p(humanabundance)	4	-1719.532	3447.354	17.602	0
psi(wetland)p(capturedays+forest+humanabundance)	6	-1717.629	3447.875	18.123	0
p(capturedays+humanabundance)	4	-1720.484	3449.259	19.507	0
psi(forest+wetland)p(humanabundance)	5	-1719.532	3449.502	19.750	0
psi(wetland)p(capturedays+humanabundance)	5	-1720.289	3451.017	21.265	0
p(forest+humanabundance)	4	-1721.506	3451.302	21.550	0
psi(agrolivestock)p(capturedays+forest)	5	-1720.575	3451.589	21.837	0
psi(wetland)p(forest+humanabundance)	5	-1721.303	3453.044	23.292	0
psi(forest+agrolivestock)p(capturedays+forest)	6	-1720.304	3453.226	23.474	0
psi(wetland+agrolivestock)p(capturedays+forest)	6	-1720.498	3453.614	23.862	0
p(humanabundance)	3	-1724.392	3454.957	25.205	0
psi(forest+wetland+agrolivestock)p(capturedays+forest)	7	-1720.273	3455.376	25.624	0
psi(wetland)p(humanabundance)	4	-1724.196	3456.681	26.929	0
psi(agrolivestock)p(forest)	4	-1725.141	3458.573	28.821	0
psi(forest+agrolivestock)p(forest)	5	-1724.839	3460.117	30.365	0
psi(forest)p(capturedays+forest)	5	-1724.906	3460.251	30.499	0
psi(wetland+agrolivestock)p(forest)	5	-1725.060	3460.558	30.806	0
psi(forest+wetland+agrolivestock)p(forest)	6	-1724.808	3462.234	32.482	0
psi(forest+wetland)p(capturedays+forest)	6	-1724.906	3462.431	32.679	0
psi(agrolivestock)p(capturedays)	4	-1729.127	3466.545	36.793	0
psi(forest)p(forest)	4	-1729.415	3467.120	37.368	0
p(capturedays+forest)	4	-1729.928	3468.147	38.394	0
psi(forest+agrolivestock)p(capturedays)	5	-1728.909	3468.256	38.504	0

psi(wetland+agrolivestock)p(capturedays)	5	-1729.057	3468.553	38.801	0
psi(forest+wetland)p(forest)	5	-1729.414	3469.2679	39.515	0
psi(wetland)p(capturedays+forest)	5	-1729.723	3469.884	40.132	0
psi(forest+wetland+agrolivestock)p(capturedays)	6	-1728.8792	3470.376	40.624	0
p(forest)	3	-1734.536	3475.246	45.494	0
psi(forest)p(capturedays)	4	-1733.497	3475.283	45.531	0
psi(agrolivestock)	3	-1734.628	3475.429	45.677	0
psi(wetland)p(forest)	4	-1734.326	3476.943	47.191	0
psi(forest+agrolivestock)	4	-1734.394	3477.078	47.326	0
psi(wetland+agrolivestock)	4	-1734.556	3477.403	47.651	0
psi(forest+wetland)p(capturedays)	5	-1733.496	3477.431	47.679	0
psi(forest+wetland+agrolivestock)	5	-1734.364	3479.166	49.414	0
p(capturedays)	3	-1738.248	3482.670	52.918	0
psi(forest)	3	-1738.945	3484.064	54.312	0
psi(wetland)p(capturedays)	4	-1738.048	3484.385	54.633	0
p(forest+wetland)	4	-1738.945	3486.181	56.429	0
psi(wetland)	3	-1743.521	3493.215	63.463	0

Supplementary Table 8 Coati Full Averaged Model Coefficients. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	1.500	0.392	3.820	0.000	***
psi(agrolivestock)	-5.623	1.630	3.449	0.000	***
psi(forest)	0.170	0.509	0.335	0.737	
p(int)	-1.266	0.117	10.811	< .000	***
p(capture days)	-0.010	0.003	2.683	0.007	**
p(forest)	-0.352	0.149	2.352	0.018	*
p(human abundance)	1.713	0.337	5.076	0.000	***

p(forest)	0.170	0.509	0.335	0.737

Supplementary Table 9 Paca Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. Df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	Loglik	QAICc	Delta	Weight
psi(agrolivestock)+p(humanabundance)	4	-374.172	618.848	0	0.103
p(humanabundance)	3	-375.998	619.669	0.820	0.068
psi(agrolivestock)p(capturedays+humanabundance)	5	-373.642	620.167	1.318	0.053
psi(agrolivestock)p(forest+humanabundance)	5	-373.681	620.229	1.380	0.051
psi(agrolivestock+forest)+p(humanabundance)	5	-374.028	620.793	1.945	0.039
psi(wetland+agrolivestock)p(humanabundance)	5	-374.105	620.919	2.070	0.036
p(capturedays+humanabundance)	4	-375.465	620.950	2.101	0.036
p(forest+humanabundance)	4	-375.469	620.957	2.108	0.036
psi(agrolivestock)p(capturedays+forest+humanabundance)	6	-373.001	621.336	2.487	0.029
psi(forest)p(humanabundance)	4	-375.739	621.396	2.547	0.028
psi(agrolivestock)p(forest)	4	-375.868	621.605	2.757	0.026
psi(wetland)p(humanabundance)	4	-375.970	621.771	2.922	0.023
psi(agrolivestock)	3	-377.406	621.958	3.109	0.021
p(capturedays+forest+humanabundance)	5	-374.786	622.026	3.177	0.021
psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-373.498	622.144	3.296	0.019
psi(forest)p(forest+humanabundance)	6	-373.523	622.184	3.335	0.019

psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-373.574	622.268	3.419	0.018
psi(wetland+agrolivestock)p(forest+humanabundance)	6	-373.611	622.328	3.479	0.018
p(forest)	3	-377.636	622.332	3.483	0.018
psi(agrolivestock)p(forest+capturedays)	5	-374.986	622.351	3.502	0.017
psi(forest)p(capturedays+humanabundance)	5	-375.206	622.709	3.860	0.015
psi(forest) p(forest+humanabundance)	5	-375.234	622.754	3.905	0.014
	2	-379.229	622.806	3.957	0.014
psi(forest+wetland+agrolivestock)p(humanabundance)	6	-373.990	622.944	4.096	0.013
p(capturedays+forest)	4	-376.754	623.046	4.197	0.012
psi(agrolivestock)p(capturedays)	4	-376.763	623.061	4.212	0.012
psi(wetland)p(capturedays+humanabundance)	5	-375.436	623.083	4.234	0.012
psi(wetland)p(forest+humanabundance)	5	-375.438	623.087	4.238	0.012
psi(forest+agrolivestock)p(capturedays+forest+humanabundance)	7	-372.844	623.325	4.476	0.011
psi(forest+wetland)p(humanabundance)	5	-375.661	623.450	4.601	0.010
psi(wetland+agrolivestock)p(capturedays+forest+humanabundance)	7	-372.931	623.467	4.618	0.010
psi(forest+agrolivestock)p(forest)	5	-375.707	623.524	4.676	0.009
psi(wetland+agrolivestock)p(forest)	5	-375.796	623.669	4.820	0.009
psi(forest)p(capturedays+forest+humanabundance)	6	-374.551	623.856	5.007	0.008
p(capturedays)	3	-378.583	623.872	5.023	0.008
psi(forest+agrolivestock)	4	-377.264	623.876	5.027	0.008
psi(wetland+agrolivestock)	4	-377.338	623.996	5.147	0.007
psi(forest)p(forest)	4	-377.407	624.109	5.260	0.007
psi(wetland)p(capturedays+forest+humanabundance)	6	-374.754	624.187	5.338	0.007

psi(forest+agrolivestock)p(capturedays+forest)	6	-374.826	624.304	5.455	0.006
psi(forest+wetland+agrolivestock)p(capturedays+humanabundance)	7	-373.460	624.327	5.479	0.006
psi(forest+wetland+agrolivestock)p(forest+humanabundance)	7	-373.485	624.368	5.519	0.006
psi(wetland)p(forest)	4	-377.603	624.426	5.578	0.006
psi(wetland+agrolivestock)p(capturedays+forest)	6	-374.914	624.446	5.597	0.006
psi(forest)	3	-378.968	624.498	5.649	0.006
psi(forest+wetland)p(capturedays+humanabundance)	6	-375.127	624.793	5.944	0.005
psi(forest+wetland)p(forest+humanabundance)	6	-375.155	624.838	5.989	0.005
psi(forest)p(capturedays+forest)	5	-376.524	624.852	6.003	0.005
psi(wetland)	3	-379.199	624.874	6.025	0.005
psi(forest+agrolivestock)p(capturedays)	5	-376.621	625.010	6.161	0.004
psi(wetland+agrolivestock)p(capturedays)	5	-376.693	625.127	6.278	0.004
psi(wetland)p(capturedays+forest)	5	-376.721	625.172	6.3235	0.004
psi(forest+wetland+agrolivestock)p(capturedays+forest+humanabundance)	8	-372.805	625.541	6.6926	0.003
psi(forest)p(capturedays)	4	-378.322	625.595	6.746	0.003
psi(forest+wetland+agrolivestock)p(forest)	6	-375.668	625.673	6.824	0.003
psi(wetland)p(capturedays)	4	-378.552	625.969	7.121	0.002
psi(forest+wetland)p(capturedays+forest+humanabundance)	7	-374.471	625.971	7.122	0.002
psi(forest+wetland+agrolivestock)	5	-377.225	625.993	7.144	0.002
psi(forest+wetland)p(forest)	5	-377.326	626.156	7.307	0.002
psi(forest+wetland+agrolivestock)p(days+forest)	7	-374.787	626.485	7.636	0.002
psi(wetland)	4	-378.886	626.513	7.664	0.002
psi(forest+wetland)p(capturedays+forest)	6	-376.442	626.931	8.082	0.001
psi(forest+wetland+agrolivestock)p(capturedays)	6	-376.582	627.158	8.309	0.001

psi(forest+wetland)p(capturedays)	5	-378.239	627.6415	8.792	0.001

Supplementary Table. 10 Paca Full Averaged Model Coefficients. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	-2.117	0.423	5.000	0.000	***
psi(agrolivestock)	2.375	1.882	1.262	0.206	
p(int)	-1.960	0.177	11.041	<0.000	***
p(human abundance)	1.338	0.533	2.511	0.012	*
p(capture days)	-0.001	0.004	0.308	0.758	
p(forest)	-0.055	0.186	0.296	0.767	
psi(forest)	0.064	0.382	0.168	0.866	

Supplementary Table 11 Peccary Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. Df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	Loglik	QAICc	Delta	Weight
psi(forest)p(forest+humanabundance)	5	-975.284	1961.006	0	0.070
psi(forest+agrolivestock)p(forest+humanabundance)	6	-974.412	1961.443	0.437	0.056
psi(agrolivestock)p(forest+humanabundance)	5	-975.503	1961.444	0.438	0.056
psi(forest)p(capturedays+forest+humanabundance)	6	-974.496	1961.611	0.604	0.052
psi(agrolivestock)p(capturedays+forest+humanabundance)	6	-974.702	1962.022	1.015	0.042
psi(forest+agrolivestock)p(capturedays+forest+humanabundance)	7	-973.621	1962.073	1.067	0.041
psi(forest)p(forest)	4	-976.891	1962.073	1.067	0.041

psi(forest+agrolivestock)p(forest)	5	-976.030	1962.498	1.491	0.033
psi(agrolivestock)p(forest)	4	-977.106	1962.503	1.497	0.033
psi(forest)+p(capturedays+forest)	5	-976.046	1962.531	1.525	0.032
psi(forest)p(humanabundance)	4	-977.164	1962.618	1.611	0.031
psi(agrolivestock)p(humanabundance)	4	-977.225	1962.740	1.733	0.029
psi(agrolivestock)p(capturedays+forest)	5	-976.245	1962.928	1.921	0.027
psi(forest+agrolivestock)p(capturedays+forest)	6	-975.178	1962.975	1.968	0.026
psi(forest+agrolivestock)p(humanabundance)	5	-976.277	1962.993	1.987	0.026
psi(forest)p(capturedays+humanabundance)	5	-976.327	1963.093	2.087	0.024
psi(forest+wetland)p(forest+humanabundance)	6	-975.275	1963.167	2.161	0.023
psi(agrolivestock)p(capturedays+humanabundance)	5	-976.377	1963.193	2.186	0.023
psi(wetland+agrolivestock)p(forest+humanabundance)	6	-975.355	1963.329	2.323	0.022
psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-975.437	1963.493	2.486	0.020
psi(forest+wetland+agrolivestock)p(forest+humanabundance)	7	-974.387	1963.604	2.598	0.019
psi(forest+wetland)p(capturedays+forest+humanabundance)	7	-974.487	1963.804	2.798	0.017
psi(wetland+agrolivestock) p(capturedays+forest+humanabundance)	7	-974.554	1963.938	2.932	0.016
psi(forest+wetland)p(forest)	5	-976.880	1964.198	3.191	0.014
psi(forest+wetland+agrolivestock)p(capturedays+forest+humanabundance)	8	-973.596	1964.266	3.260	0.013
psi(wetland+agrolivestock)p(forest)	5	-976.949	1964.337	3.330	0.013
psi(forest+wetland+agrolivestock)p(forest)	6	-976.000	1964.618	3.612	0.011
psi(wetland+agrolivestock)p(humanabundance)	5	-977.093	1964.624	3.617	0.011
psi(forest+wetland)p(capturedays+forest)	6	-976.035	1964.687	3.681	0.011
psi(forest+wetland)p(humanabundance)	5	-977.156	1964.749	3.743	0.010
psi(wetland+agrolivestock)p(capturedays+forest)	6	-976.088	1964.794	3.788	0.010
psi(forest)	3	-979.466	1965.105	4.098	0.009
psi(wetland+agrolivestock)p(humanabundance+capturedays)	6	-976.244	1965.107	4.101	0.009
psi(forest+wetland+agrolivestock)p(humanabundance)	6	-976.254	1965.125	4.119	0.009

psi(forest+wetland+agrolivestock)p(capturedays+forest)	7	-975.149	1965.127	4.121	0.008
psi(agrolivestock)	3	-979.503	1965.179	4.173	0.008
psi(forest+wetland)p(capturedays+humanabundance)	6	-976.319	1965.256	4.249	0.008
psi(forest)p(days)psi(agrolivestock)p(capturedays)	4	-978.533	1965.356	4.350	0.008
psi(forest+agrolivestock)	4	-978.557	1965.405	4.399	0.007
psi(forest+agrolivestock)	4	-978.599	1965.487	4.481	0.007
psi(forest+wetland+agrolivestock)p(capturedays+humanabundance)	7	-975.413	1965.656	4.650	0.006
psi(forest+agrolivestock)p(capturedays)	5	-977.659	1965.756	4.749	0.006
p(forest+humanabundance)	4	-979.260	1966.810	5.803	0.003
psi(wetland+agrolivestock)	4	-979.359	1967.008	6.002	0.003
psi(forest+wetland)	4	-979.454	1967.198	6.192	0.003
psi(wetland+agrolivestock)p(capturedays)	5	-978.413	1967.265	6.259	0.003
p(days+forest+humanabundance)	5	-978.455	1967.349	6.342	0.002
psi(forest+wetland)p(days)	5	-978.521	1967.481	6.474	0.002
psi(forest+wetland+agrolivestock)	5	-978.569	1967.576	6.569	0.002
p(forest)	3	-980.805	1967.783	6.776	0.002
p(humanabundance)	3	-980.843	1967.858	6.852	0.002
psi(forest+wetland+agrolivestock)p(days)	6	-977.629	1967.875	6.869	0.002
p(capturedays+forest)	4	-979.947	1968.185	7.179	0.001
p(capturedays+humanabundance)	4	-979.995	1968.281	7.275	0.001
psi(wetland)p(forest+humanabundance)	5	-978.991	1968.420	7.413	0.001
psi(wetland)p(capturedays+forest+humanabundance)	6	-978.186	1968.990	7.984	0.001
psi(wetland)p(forest)	4	-980.523	1969.337	8.330	0.001
psi(wetland)p(humanabundance)	4	-980.592	1969.474	8.467	0.001
psi(wetland)p(capturedays+forest)	5	-979.667	1969.772	8.766	0
psi(wetland)p(capturedays+ humanabundance)	5	-979.744	1969.926	8.920	0
p(capturedays)	3	-982.065	1970.303	9.296	0
psi(wetland)	3	-982.734	1971.640	10.634	0
psi(wetland)p(capturedays)	4	-981.799	1971.889	10.882	0

Supplementary Table 12 Peccary Full Averaged Model Coefficients

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	-0.261	0.546	0.478	0.633	
psi(forest)	0.876	0.813	1.077	0.281	
p(int)	-2.055	0.196	10.449	<0.000	***
p(forest)	-0.384	0.262	1.466	0.143	
p(human abundance)	0.765	0.718	1.065	0.287	
psi(agrolivestock)	-1.792	1.944	0.922	0.357	
p(capture days)	-0.002	0.004	0.545	0.586	

Supplementary Table 13 White-tailed deer Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. Df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	loglik	QAICc	Delta	Weigh
psi(forest+wetland+agrolivestock)p(capturedays+forest+humanabundance)	8	-1788.45	3593.992	0	0.483
psi(wetland+agrolivestock)+p(capturedays+forest+humanabundance)	7	-1789.83	3594.491	0.499	0.376
psi(forest+wetland)p(capturedays+forest+humanabundance)	7	-1791.70	3598.244	4.252	0.057

psi(agrolivestock)p(capturedays+forest+humanabundance)	6	-1793.34	3599.310	5.318	0.033
psi(forest+agrolivestock)p(capturedays+forest+humanabundance)	7	-1792.52	3599.873	5.881	0.025
psi(forest+wetland+agrolivestock)p(capturedays+forest)	7	-1793.58	3602.005	8.013	0.008
psi(wetland+agrolivestock)p(capturedays+forest)	6	-1795.36	3603.338	9.346	0.004
psi(forest+wetland+agrolivestock)p(forest+humanabundance)	7	-1794.65	3604.143	10.151	0.003
psi(wetland+agrolivestock)p(forest+humanabundance)	6	-1796.02	3604.665	10.673	0.002
psi(forest)p(capturedays+forest+humanabundance)	6	-1796.26	3605.154	11.162	0.001
psi(forest+wetland)p(capturedays+forest)	6	-1796.98	3606.593	12.600	0
psi(forest+agrolivestock)p(capturedays+forest)	6	-1797.82	3608.275	14.283	0
psi(agrolivestock)p(capturedays+forest)	5	-1799.00	3608.455	14.463	0
psi(forest+wetland)p(forest+humanabundance)	6	-1798.01	3608.64	14.656	0
psi(agrolivestock)p(forest+humanabundance)	5	-1799.53	3609.516	15.524	0
psi(forest+agrolivestock)p(forest+humanabundance)	6	-1798.71	3610.049	16.057	0
psi(wetland)p(capturedays+forest+humanabundance)	6	-1800.03	3612.684	18.692	0
psi(forest)p(capturedays+forest)	5	-1801.39	3613.233	19.241	0
psi(forest+wetland+agrolivestock)p(forest)	6	-1800.49	3613.614	19.622	0

psi(wetland+agrolivestock)p(forest)	5	-1802.28	3614.998	21.006	0
p(forest+humanabundance)	5	-1802.50	3615.443	21.451	0
p(capturedays+forest+humanabundance)	5	-1802.75	3615.943	21.950	0
psi(forest+wetland)p(forest)	5	-1803.97	3618.388	24.396	0
psi(forest+agrolivestock)p(forest)	5	-1804.74	3619.931	25.939	0
psi(agrolivestock)p(forest)	4	-1805.93	3620.169	26.177	0
psi(wetland)p(capturedays+forest)	5	-1806.27	3622.997	29.005	0
psi(wetland)p(humanabundance)	5	-1806.36	3623.161	29.169	0
psi(forest)p(forest)	4	-1808.35	3625.004	31.012	0
p(capturedays+forest)	4	-1808.76	3625.811	31.818	0
p(forest+humanabundance)	4	-1809.01	3626.326	32.333	0
p(forest+wetland)	4	-1813.38	3635.052	41.060	0
p(forest)	3	-1815.81	3637.793	43.801	0
psi(forest+wetland+agrolivestock)p(capturedays+humanabundance)	7	-1817.50	3649.834	55.842	0
p(capturedays+humanabundance)	6	-1818.92	3650.471	56.478	0
psi(forest+wetland)p(capturedays+humanabundance)	5	-1822.47	3655.385	61.393	0

psi(forest+agrolivestock)p(capturedays+humanabundance)	6	-1821.56	3655.748	61.756	0
psi(forest)p(capturedays+humanabundance)	5	-1825.47	3661.379	67.387	0
psi(forest+wetland+agrolivestock)p(humanabundance)	6	-1824.57	3661.761	67.768	0
psi(wetland+agrolivestock)p(humanabundance)	5	-1825.98	3662.411	68.419	0
psi(forest+wetland)p(humanabundance)	5	-1828.37	3667.184	73.192	0
psi(agrolivestock)p(humanabundance)	4	-1829.53	3667.358	73.365	0
psi(forest+agrolivestock)p(humanabundance)	5	-1828.63	3667.705	73.712	0
psi(wetland)p(capturedays+humanabundance)	5	-1830.15	3670.753	76.761	0
p(capturedays+humanabundance)	4	-1832.48	3673.260	79.268	0
psi(forest)p(humanabundance)	4	-1832.57	3673.434	79.442	0
psi(forest+wetland+agrolivestock)p(capturedays)	6	-1832.85	3678.328	84.336	0
psi(wetland+agrolivestock)p(capturedays)	5	-1834.79	3680.027	86.035	0
psi(wetland)p(humanabundance)	4	-1837.29	3682.871	88.879	0
psi(forest+wetland)p(capturedays)	5	-1836.56	3683.566	89.574	0
psi(forest+agrolivestock)p(capturedays)	5	-1837.16	3684.768	90.776	0
psi(agrolivestock)p(capturedays)	4	-1838.51	3685.325	91.333	0

p(humanabundance)	3	-1839.59	3685.365	91.373	0
psi(forest)p(capturedays)	4	-1840.87	3690.048	96.055	0
psi(forest+wetland+agrolivestock)	5	-1841.15	3692.750	98.758	0
psi(wetland+agrolivestock)	4	-1843.07	3694.446	100.454	0
psi(forest+wetland)	4	-1844.89	3698.080	104.088	0
psi(forest+agrolivestock)	4	-1845.47	3699.233	105.241	0
psi(agrolivestock)	3	-1846.80	3699.789	105.797	0
psi(wetland)p(capturedays)	4	-1846.74	3701.779	107.787	0
p(capturedays)	3	-1849.02	3704.231	110.238	0
psi(forest)	3	-1849.22	3704.622	110.630	0
psi(wetland)	3	-1855.10	3716.380	122.388	0
	2	-1857.39	3718.869	124.877	0

Supplementary Table 14 Deer Full Averaged Model Coefficients. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	1.168	0.620	1.883	0.059	.
psi(forest)	0.790	0.955	0.827	0.408	

psi(wetland)	12.654	7.391	1.712	0.086	.
psi(agrolivestock)	-5.905	2.077	2.843	0.004	**
p(int)	-2.190	0.122	17.832	< 0.000	***
p(capture days)	0.011	0.003	3.528	0.000	***
p(forest)	1.069	0.142	7.498	< 0.000	***
p(human abundance)	-1.470	0.456	3.221	0.001	**

Supplementary Table 15 Jaguar Complete Occupancy and Detection Probability Models. Averaged Models with delta lower than 2 are highlighted in yellow. Df= number of parameters, loglik= Logistic Likelihood, QAICc= Quasi Akaike Information Criterion value, delta= relative difference in QAICc values, w= model weight

Model	df	loglik	QAICc	Delta	Weight
psi(peccary+armadillo)p(capturedays+forest+humanabundance)	7	-430.790	876.410	0	0.477
psi(peccary)p(capturedays+forest+humanabundance)	6	-432.875	878.368	1.957	0.179
psi(armadillo+settlements)p(forest+humanabundance)	6	-433.302	879.223	2.812	0.116
psi(armadillo+peccary)p(humanabundance)	5	-435.013	880.464	4.053	0.062
psi(peccary)p(humanabundance)	4	-436.642	881.574	5.163	0.036
psi(settlements)p(forest)	5	-435.923	882.283	5.873	0.025
psi(armadillo+peccary)p(capturedays+humanabundance)	6	-434.929	882.476	6.065	0.022
psi(peccary+settlements)p(humanabundance)	5	-436.239	882.917	6.506	0.018
psi(peccary)p(capturedays+humanabundance)	5	-436.560	883.559	7.148	0.013
psi(peccary)p(capturedays+humanabundance)	6	-435.562	883.743	7.332	0.012
psi(peccary+settlements)p(forest)	5	-436.660	883.759	7.348	0.012

psi(settlements)p(capturedays+forest+humanabundance)	6	-435.620	883.858	7.447	0.011
psi(armadillo+peccary+settlements)p(humanabundance)	6	-437.189	886.996	10.585	0.002
p(armadillo+peccary+settlements)	5	-438.360	887.159	10.748	0.002
p(armadillo+settlements)p(capturedays+forest+humanabundance)	7	-436.518	887.866	11.455	0.001
psi(armadillo)p(forest+humanabundance)	5	-438.808	888.054	11.643	0.001
p(forest+humanabundance)	4	-440.211	888.712	12.301	0.001
psi(armadillo+peccary+settlements)p(forest+humanabundance)	7	-437.277	889.384	12.973	0
psi(armadillo)p(capturedays+forest+humanabundance)	6	-438.791	890.201	13.790	0
p(capturedays+forest+humanabundance)	5	-440.203	890.845	14.434	0
psi(armadillo+peccary)p(capturedays+forest)	6	-439.218	891.053	14.642	0
psi(armadillo+peccary+settlements)p(capturedays+forest+humanabundance)	8	-437.225	891.526	15.115	0
psi(settlements)p(forest)	4	-441.928	892.146	15.736	0
psi(armadillo+peccary+settlements)p(forest)	6	-440.059	892.735	16.324	0
psi(peccary+settlements)p(capturedays+forest+humanabundance)	7	-439.315	893.460	17.049	0
psi(road+settlements)p(capturedays+forest+humanabundance)	7	-439.445	893.721	17.310	0
psi(peccary)p(capturedays+forest)	5	-441.902	894.243	17.832	0
psi(armadillo+peccary+roads)p(capturedays+forest+humanabundance)	8	-438.787	894.649	18.238	0
psi(peccary+settlements)	4	-443.858	896.007	19.596	0
psi(peccary+roads+settlements)p(capturedays+forest+humanabundance)	8	-439.975	897.025	20.614	0
psi(settlements)p(capturedays+forest)	5	-443.691	897.821	21.410	0
psi(armadillo+roads+settlements)p(capturedays+forest+humanabundance)	8	-440.416	897.907	21.496	0
psi(armadiilo+settlements)p(forest)	5	-443.841	898.121	21.710	0
psi(armadillo+peccary)	4	-445.310	898.911	22.500	0
psi(armadillo+settlements)p(capturedays+forest)	6	-443.333	899.285	22.874	0

psi(peccary+settlements)p(capturedays+forest)	6	-443.675	899.968	23.557	0
psi(armadillo+peccary)p(capturedays)	5	-445.104	900.647	24.236	0
psi(peccary)	3	-447.409	900.991	24.580	0
psi(peccary+roads)p(capturedays+forest+humanabundance)	7	-443.801	902.433	26.022	0
psi(peccary)p(capturedays)	4	-447.208	902.707	26.296	0
psi(armadillo)p(forest)	4	-447.409	903.108	26.697	0
psi(peccary+roads+settlements)p(forest+humanabundance)	7	-444.887	904.604	28.193	0
p(forest)	3	-449.243	904.659	28.248	0
psi(armadillo)p(capturedays+forest)	5	-447.332	905.103	28.692	0
p(capturedays+forest)	4	-449.180	906.651	30.240	0
psi(armadillo+settlements)p(humanabundance)	5	-448.464	907.366	30.956	0
psi(armadillo+peccary+roads+settlements)p(humanabundance)	7	-447.286	909.402	32.991	0
psi(settlements)p(humanabundance)	4	-450.844	909.978	33.567	0
psi(armadillo+peccary+settlements)p(capturedays+forest)	7	-448.018	910.867	34.456	0
p(humanabundance)	3	-452.498	911.168	34.757	0
psi(armadillo)p(humanabundance)	4	-452.228	912.747	36.336	0
p(capturedays+humanabundance)	4	-452.403	913.097	36.686	0
psi(armadillo+peccary+roads+settlements)p(capturedays+humanabundance)	8	-448.275	913.624	37.213	0
psi(armadillo)p(capturedays+humanabundance)	5	-452.131	914.701	38.290	0
psi(armadillo+peccary+roads)p(forest+humanabundance)	7	-449.973	914.776	38.365	0
psi(armadillo+peccary+roads+settlements)p(capturedays+forest+humanabundance)	9	-447.942	915.237	38.826	0
psi(settlements)	3	-455.581	917.334	40.923	0
psi(armadillo+peccary+roads+settlements)p(forest)	7	-451.555	917.940	41.529	0
psi(peccary+roads)p(capturedays+humanabundance)	6	-452.848	918.315	41.904	0
psi(armadillo+roads+settlements)p(capturedays+humanabunadnce)	7	-452.051	918.931	42.520	0

psi(armadillo+roads+settlements)p(days+humanabundance)	8	-451.160	919.396	42.985	0
psi(roads+settlements)p(capturedays+forest)	6	-453.658	919.934	43.523	0
psi(roads)p(forest+humanabundance)	5	-456.118	922.674	46.263	0
psi(armadillo+peccary+roads)p(forest)	6	-455.307	923.232	46.821	0
psi(armadillo+peccary+roads)p(humanabundance)	6	-455.465	923.549	47.138	0
psi(peccary+roads)p(forest)	5	-456.787	924.012	47.601	0
psi(peccary+roads)p(forest+humanabundance)	6	-455.953	924.524	48.113	0
psi(armadillo+roads)p(forest+humanabundance)	6	-456.052	924.722	48.311	0
psi(peccary+roads+settlements)p(capturedays+forest)	7	-455.502	925.834	49.423	0
psi(armadillo+roads)p(capturedays+forest+humanabundance)	7	-456.377	927.585	51.174	0
psi(roads)p(capturedays+forest+humanabundance)	6	-457.811	928.240	51.830	0
psi(roads+settlements)p(forest+humanabundance)	6	-457.987	928.591	52.181	0
psi(armadillo+roads+settlements)p(forest+humanabundance)	7	-458.115	931.059	54.648	0
psi(peccary)p(forest+humanabundance)	5	-461.029	932.496	56.085	0
psi(armadillo+roads)p(forest)	5	-461.300	933.039	56.628	0
psi(armadillo+peccary)p(forest+humanabundance)	6	-461.029	934.676	58.265	0
psi(armadillo+settlements)	4	-463.840	935.970	59.559	0
psi(armadillo+peccary+roads)p(capturedays+forest)	7	-462.054	938.938	62.527	0
psi(peccary+roads+settlements)p(forest)	6	-463.947	940.512	64.101	0
	2	-468.888	941.863	65.452	0
psi(roads)p(capturedays+forest)	5	-465.927	942.291	65.881	0
psi(roads)p(forest)	4	-467.161	942.612	66.201	0
psi(roads+settlements)p(forest)	5	-466.175	942.789	66.378	0
psi(armadillo+roads)p(capturedays+forest)	6	-465.150	942.919	66.508	0
psi(armadillo)	3	-468.382	942.936	66.525	0
p(capturedays)	3	-468.669	943.511	67.100	0
psi(peccary+roads)p(capturedays+forest)	6	-465.555	943.728	67.317	0
psi(peccary+roads)p(humanabundance)	5	-467.043	944.524	68.113	0
psi(armadillo)p(capturedays)	4	-468.161	944.611	68.200	0

psi(armadillo+roads+settlements)p(forest)	6	-467.382	947.381	70.970	0
psi(peccary+roads)p(capturedays)	5	-468.602	947.641	71.231	0
psi(armadillo+peccary+roads)p(capturedays+humanabundance)	7	-467.040	948.910	72.499	0
psi(peccary)p(forest)	4	-470.568	949.426	73.015	0
psi(armadillo+peccary+roads)p(capturedays)	6	-469.272	951.163	74.752	0
psi(armadillo+peccary)p(forest)	5	-470.568	951.574	75.163	0
psi(roads)p(humanabundance)	4	-473.735	955.761	79.350	0
psi(armadillo+peccary+roads)	5	-473.054	956.546	80.135	0
psi(armadillo+roads)p(humanabundance)	5	-474.114	958.667	82.256	0
psi(roads)	3	-479.090	964.354	87.943	0
p(armadillo+roads)	4	-485.654	979.599	103.188	0
psi(peccary+roads)	4	-497.698	1003.68	127.275	0
psi(armadillo+peccary+roads+settlements)	6	-503.958	1020.535	144.124	0
psi(settlements)p(capturedays)	4	-515.360	1039.010	162.599	0
psi(settlements)p(capturedays+humanabundance)	5	-514.996	1040.431	164.020	0
psi(armadillo+settlements)p(capturedays)	5	-515.792	1042.022	165.611	0
psi(armadillo+settlements)p(capturedays+humanabundance)	6	-515.423	1043.464	167.053	0
psi(peccary+settlements)p(capturedays)	5	-516.549	1043.536	167.125	0
psi(peccary)p(capturedays+humanabundance)	6	-516.171	1044.960	168.549	0
psi(armadillo+peccary+settlements)p(capturedays)	6	-516.964	1046.547	170.136	0
psi(armadillo+peccary+settlements)p(capturedays+humanabundance)	7	-516.583	1047.997	171.586	0

psi(roads+settlements)p(capturedays)	5	-520.260	1050.958	174.547	0
psi(roads+settlements)p(capturedays+humanabundance)	6	-519.755	1052.128	175.717	0
psi(armadillo+roads+settlements)p(capturedays)	6	-521.049	1054.716	178.306	0
psi(armadillo+roads+settlements)p(capturedays+humanabundance)	7	-520.538	1055.905	179.494	0
psi(peccary+roads+settlements)p(capturedays)	6	-522.866	1058.350	181.939	0
psi(peccary+roads+settlements)p(captruredays+humanabundance)	7	-522.336	1059.502	183.091	0
psi(armadillo+peccary+roads+settlements)p(capturedays)	7	-523.538	1061.907	185.496	0
psi(armadillo+peccary+roads+settlements)p(capturedays+humanabundance)	8	-523.005	1063.085	186.674	0
psi(roads)p(capturedays)	4	-531.828	1071.946	195.535	0
psi(roads)p(capturedays+humanabundance)	5	-531.303	1073.045	196.634	0
psi(armadillo+roads)p(capturedays)	5	-533.589	1077.617	201.206	0
psi(capturedays+humanabundance)p(armadillo+roads)	6	-533.063	1078.745	202.334	0
psi(roads+settlements)	4	-587.252	1182.795	306.384	0
psi(roads+settlements)p(humanabundance)	5	-587.060	1184.558	308.147	0
psi(armadillo+roads+settlements)	5	-589.503	1189.444	313.033	0
psi(armadillo+roads+settlements)p(humanabundance)	6	-589.311	1191.241	314.830	0

psi(peccary+roads+settlements)	5	-595.163	1200.765	324.354	0
psi(peccary+roads+settlements)p(humanabundance)	6	-594.968	1202.554	326.143	0

Supplementary Table 16 Jaguar Full Averaged Model Coefficients. Significant codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

	Estimate	Std. error	Z value	Pr (> |z|)	
psi(int)	-4.871	3.044	1.600	0.109	
psi(armadillo)	-12.048	11.201	1.076	0.282	
psi(peccary)	15.563	4.586	3.393	0.000	***
p(int)	-3.610	0.514	7.020	0.000	***
p(capture days)	0.001	0.007	0.237	0.812	
p(forest)	1.497	0.575	2.602	0.009	**
p(human abundance)	-16.681	5.573	2.993	0.002	**