The Application of Occupancy Modeling to Evaluate the Determinants of Distribution of Jaguars *Panthera onca*, Pumas *Puma concolor*, and Valued Prey Species in a Protected Area

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

In the past four decades, both biodiversity and individual populations of numerous species in the tropics have consistently declined. Tropical forests constitute only 6% to 7% of the Earth's surface, yet they contain more than half of all species richness, making them a significant reservoir for global biodiversity. Maintaining healthy populations of both predators and prey in the tropics is therefore crucial for supporting dynamic ecosystems and for preserving biodiversity. As apex predators, jaguars *Panthera onca* and pumas *Puma concolor* play a critical role in helping to support dynamic tropical ecosystems. Correspondingly, prey species of value to these felids are equally important. Ecological models have become valuable tools for facilitating an understanding of how species distribution is influenced by natural landscape variables and anthropogenic factors. The objectives of this study were to utilize hierarchical occupancy modeling to assess if jaguars, pumas, and valued prey species (brocket deer *Mazama sp*., white-tailed deer *Odocoileus virginianus*, collared peccary *Pecari tajacu*, white-lipped peccary *Tayassu pecari*, lowland paca *Cuniculus paca*, Central American agouti *Dasyprocta punctate*, and white-nosed coati *Nasua narica*) are non-randomly distributed across the Calakmul Biosphere Reserve in Campeche, Mexico, and how natural and anthropogenic features are influential in shaping this distribution. Because felid distribution is thought to largely depend on prey availability, latent occupancy estimates for focal prey were also incorporated into occupancy models for jaguars and pumas. Spoor sampling was conducted using line transects in four survey areas throughout the core and buffer zone of the reserve from June 25th to August 8th, 2013. Detection histories for focal species were utilized for occupancy modeling that was completed in the 'unmarked' package in R. It was determined that distribution was random for brocket and white-tailed deer species, was largely random for collared peccary, and non-random for white-lipped peccary, large prey as a group, and medium prey species collectively. Model averaged occupancy of collared peccary was 30% higher than it was for white-lipped peccary and occupancy was weakly associated with increasing tree species richness. White-lipped peccary occupancy was lower in areas with decreased tree species richness and diminished total basal area, likely corresponding to disturbed habitat. Occupancy of large prey as a collective group had a weak negative association with proximity to water (aguadas specifically). A weak association of site (survey area) was found for occupancy of medium prey collectively, as models exhibited higher occupancy estimates for the survey areas located in the core zone of the CBR, which is an area intended to be free of disturbance. Distribution of jaguars and pumas was found to be primarily influenced by occupancy of brocket deer and medium prey species. There was also a weak negative association with proximity to an aguada. Results from this study reinforce the need for evaluating tropical species occupancy, as understanding the factors that are influential in determining distribution is quite complex. Due to the troubling status of jaguars and pumas, understanding how landscape variables, as well as prey occupancy, influences their distribution is of utmost importance to ensure that critical habitat is protected and/or restored and that human-wildlife conflicts are minimized. This study is the first to explicitly integrate both landscape variables and latent occupancy of prey species as covariates in occupancy models for jaguars and pumas and it adjoins only a handful of studies that model occupancy of the focal species in Mexico.

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Dedication

This thesis is dedicated to my incredible, wonderful, enchanting, and inquisitive, daughter, Isla. Never believe that you can’t because you are capable of anything. To quote William Shakespeare, “And though she be but little, she is fierce.” This could not be truer for my little girl and I could not be more proud. I love you with all my heart.

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Chapter 1 Introduction and Literature Review

1.1 Global Biodiversity and Wildlife Population Declines

In 2002, 193 parties to the Convention on Biological Diversity (CBD) committed to achieve a significant reduction in the current rate of biodiversity loss by 2010. Using a framework of indicators created by the CBD, Butchart et al. (2010) determined that global biodiversity has declined consistently over the past four decades, with notable decreases in the diversity and extent of vertebrates and also in the coverage of forests. The International Union for Conservation of Nature (IUCN) Red List categorizes all species into one of eight categories based on their risk for extinction (IUCN, 2013). According to this list, almost one-fifth of extant vertebrates are classified as Threatened; however, when the uncertainty for species with insufficient data for determining risk of extinction is included in this assessment, between 16% and 33% of vertebrates and almost 40% of all mammals are actually classified as Threatened (Hoffmann et al., 2010). Large carnivores have been particularly affected, with 17% of species listed as Threatened, including 20% of all felids (Zarco-González, Monroy-Vilchis, & Alaníz, 2013; Zarco-González, Monroy-Vilchis, Rodríguez-Soto, & Urios, 2012). Tropical forests constitute only 6% to 7% of the Earth's surface, yet they contain more than half of all species richness, making them a significant reservoir for global biodiversity (Dirzo & Raven, 2003; Licona, Mccleery, Collier, Brightsmith, & Lopez, 2011). Concurrently, the majority of threatened species occur in tropical countries and extensive tracts of tropical habitat have already been degraded (Chazdon et al., 2009; Dirzo & Raven, 2003). Tropical biodiversity is not restricted to reserves and parks; over 90% of the tropics lies beyond these borders and is therefore vulnerable to anthropogenic pressures. The interface between protected areas and unprotected ones is not definitive, as despite their shielded status, parks and reserves are often directly and indirectly still negatively affected by anthropogenic activities, threatening ecosystems and wildlife populations within and beyond their borders (Chazdon et al., 2009).

Anthropogenic activities are the primary cause of declines in wildlife populations and biodiversity loss in the tropics (Chazdon et al., 2009). Particularly impactful activities include: deforestation (Dirzo & Raven, 2003; Wright & Muller-Landau, 2006); habitat fragmentation from development, agriculture, roads and trails (Zeilhofer, Cezar, Tôrres, de Almeida Jácomo, & Silveira, 2014); hunting and poaching (Hoffmann et al., 2010; Reyna-Hurtado & Tanner, 2007; Rodríguez-Soto, Monroy-Vilchis, & Zarco-González, 2013), and human-wildlife conflict (Erb, McShea, & Guralnick, 2012; Schuette, Wagner, Wagner, & Creel, 2013). Of all of these actions, habitat loss/disturbance is the most significant risk to mammals with 89% of threatened mammals being affected, followed by hunting and poaching, especially in the tropics, where it impacts 34% of all threatened mammal species (Dirzo & Raven, 2003). Large carnivores, particularly felids in the tropics, are highly susceptible to anthropogenic pressures due to their requirements for ample prey and large home ranges (Arroyo-Arce, Guilder, & Salom-Pérez, 2014; Hoffmann et al., 2010), which are often fragmented by human-modified landscapes (Hoffmann et al., 2010; Srivathsa, Karanth, Jathanna, Kumar, & Karanth, 2014; Zanin, Palomares, & Brito, 2014), low density and reproductive rates (Ripple et al., 2014), and their increased risk for human-wildlife conflict (Inskip & Zimmermann, 2009; Schuette et al., 2013; Zeller, 2007).

1.2 Predator and Prey Dynamics

Maintaining healthy populations of both predators and prey is crucial for supporting dynamic ecosystems and preserving biodiversity (Ripple et al., 2014). This importance is demonstrated by felid-prey interactions in tropical ecosystems. Changes in the status of wild cat populations can have trophic effects on pollination and pollinators, seed dispersal, seed predators, folivores, mesopredators, woody plant recruitment, bird abundance, ungulate disease prevalence, and soil carbon/nitrogen ratios (Jorge, Galetti, Ribeiro, & Ferraz, 2013; Ripple et al., 2014; Salo, Banks, Dickman, & Korpimäki, 2010). From a top-down ecological perspective, when felid populations decline, a tropic cascade can ensue where populations of prey (e.g. ungulates) become hyperabundant, until restricted by the carrying capacity of their environment (Salo et al., 2010). In the meantime; however, intense grazing reduces the quantity and diversity of palatable plant species, increases plant defenses, reduces plant recruitment, and lowers carrying capacity for consumers overall (Jorge et al., 2013; Ripple et al., 2014; Zanin et al., 2014). Declines in populations of top predator felids can result in changes in the ecosystem as a result of mesopredator release where intraguild competition is reduced allowing for expansion of mesopredator distribution and abundance, and increased predation pressure overall (Ripple et al., 2014; Salo et al., 2010; Schuette et al., 2013). When apex felids are productive it is often indicative that the entire ecosystem is dynamic and diverse (Ripple et al., 2014; Sergio, Newton, Marchesi, & Pedrini, 2006). Large cats require sizeable home ranges with habitat that is suitable for hunting and houses prey that is ample or easily captured within their home range (Arroyo-Arce et al., 2014; Hoffmann et al., 2010); therefore, sites capable of providing this will automatically be sufficient for smaller, less demanding species (Sergio et al., 2006). Another reason that this is often found to be true is that the if carnivores are able to persist during times of scarcity through prey switching behaviour, it is indicative that there is a diversity of prey available as the diets of large carnivores are primarily comprised of a few preferred species and a multitude of minor prey species (Sergio et al., 2006). The status of felids can therefore be used as an indicator for the health of an ecosystem and as an early warning sign of ecological decline (Niemi & McDonald, 2004).

Prey species play an equally crucial role in felid-prey relationships and in the functioning of tropical ecosystems by influencing forest structure and plant diversity through seed dispersal, seed predation and herbivory (Ahumada, Hurtado, & Lizcano, 2013; Hass & Valenzuela, 2002; Licona et al., 2011). For example, reductions in ungulate populations can gradually lead to reduced dispersal of large seeded plants, increased conspecific competition, and decreases in the overall diversity of plant species (Licona et al., 2011). Declines in prey abundance may alter reproduction of felids by delaying the age of first reproduction, reducing litter sizes, and increasing offspring and adult mortality (Foster, Harmsen, & Doncaster, 2010; Fuller & Sievert, 2001). The home range of wild cats is generally impacted by the availability of prey and habitat quality, with the home range increasing as these two factors become less accessible (Petracca, Ramirez-Bravo, & Hernandez-Santin, 2013). As female cats increase their home range in response to diminished prey availability, male felids will in turn expand their range to follow the females. This results in a higher proportion of transient and dispersing individuals, which negatively influences viability (Conde et al., 2010; Fuller & Sievert, 2001; Stander, Haden, Kaqece, & Ghau, 1997). In areas where larger prey species are depleted, livestock may supplement the diet of large felids (de Azevedo & Conforti, 2008); therefore, the predation of livestock is often inversely associated with availability of preferred wild prey (Foster et al., 2010). This often leads to negative attitudes, misperceptions of threat, and persecution of apex felids (Zimmermann, Walpole, & Leader Williams, 2005). In Mexico for example, where hunting of jaguar *Panthera onca* is illegal, there is growing concern that increased predation of livestock will result in intensified human-jaguar conflicts, eventually leading to the poaching of these iconic cats (K. Slater, email communication, October 4, 2013).

1.3 Focal Species

1.3.1 Predators

As a result of the aforementioned anthropogenic stresses, large carnivores have become some of the most threatened species globally (Ripple et al., 2014). Their ability to exert significant influence on ecosystem structure and their high risk for extinction makes conservation of large felids exceedingly vital (Ripple et al., 2014). As the Neotropics' largest and second largest top predators, jaguars and pumas *Puma concolor* are critical for supporting tropical ecosystem functioning and dynamics (Jorge et al., 2013). Jaguars are currently classified as Near Threatened by the IUCN and as Endangered in Mexico by the Secretaria de Medio Ambiente Y Recursos Naturales (Caso et al., 2015; Rodríguez-Soto et al., 2013). Pumas are classified by the IUCN as a Species of Least Concern; however, they are listed as Near Threatened in Brazil and as Vulnerable outside the Amazon Basin (Table 1-1). Little is actually known for sure about their status and it is thought that on-going habitat destruction, fragmentation, and prey decline may threaten their stable state (Negroes et al., 2010; Nielsen et al., 2015).

The troubled status of jaguars and pumas has evolved from a variety of pressures, including: habitat fragmentation, destruction, and loss; poaching; and the direct hunting of their prey (Dirzo & Raven, 2003; Erb et al., 2012; Hoffmann et al., 2010; Reyna-Hurtado & Tanner, 2007; Rodríguez-Soto et al., 2013; Schuette et al., 2013; Wright & Muller-Landau, 2006; Zeilhofer et al., 2014). Habitat disturbance can impact jaguars and pumas in numerous ways, including: loss of suitable habitat; barriers to dispersion; changes in intraguild competition; alteration of population genetic structure, and loss of genetic diversity (Rabinowitz & Zeller, 2010; Zanin et al., 2014). Historically, jaguars used to be found from the southern United States to southern Argentina (Ceballos, Chavez, Rivera, & Manterola, 2002). As a result of habitat loss, it is estimated that only 56% of original jaguar habitat range remains (Rodríguez-Soto et al., 2011; Zanin, Palomares, & Brito, 2015), from the southern border of the United States to northern Argentina (Zeller, 2007). The species will utilize a variety of habitats (Zeller, 2007), and while they have been found to show a preference for areas proximal to water (de Azevedo & Murray, 2007; Sollmann et al., 2012; Zeilhofer et al., 2014), that are more densely forested (Colchero et al., 2011), and at increased distance from human settlement (Arroyo-Arce et al., 2014), generally distribution is thought to largely depend on prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Stander et al., 1997).

The diets of jaguars are highly variable with between eight and 24 prey species documented in their diet at any one site (Foster et al., 2010). While large prey provide the most caloric energy, medium prey that has the least risk associated with predation is often equally beneficial to supplement their diet (Novack, Main, Sunquist, & Labisky, 2005; Polisar et al., 2003). Jaguars are adaptable and opportunistic hunters that consume prey relative to its abundance, and can take down prey as large as they are (Foster et al., 2010; Weckel, Giuliano, & Silver, 2006). Their preferred prey species include armadillo *Dasypus novemcinctus*, lowland paca *Cuniculus paca*, brocket deer [the red *Mazama americana* and Yucatán brown *M. pandora* (referred to as brocket deer *Mazama sp*. hereafter)], white-tailed deer *Odocoileus virginianus*, white-lipped peccary *Tayassu pecari*, collared peccary *Pecari tajacu* and white-nosed coati *Nasua narica* (Foster et al., 2010; Novack et al., 2005; Slater, 2014; Weckel et al., 2006). Jaguars are also able to switch to alternative prey or 'buffer species' during times when preferred prey species are scarce (Novack et al., 2005). In the Cookscomb Basin Wildlife Sanctuary in Belize jaguars took smaller prey and less variety of species in buffer zones where hunters likely had depleted the area of larger game species such as deer and white-lipped peccary (Foster et al., 2010). In areas where larger prey (white-lipped peccary and deer) is depleted from human hunting, collared peccary and medium prey species may contribute greatly to sustaining jaguar populations (Foster et al., 2010).

Pumas are widespread throughout the Americas over a larger range of habitats and altitudes and they are sympatric with jaguars throughout most of Central and South America (Negroes et al., 2010; Nielsen, Thompson, Kelly, & Lopez-Gonzalez, 2015; Novack et al., 2005). Pumas are largely habitat generalists; however, the species can display a tendency to occupy drier areas, possibly because they are deterred by the higher jaguar presence around water (Angelieri, Adams-Hosking, Ferraz, de Souza, & McAlpine, 2016; Romero-Muñoz, Maffei, Cuéllar, & Noss, 2010; Sollmann et al., 2012). The species is less elusive than jaguars and can adapt to various environments (Angelieri et al., 2016), even hunting near human presence (Zarco-González et al., 2013), although they generally avoid highly modified habitats (Angelieri et al., 2016).

In areas where jaguars and pumas coexist, pumas are smaller in size, which is thought to be an evolved response to reduce competition, as pumas are often pressured into selecting smaller prey (Gómez-Ortiz & Monroy-Vilchis, 2013; Novack et al., 2005). Preferred prey species for pumas include: white-tailed deer; brocket deer; Central American agouti *Dasyprocta punctate*, and paca (Foster, 2010; Novack et al., 2005). When prey are abundant, sympatric jaguars and pumas will generally prey upon both medium and large species at similar rates; however, usually, pumas demonstrate more generalist behaviour patterns overall and jaguars tend to have a preference for larger prey (Gómez-Ortiz & Monroy-Vilchis, 2013). Body size of both cats tends to increase further from the equator; however, which corresponds to a preference for generally larger prey overall by both cat species (Gómez-Ortiz & Monroy-Vilchis, 2013; Novack et al., 2005). While jaguars and pumas are both known to prey upon peccary species, unlike jaguars, pumas more often prefer juveniles to adults. Peccaries live in groups and possess canine teeth that are almost as large as and as sharp as those of the jaguar (Polisar et al., 2003). Jaguars possess a more powerful bite than pumas;

therefore predation on juvenile peccaries with weaker defenses would be less of a risk of injury for pumas (Foster et al., 2010; Polisar et al., 2003).

As habitat ranges decline and humans colonize previously uninhabited wildlife areas, conflicts between large felids and people have emerged (Zarco-González et al., 2013). Competition occurs between large cats and humans, not only for space, but also for their prey, as both colonization and the human hunting of wildlife reduces the availability of prey (Foster et al., 2010). Several studies of jaguars and pumas in Mexico have shown that diet choices are largely distinctive between the two cats (Gómez-Ortiz & Monroy-Vilchis, 2013; Rosas-Rosas & Bender, 2012), except when large prey is scarce due to hunting activities leading to increased predation on medium sized species by both cats (Novack et al., 2005). Novack et al. (2005) suggest that there is lower abundance of jaguars in areas where human harvesting of their preferred prey occurs versus non-hunted areas. Unfortunately, in areas where humans deplete larger prey species through hunting, livestock may supplement the diets of jaguars and pumas that range in these unprotected areas (de Azevedo & Conforti, 2008).

As the third (jaguar) and fourth (puma) largest felid species, the risk for conflict is substantial for these cats, as the severity of conflict increases with the body mass of felids (Inskip & Zimmermann, 2009). Because pumas show less elusive behaviour than jaguars and often hunt closer to human settlements, they have an even greater risk for conflict (Inskip & Zimmermann, 2009). In areas where jaguars and pumas are sympatric, the majority of studies that investigate livestock depredation only examine the incidence of jaguar attacks; this has resulted in scarce data on the incidence of puma and livestock depredation as well as on puma-human conflict. It is thought that the impact of depredation by pumas, as well as the incidence of conflict is therefore underestimated (Zarco-González et al., 2013). This is troublesome for jaguars as many livestock attacks by pumas are wrongfully attributed to the larger felid, thus increasing the potential for poaching of jaguars (Rosas-Rosas & Bender, 2012).

The predation of livestock is often inversely associated with availability of preferred wild prey (Foster, 2010; Inskip & Zimmermann, 2009). In and around Iguacu National Park in Brazil, it was found that jaguars have made a dietary shift towards livestock in response to a decline in white-lipped peccaries, which are hunted by local people (de Azevedo & Conforti, 2008). Not surprisingly, depredation of livestock is also higher where there are poor livestock husbandry and management practices, such as: ineffectual guarding or herding; lack of or inadequate containment of livestock at night, and the placement of grazing pastures within or close to felid habitat (Inskip & Zimmermann, 2009). Many cattle ranches are located in previously prime jaguar habitat; this inevitably results in livestock becoming prey for jaguars, especially when proper livestock management practices are not implemented (Polisar et al., 2003; Zimmermann et al., 2005). Livestock depredation can significantly impact the livelihoods of local farmers and thus generate negative attitudes and persecution of jaguars and pumas, leading to the slaughter of these cats. In Central and South America conflict between jaguars and cattle ranchers is common and does result in the illegal poaching of jaguars (Zimmermann et al., 2005). It is thought that poaching is the factor most limiting to the range of the jaguar (Zeller, 2007) and that it is their greatest threat to survival in Mexico (Zarco-González et al., 2013). Depredation of cattle by pumas tends to only occur in the presence of poor livestock management practices. Unfounded perceptions of puma depredation have resulted in the deaths of more than 40 pumas between 2002 and 2012 in Sierra Nanchititla Natural Park alone (a 663.93km2 area in central Mexico) (Gómez-Ortiz & Monroy-Vilchis, 2013). While large felids undeniably pose a risk to livestock and are responsible for losses due to depredation, ironically these cats actually provide a benefit to local subsistence farmers by limiting wild herbivore populations, allowing productive pastoralism and minimizing disease transfer to livestock (Ripple et al., 2014).

1.3.2 Prey

As previously mentioned, preferred prey species of jaguars and pumas include: brocket deer, white-tailed deer, collared peccary, white-lipped peccary, lowland paca, Central American agouti, and coati. (See Table 1-1 for a summary of the focal species and their respective conservation statuses.) Like jaguars and pumas, prey species are equally crucial for supporting the functioning of healthy ecosystems and biodiversity (Jorge et al., 2013; Ripple et al., 2014). The Yucatán brown brocket deer species is listed at Threatened by the IUCN, as there is no information available on its status outside of the Calakmul region in Mexico and also because of continuous population declines as a result of habitat loss. However, it is known that it is fairly abundant in Calakmul (IUCN, 2013). The red brocket deer is listed as Data Deficient due to taxonomic uncertainty. It is believed to be widespread from Mexico to South America and to be overhunted in some of it's range but occurring at natural densities in most areas (IUCN, 2013). Studies have shown that brocket deer are able to tolerate some degree of hunting pressure and habitat fragmentation, as they have been found to occur at higher population levels in these areas compared to other ungulates (Reyna-Hurtado & Tanner, 2007). They prefer high canopy forests with increased fruit density and areas that are proximal to water (Ahumada et al., 2013; Petracca et al., 2013; Zeller, Nijhawan, Salom-Pérez, Potosme, & Hines, 2011).

White-tailed deer are largely habitat generalists (Petracca et al., 2013; Zeller et al., 2011), but are also known to be highly adaptable to human-modified landscapes. They will occupy areas where fragmentation and clear-cutting, especially in the presence of croplands, has occurred. Higher abundances are also found in human-hunted areas, compared to other species, like white-lipped peccary that are not as adaptable to disturbance (Petracca et al., 2013; Reyna-Hurtado & Tanner, 2007). It is likely that increased occupancy in hunted areas is actually related to the presence of forest fragmentation and farming, where the species is able to capitalize on crops as a food source and as ideal habitat (Novack et al., 2005; Santos-Fita, Naranjo, & Rangel-Salazar, 2012). Both brocket deer and white-tailed deer are prized game species for human hunters in the tropics (Reyna-Hurtado & Tanner, 2007; Santos-Fita et al., 2012). Nonetheless, they are both often ubiquitous, providing a food source for both human and wildlife predators alike (Novack et al., 2005; Reyna-Hurtado & Tanner, 2007; Santos-Fita et al., 2012).

Collared peccary are generally abundant in their range (Santos-Fita et al., 2012), live in herds comprised usually of fewer than 10 individuals (Peres, 1996), and are prized game for hunters, as well as jaguars and pumas (Polisar et al., 2003; Santos-Fita et al., 2012). The species is highly adaptable to disturbance, as abundance generally does not differ greatly between human hunted and non-hunted sites, or in forests that are fragmented/disturbed compared to ones that are primary vegetation, even in the presence of substantial hunting pressures (Petracca et al., 2014; Reyna-Hurtado & Tanner, 2007). Collared peccary capitalize on crops as a food source when available, similar to white-tailed deer, and compete with other animals including agoutis for seeds and pacas and coatis for fruit (Ahumada et al., 2013; Hass & Valenzuela, 2002; Petracca et al., 2014). It is likely that their adaptability for living in either disturbed forest, as well as primary forest has allowed them to tolerate anthropogenic disturbance to a greater degree than white-lipped peccary (Peres, 1996; Reyna-Hurtado & Tanner, 2007).

White-lipped peccary have been found at lower abundance, (up to three times lower), in areas where hunting occurs and have even been known to completely disappear from heavily hunted areas in the Amazon Basin, in Mexico, and in Guatemala (Peres, 1996; Reyna-Hurtado, Naranjo, Chapman, & Tanner, 2010; Reyna-Hurtado & Tanner, 2007). The species is likely impacted to a greater degree by fragmentation and agriculture, as they require large intact home ranges (>100km2) (Reyna-Hurtado, Rojas-Flores, & Tanner, 2009). Furthermore, they are greatly affected by human presence, as they have an increased susceptibility to disease transmission from domestic animals (Reyna-Hurtado & Tanner, 2007). These factors, in combination with hunting pressures likely lead to the emigration of white-lipped peccary out of areas with higher human occupation and into sites with less disturbance (Petracca et al., 2014; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007). Populations of white-lipped peccary have been declining in Mexico and Central America since the 1950's, with the only remaining ones found in four of the seven states they formerly occupied. They are a unique social ungulate, living in groups of 20 to 300 individuals, which intensifies their vulnerability to hunting, as in a group setting multiple individuals can be killed at once (Peres, 1996; Reyna-Hurtado et al., 2010). In areas where populations of white-lipped peccary are declining, it is common to observe groups of less than 10, which is likely a response to increased hunting pressure (Reyna-Hurtado et al., 2010). In Mexico, Reyna-Hurtado et al. (2010) observed that the mean size of groups of white-lipped peccary in hunted areas was 16 and in non-hunted areas 25, which suggests that populations are being affected by hunting. White-lipped peccary are significant to the functioning of Neotropical ecosystems through their highly frugivorous habits. Seed predation, dispersal, trampling, and rooting all play a critical part in plant survival, recruitment, and distribution. The species also plays a unique role in the creation and maintenance of wallows, which serve as critical habitat for many species, and they are a significant food source for jaguars and pumas and (Altrichter et al., 2012). The IUCN has recently changed the status of white-lipped peccary from "Near Threatened" to "Vulnerable" due to the rising evidence of these anthropogenic threats, primarily deforestation, habitat disturbance, and hunting, to the survival of this species (Altrichter et al., 2012; Petracca et al., 2014).

While large prey provide the most caloric energy for apex predators, like jaguars and pumas, medium prey that has the least risk associated with predation is often equally beneficial to supplement the diets of jaguars and as a primary food source for pumas (Novack et al., 2005; Polisar et al., 2003). Despite their smaller stature, medium prey species also are crucial for the functioning of healthy ecosystems as well (Ripple et al., 2014). Pacas are small rodent herbivores native to Latin America

(Govoni & Fielding, 2001); their preferred food source is soft fruits, which is also a food choice of peccaries and coatis (Ahumada et al., 2013; Hass & Valenzuela, 2002). They are considered to be habitat generalists (Zeller et al., 2011). While they are listed as a species of Least Concern by the IUCN, Ahumada et al., (2013) showed that populations in northern Costa Rica have significantly declined, likely due to poor management of hunting practices and/or increased competition for food with agoutis and peccaries. They are frequently harvested by subsistence hunters for food and income, and as a result, the species is considered a risk for extinction by many countries autonomously. This has resulted in the development of laws aimed at controlling the hunting of pacas in Panama, El Savador, Nicaragua, Costa Rica, Surinam, Mexico, and Venezuela (Govoni & Fielding, 2001).

Agoutis are also rodents that share much of the same geographic range as the slightly larger paca species (Govoni & Fielding, 2001). The species competes for palm seeds with collared peccary, which are more efficient at obtaining this food source. Agoutis have been considered to be adaptable habitat generalists; however, some studies have found that they prefer tall lowland forested habitats with high palm diversity and increased abundance of palm nuts, which is their preferred food source (Ahumada et al., 2013; Govoni & Fielding, 2001; Zeller et al., 2011). They are also listed as a species of Least Concern by the IUCN; however, a gradual reduction in populations has been shown in some areas throughout their range due to declining habitat and hunting (Govoni & Fielding, 2001).

Coatis belong to the family of Procyonidae. The species has a large range from the southern United States to South America (IUCN, 2013). They are omnivores and their diet consists mainly of fruit and terrestrial invertebrates (Hass & Valenzuela, 2002; Novack et al., 2005). Female coatis live in groups of 5-40 individuals, along with juveniles of both sexes, while males leave the group at sexual maturity (Hass & Valenzuela, 2002). Coatis adapt well to human influence with increased densities in areas closer to settlements and where hunting occurs (Novack et al., 2005). Despite being listed by the IUCN as a species of Least Concern, there is little knowledge of the status of the species in Central America, and known population declines in Mexico and the United States (IUCN, 2013).

Table 1-1: Species names and conservation status of each focal species as designated by the International Union for Conservation of Nature (IUCN), Mexico's Secretaria de Medio Ambiente Y Recursos Naturales, and Brazil's Ministério do Meio Ambiente.

Binomial Name	Common Name	Status*	Reporting Agency
Panthera onca	jaguar	NT	IUCN
		EN in Mexico	Secretaria de Medio Ambiente Y Recursos Naturales
Puma concolor	puma	LC	IUCN
		NT in Brazil	Ministério do Meio Ambiente
Mazama pandora	Yucatán brown brocket deer	VU	IUCN
Mazama americana	red brocket deer	DD	IUCN
Odocoileus virginianus	white-tailed deer	LC	IUCN
Pecari tajacu	collared peccary	LC	IUCN
Tayassu pecari	white-lipped peccary	VU	IUCN
Cuniculus paca	lowland paca	LC	IUCN
Dasyprocta punctate	Central American agouti	LC	IUCN
Nasua narica	white-nosed coati	LC	IUCN

*NT=Near Threatened; EN=Endangered; LC=Least Concern; VU=Vulnerable; DD=Data Deficient

1.4 Monitoring the Status of Felids and Their Prey

The importance of maintaining healthy populations of jaguars, pumas, and their prey for the support of dynamic tropical ecosystems has been widely recognized (Conde et al., 2010; Fuller & Sievert, 2001; Jorge et al., 2013; Ripple et al., 2014). Knowledge of the status of wildlife through indicators such as abundance and occupancy is equally critical for informing conservation decision-making, management, and policy-making (Stanley & Royle, 2005). As determined by the Wildlife Conservation Society's Jaguar Conservation Program, of the 90 Jaguar Conservation Units areas (areas which are critical to jaguar conservation) totaling 1.9million km2, only 28% is in protected areas and of that, just 1% is adequately protected (Zeller, 2007). The interface between protected areas and unprotected ones is not definitive, as despite their protected status, parks and reserves are often directly and indirectly still negatively affected by anthropogenic pressures, threatening ecosystems within and beyond the borders (Chazdon et al., 2009). Understanding occupancy and distribution is therefore critical for evaluating how wildlife uses protected and unprotected habitat and for understanding how anthropogenic pressures can radiate beyond the borders of protected areas, affecting jaguars and other species that reside within and around them, and ultimately the ecosystem as a whole.

What is not well established, is how best to assess and draw accurate inferences about the occupancy, distribution, and status of focal species. There are a multitude of methods utilized, some of which include: multiple regression and general linear modeling (Conde et al., 2010; Harmsen, Foster, Silver, Ostro, & Doncaster, 2009); Bayesian movement models (Colchero et al., 2011), landscape metrics (Zanin, Palomares, et al., 2015; Zeilhofer et al., 2014); ensemble models (Rodríguez-Soto et al., 2013), and maximum entropy (MAXENT) (Zarco-González et al., 2012). Hierarchical occupancy modeling that incorporates imperfect detection is an additional tool that is increasingly being used for evaluating occupancy of jaguars, pumas, and their prey species, in order to identify crucial habitat for protection and/or restoration (Arroyo-Arce et al., 2014; Srivathsa et al., 2014).

Occupancy modeling is widely used globally as a surrogate to abundance, as it is often not possible to census the entire population of a species (Hines et al., 2010; MacKenzie & Nichols, 2004; Mackenzie et al., 2006; Stanley & Royle, 2005; Welsh, Lindenmayer, & Donnelly, 2013). Occupancy is simply the proportion of a study area that is occupied by the species of interest whereas; abundance is the total number of individuals in a population (Mackenzie et al., 2006). Occupancy estimation sampling usually requires less effort than abundance surveys and is sometimes the only viable option for rare species (e.g. jaguars), where it would be essentially impossible to estimate abundance (Mackenzie et al., 2006; Zeller et al., 2011). It is a useful approach for evaluating species because of the flexibility of methods that can be used to obtain the detection and non-detection data needed for creating detection histories (Zeller et al., 2011). Methods include: spoor sampling (Karanth et al., 2011; Licona et al., 2011; Reyna-Hurtado & Tanner, 2007; Stanley & Royle, 2005); distance sampling (Dénes, Silveira, & Beissinger, 2015); camera-trapping (Ahumada et al., 2013; Arroyo-Arce et al., 2014; Licona et al., 2011; Negroes et al., 2010; Silver et al., 2004; Sollmann et al., 2012); interview data (Arroyo-Arce et al., 2014; Petracca et al., 2014, 2013; Zeller et al., 2011), and radio-telemetry (Conde et al., 2010; Núñez-Pérez, 2011). Furthermore, it allows for integration of covariates into analysis, providing valuable information about the factors that influence habitat use (Zeller et al., 2011).

Occupancy modeling has been widely used for the focal prey species in Central and South America, including studies in: Peru (Licona et al., 2011); Brazil (Jorge et al., 2013); Costa Rica (Ahumada et al., 2013), and Nicaragua (Zeller et al., 2011). Despite its widespread usage, there is very little research on the occupancy of prey species in tropical Mexico (Petracca et al., 2013; Reyna-Hurtado & Tanner, 2007).

Occupancy modeling is an effective method for acquiring valuable information on the influence of landscape variables on carnivore distribution (Harmsen et al., 2009; Reed, 2011; Stander, 1998). Density and occupancy studies that evaluate the influence of these factors on the distribution of jaguars and pumas have been done throughout Central and South America, including studies in: Belize (Petracca et al., 2013; Silver et al., 2004); Nicaragua (Petracca et al., 2014; Zeller et al., 2011); Costa Rica (Ahumada et al., 2013); Brazil (Negroes et al., 2010; Sollmann et al., 2012; Zanin, Palomares, et al., 2015), and Mexico (Núñez-Pérez, 2011; Rosas-Rosas & Bender, 2012). Despite the fact that felid distribution is thought to largely depend on prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Stander et al., 1997), there is very little research on how prey occupancy is influential in shaping the distribution of large carnivores, especially jaguars and pumas. When prey variables are incorporated into modeling it is often done using indices such as overall prey biomass or density (Karanth et al., 2011; Midlane, O'Riain, Balme, Robinson, & Hunter, 2014; Negroes et al., 2010; Robinson, Bustos, & Roemer, 2014), general presence or absence of prey (Alexander, Shi, Tallents, & Riordan, 2015; Harihar & Pandav, 2012; Petracca et al., 2013), photo-trap rates (Sunarto, Kelly, Parakkasi, & Hutajulu, 2015), or prey richness (Negroes et al., 2010; Zanin, Sollmann, et al., 2015). Hierarchical occupancy modeling is therefore a valuable tool for assessing how all of these factors, (anthropogenic pressures, landscape features, and prey availability), influence the distribution of jaguars and pumas (Arroyo-Arce et al., 2014; Fiske et al., 2014; Srivathsa et al., 2014).

1.5 Modeling Approach

Knowledge of abundance of a species of interest is essential for many aspects of ecological understanding and management implications. For elusive species, such as jaguar and puma, it is extremely difficult, time-consuming, and costly to conduct direct counts to develop indices for abundance (Stanley & Royle, 2005). Consequently, indirect indices, where the index is based on signs indicating the animals presence, such as spoor, tracks, or hair, is often used for developing estimates of abundance and/or occupancy (Stanley & Royle, 2005). In theory, the two state variables, occupancy and abundance, should be positively correlated (MacKenzie & Nichols, 2004). Detection probability (ρ), which is the likelihood that an individual will be detected, is an important consideration when developing occupancy estimates as it cannot be explicitly known that all members of a species in the sample area will be sampled (Fiske & Chandler, 2011; Mackenzie et al., 2006). Because individuals may be present but not actually detected (imperfect detection), a naïve count will underestimate the true proportion of sites that are occupied (MacKenzie et al., 2002; Mackenzie et al., 2006). This can be overcome however, by the use of occupancy models. These models utilize a detection history to calculate a detection probability, which is then applied to adjust the naïve occupancy and to give an estimate of occupancy probability (φ). The occupancy probability can be interpreted as the probability of a site being occupied or as the proportion of the site that is likely occupied (Midlane et al., 2014).

Hierarchical occupancy modeling offers a unified framework for analysis that uses repeated presence-absence (detection/non-detection) data to model and adjust for the detection process (Kery, Chandler, & Royle, 2012; Welsh et al., 2013). It recognizes that two processes influence observations: the first is a state process, which determines occupancy at each site, while the second is a detection (observation) process, that yields observations that are provisional on the state process (Fiske & Chandler, 2011; Kery et al., 2012). A Bernoulli distribution describes both of these state processes by combining the canonical model for species occurrence and imperfect detection. Because the second is conditional on the first, the false positive errors are essentially negated (Kery et al., 2012).

The occupancy model for the state process is:

$$z_i \sim Bernoulli\ (\varphi)$$

The occupancy model for the detection process is:

$$y_{ij} \sim Bernoulli\ (z_i \rho_{ij})$$

The latent variable z_i represents the true state of occurrence at site i, φ is the expected value of z_i, y_{ij} is the observed value of occurrence at site i during survey j, and ρ_{ij} is the detection probability of the all individuals of a species at site i during survey j. The site-occupancy model can be interpreted as a hierarchical extension to a Bernoulli generalized linear model (GLM), logistic regression, or two linked GLMs (Kery et al., 2012). There are five main assumptions that have to be considered for occupancy models:

1. Closure: occupancy does not change during the survey period. This often requires that survey seasons occur over a short enough time period relative to the dynamics of the distribution of the target species (Kery et al., 2012);
2. No false positive errors: this can be avoided by discarding observations where the species id is uncertain. False positive errors can result in significant bias in the occupancy estimator (Kery et al., 2012);
3. Independence of detection histories at each location and detection of species: non-independence can result in overstated precision of the occupancy estimates, as well as biases in the parameter estimates. Independence can be encouraged by ensuring adequate spatial separation of sites and also by defining appropriate survey-specific covariates (e.g. if a species was detected at site i before survey j (Mackenzie et al., 2006);

4. Homogeneity of detection at the sites: this assumption states that detection probability is constant across all sites and surveys or that it is a function of the covariates for the site. Detection probability can in fact vary due to a variety of factors, including: environment (e.g. weather), seasonal behaviour patterns, habitat features, observer differences, and also the size of the local populations at each site (Mackenzie et al., 2006). Heterogeneity in detection probability can often result in negatively biased occupancy estimates, which results in underestimates of occupancy. Careful study design as well as incorporation of site-specific covariates can minimize its effects (Kery et al., 2012; Mackenzie et al., 2006), and
5. Parametric Assumptions: this assumption states that the two Bernoulli distributions for occupancy and detection are a reasonable abstraction of reality (Kery et al., 2012).

1.6 Modeling Covariates

Felid-prey interactions and consequently, the dynamics of the ecosystem and biodiversity, are all influenced by anthropogenic pressures (Butchart et al., 2010; Ripple et al., 2014; Terborgh et al., 2001; Vester, Lawrence, Eastman, Turner II, & Calme, 2007), prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Stander et al., 1997), and landscape variables (Woodroffe, 2001). Occupancy modeling allows for integration of site-level or observation-level covariates into analysis through a logit link function (Kery et al., 2012; Zeller et al., 2011). Site-level covariates include variables that can influence both detection and observation. They are characteristic to the sampling site, such as habitat type, canopy cover, elevation, and distance to a water source. These variables may differ between sites, but do not change during a sampling season. Observation-level covariates are those that influence detection only and can vary among every survey of any unit, such as temperature, time, and the observer doing the sampling (Mackenzie, 2012). There are also two forms of covariates that can be included in the models in 'unmarked'; continuous or categorical. Continuous variables can take on any value between $+/- \infty$, and can include data on rainfall, temperature, latitude etc. (Mackenzie, 2012). Categorical variables can be represented by binary indicator (or dummy) variables, either 0 or 1, or an ordinal categorical variable can be used when the relative difference between each of the numeric values is similar to the difference in the ordinal value. For example if a covariate is habitat quality, with three categories being low (1), medium (2), and high quality (3), the difference between low and medium is similar to that between medium and high, as the ordinal values differ by one (Mackenzie, 2012). The logit link function converts linear combinations of covariate values into a value between 0 and 1 on a scale of probability (Mackenzie et al., 2006). The equation for the logit link function for variables related to occupancy is as follows:

$$\text{logit}(\varphi_i) = x_i\beta$$

The variable x_i represents the values for the site-level or observation-level covariate of interest at the ith sampling unit, while β is the estimated regression coefficient representing the value of the covariates corresponding effects (Fiske & Chandler, 2011; Mackenzie et al., 2006). The equation for the logit link function for variables related to detection is as follows:

$$\text{logit}(\rho_{ij}) = v_{ij}\alpha$$

The variable v_{ij} represents the values for the observation-level covariates of interest at site i during survey j, while α is the estimated regression coefficient representing the value of the covariates corresponding effects (Fiske & Chandler, 2011). For this study, only site-level covariates were included as the primary focus was on occupancy of target prey species as a function of habitat features, rather than on detection. Detection was held constant for all models, under the assumption that the covariates commonly modeled for detection would be found to have negligible influence. For example, the affect of observer on detection was not a concern as multiple observers were rotated for each survey between the different transects. The use of trained researchers and/or experienced volunteers within different observer groups has been shown to minimize variation of observations between surveys (Darwall & Dulvy, 1996; Edgar & Stuart-Smith, 2009). The pairing/grouping of observers together has also been found to minimize the effects of identification errors and improve accuracy of data through consultation and discussion of observations (Bernard, Götz, Kerwath, & Wilke, 2013). Also, several (>4) replicate surveys were completed for each transect, which reduced the problem of imperfect detection by minimizing the likelihood of not detecting a species despite the site being occupied (Guillera-Arroita, Lahoz-Monfort, MacKenzie, Wintle, & McCarthy, 2014). Finally, the detection process is accounted for in the inherent nature of a single-state site occupancy model through the incorporation of the canonical model for imperfect detection (Kery et al., 2012).

When evaluating the influence variables on the occupancy of a species, it is necessary to test for correlation between the variables (collinearity), as the presence of collinearity can result in confusing results that show that none of the covariates are significant, yet suddenly become so if one covariate is removed from the equation. This ultimately can lead to type II errors (i.e. not rejecting the null hypothesis despite it being untrue) (Zuur, Ieno, & Elphick, 2010). For this study, I used variance inflation factor (*VIF*) to check for collinearity between variables. The *VIF* for a variable, Xj is the square root of the inverse of the R^2_j value of the regression of the variable Xj against all of the other explanatory variables (Zuur et al., 2010).

$$VIF_j = \sqrt{\frac{1}{(1 - R_j^2)}}$$

High *VIF* values indicate that the presence of collinearity, which suggests that most of the variation in the variable can be explained by the other covariates. To resolve this issue, a preselected *VIF* threshold (as high as 10, or as low as 3 for a more conservative analysis) is chosen and variables with *VIF*s >threshold are sequentially removed one at a time with the highest ones removed first and then the analysis repeated until only variables with a *VIF*<threshold remain (Zuur et al., 2010).

1.7 Model Fitting and Selection

1.7.1 Model Fitting

Before beginning an occupancy analysis careful consideration of what is being investigated and why should be carried out in order to create a reasonable and deliberate candidate set of 4-20 models. Furthermore, the variables chosen for modeling, and therefore the candidate model set, should be selected based on scientific reasoning with a priori knowledge of the focal species taken into account. The alternative approach is known as data dredging, which refers to creating a vast candidate model set of greater than 70 models that likely have more interaction parameters than the data can support. Data dredging can lead to over-fitted models and spurious results (Burnham & Anderson, 2002). Once the candidate model set is selected, the most general model (global model) that encompasses all possible covariates and is therefore the most complex with the greatest number of parameters should be assessed for goodness-of-fit and to check for overdispersion (Burnham & Anderson, 2002; Mackenzie et al., 2006). Because the global model is the most highly parameterized, if this model fits the data adequately then it would be inferred that any models that are less parameterized and thus more parsimonious would also fit the data (Burnham & Anderson, 2002; Cooch & White, 2002). Goodness-of-fit can be evaluated using methods developed by Mackenzie & Bailey (2004), which utilizes the Pearson chi-square (X^2) test statistic, a parametric bootstrap approach. The overdispersion parameter (ĉ) is then estimated using the X^2_{obs} from the observed data and the average X^2_B from the bootstrapped data according to the following equation (Mackenzie & Bailey, 2004):

$$\hat{c} = \frac{X^2_{obs}}{\overline{X^2_B}}$$

If ĉ is approximately equal to one then it can be inferred that the model adequately fits the data; however, overdispersion is indicated if ĉ>1, underdisperison if ĉ <1, and lack-of fit demonstrated if ĉ>4 (Durso, Willson, & Winne, 2011; Mackenzie & Bailey, 2004; Mazerolle, 2015). Overdispersion simply means that there is likely more variation in the observed data than expected by the model (Mackenzie & Bailey, 2004). If ĉ for the global model is >1 then the value of ĉ is then applied to all subsequent models derived from the global model. If ĉ <1 then subsequent models are run without adding the overdispersion parameter and ĉ is fixed at one (Mazerolle, 2015).

1.7.2 Model Selection

Akaike's Information Criterion (AIC) has become increasingly prevalent and beneficial for analyzing ecological data (Durso et al., 2011; Hines et al., 2010; Karanth et al., 2011; Mackenzie & Bailey, 2004). By minimizing the AIC values, the most parsimonious models for the data can be identified. Rather than selecting models based on the absolute magnitude of AIC value, the differences in AIC (ΔAIC) among the various models can be evaluated (Mackenzie et al., 2006). Models with a delta AICc (ΔAICc) <2 have substantial empirical support, those with values between 4 and 7 have substantially less support, and those with a difference >10 essentially have no support (Burnham &

Anderson, 2002; Reed, 2011). AICc values also form the basis for AICc weights (AICcw), which sum to one for all models of the set. These can further aid in assessing which models and covariates have more support and relative goodness-of-fit (Petracca et al., 2013). A top ranking set of models that best explain the data can then be identified and utilized for multimodel inference via model averaging (Burnham & Anderson, 2002). Model averaging is a method that calculates a coefficient estimate ($\widehat{\hat{\beta}}_{\imath}$) from the candidate models in which the parameter of interest appears as follows (Symonds & Moussalli, 2011):

$$\widehat{\hat{\beta}}_{\imath} = \frac{\sum_{i=1}^{R} w_i \widehat{\hat{\beta}}_{\imath}}{\sum_{i=1}^{R} w_i}$$

Model averaging is used to produce parameter and error estimates that are derived from multiple models by weighting each averaged parameter estimate. This minimizes the influence that variables with low AIC weights have so that they exert little to no influence on the predicted parameters (Symonds & Moussalli, 2011). Model averaging is particularly useful when a variable occurs in all of the models in a set or when wanting to make predictions and no one model is identified as convincingly best (Burnham & Anderson, 2002). Furthermore, model averaging can result in an estimator with reduced bias and improved precision compared to an estimator originating from the top model alone (Burnham & Anderson, 2002).

1.8 Research Objectives

Felid-prey interactions and consequently, the dynamics of the ecosystem and biodiversity, are influenced by anthropogenic pressures (Butchart et al., 2010; Reyna-Hurtado et al., 2010; Ripple et al., 2014; Terborgh et al., 2001; Vester et al., 2007), landscape variables (Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2013; Woodroffe, 2001), and prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Novack et al., 2005; Stander et al., 1997). Due to the crucial functions that jaguars and pumas have for supporting tropical ecosystem functioning and dynamics (Jorge et al., 2013), as well as their troubled statuses (Caso et al., 2015; Negroes et al., 2010; Nielsen et al., 2015; Rodríguez-Soto et al., 2013), research on these iconic cats and the prey species they depend on is incredibly vital. As such, my objectives for this study were to assess if jaguars, pumas, and valued prey species (brocket deer, white-tailed deer, collared peccary, white-lipped peccary, lowland paca, Central American agouti, and white-nosed coati) are non-randomly distributed across a tropical region and how natural and anthropogenic features are influential in shaping this distribution. My final objective was to incorporate latent occupancy estimates for focal prey into occupancy models for jaguars and pumas to evaluate the relative influence of prey occupancy on the distribution of these felids.

This research was done in collaboration with Operation Wallacea. I collected data along with a large team of ecologists, academics, field staff, and volunteers. Data collection methods were as per Operation Wallacea field protocols.

Chapter 2 Study Site

2.1 Geography

As previously mentioned, the majority of threatened species occur in tropical forests; Mexico has the fourth highest amount of threatened species, behind Indonesia, Brazil, and China (Dirzo & Raven, 2003). Concurrently, Mexico has between 8% and 12% of all species, including six felid species (Zarco-González et al., 2013). Protected areas, such as biosphere reserves are considered to be the most effective way to protect biodiversity when they have the support and the cooperation of local people (Licona et al., 2011). This research was conducted in the Calakmul Biosphere Reserve (CBR), which covers around one-third of the southern Yucatán region in the state of Campeche, Mexico. The CBR contains the largest protected area of tropical forest (723,185 hectares) in Mexico and adjoins two state reserves: Balam-kim and Balam-ku. The total area of the combined reserves is 1,200,000 hectares; however, the surrounding forest gives rise to a total of over four million hectares of forest (García-Frapolli, Ramos-Fernández, Galicia, & Serrano, 2009; Slater, 2014). The CBR borders the Maya Biosphere Reserve in Guatemala and the Society Hall Nature Reserve in Belize and is also a component of the MesoAmerican Biological Corridor (MBC) (García-Frapolli et al., 2009; Vester et al., 2007). The reserve has the largest wild feline population in North America, including the highest reported density of jaguar in Central America, with an estimated population size of 800 individuals, making it a top priority site for the conservation of jaguars (Colchero et al., 2011; García-Frapolli et al., 2009; Vester et al., 2007).

The climate of the Campeche state is warm and sub-humid with a mean temperature of 24.6°C. The topography is fairly flat with shallow rocky soils, and there are no rivers or streams within the reserve, only aguadas (ponds) (Figure 2-1). The aguadas form during the rainy season (May to October) and some can remain into the dry season, which runs from December until May. Annual precipitation (1,076mm/year average) increases from the north to the south of the reserve (Reyna-Hurtado et al., 2010; Slater, 2014). The forest is primarily tropical semi-deciduous with a mean canopy height of 20-30m (Slater, 2014) and the chicozapote *Manilkara zapota* tree, also known as chicle, is the most abundant tree species (Ericson, 2006; Smardon & Faust, 2006). A patchwork of mature and disturbed forest, secondary growth of less than 25 years old, and savannah type flood plains comprises the flora of the reserve (Slater, 2014). Most precipitation in the CBR percolates through the limestone with some surface water entering the aguadas (Reyna-Hurtado et al., 2010). Procurement of water for cattle, irrigation, and even household use is an ongoing concern that residents face due to a lack of abundant surface water and accessible ground water (Smardon & Faust, 2006).

Figure 2-1: Aguada at Hormiguero camp in the Calakmul Biosphere Reserve, Mexico.

2.2 Historical Background and Current Demography

The CBR was created in 1989 and accepted into the United Nations network of biosphere reserves in 1993 (Ericson, 2006; García-Frapolli et al., 2009). It was created in response to international concerns that rampant deforestation in the southern Yucatán region would threaten carbon stocks and, biota, and habitat (Vester et al., 2007). Before the 1970's the area had remained relatively undisturbed since ancient Mayan civilizations abandoned it 1,100 years ago (Reyna-Hurtado et al., 2010). The history of the CBR has not been one of seamless transitions or of cooperation among stakeholders. When the reserve was established, the Mexican federal government actively promoted the expansion of agriculture and cattle ranching within the buffer zone, which resulted in an influx of immigrants to the area, whose lifestyles contrasted with the local indigenous populations that already resided here (García-Frapolli et al., 2009). When the reserve was established local residents were completely excluded from the CBR creation process; to the point where many were not even aware it existed until a year into the process (Haenn, 1999). A lack of communication and knowledge sharing led to misconception by conservation agencies that local inhabitants were apathetic to conservation, and local people felt that their right to subsist was restricted (García-Frapolli et al., 2009). The CBR is comprised of a core zone, which under the guidelines of the Man and Biosphere (MAB) program, is intended to be free of human settlement and disturbance, and a buffer zone, where settlement and activities that do not impact ecosystem services are supported (Ericson, 2006). Unfortunately due to poor design, lack of consultation with local people, and a disregard for existing land tenure when the reserve was established, the reserve was created with ill-advised socio-ecologically boundaries. The reserve was designed contrary to the considerations of the MAB program, as it is divided by two highways, it includes some private lands where cattle ranching occurs, and it disregarded existing land tenure by crossing ejidos (land that is communally owned and managed by peasants or indigenous people) and private lands (García-Frapolli et al., 2009).

The 248,260ha core is split between the north and the south by Federal Highway 86 with approximately 16,000ha of private lands in the north where ranching occurs. Inhabitants residing in the south core zone (~350,000ha) were relocated after the CBR was created (Colchero et al., 2011; Reyna-Hurtado et al., 2010). Around 35,000 people live within traditional Mayan villages inside the reserve, in the buffer zone, and in the surrounding lands, with immigration into the area still occurring today (Reyna-Hurtado et al., 2010). There are 114 ejidos in the CBR region, covering 22.6% of the CBR total area (García-Frapolli et al., 2009; Vester et al., 2007). Primary sources of income include slash and burn agriculture and logging for timber harvesting (Reyna-Hurtado & Tanner, 2007). Most of its residents are largely peasant and practice swidden agriculture or cattle ranching (García-Frapolli et al., 2009). Crops such as corn, beans, and squash are often harvested for subsistence with chili peppers and black pepper grown for commercial harvest. Honey, timber, charcoal, mahogany seeds, and palm leaves are also extracted/harvested commercially (Santos-Fita et al., 2012). Chicle was historically harvested for chewing gum, and today is still harvested primarily for latex (Ericson, 2006; Smardon & Faust, 2006).

2.3 Ecological Concerns

As a result of forest clearing for timber extraction and agriculture, including cattle grazing, only a small percentage of the original forest in the CBR remains (Ericson, 2006). As of the year 2000, it was hypothesized that land cover changes, (primarily deforestation), are responsible for the reduction of habitat for 32 of the 54 mammal species in the southern Yucatán and for the reported decline in jaguar populations in the CBR. This has resulted in concerns about loss of habitat, expanded barriers for biota movement, diminished biodiversity, and an increase in exposure of wildlife to humans (Vester et al., 2007).

In rural areas throughout the tropics various prey species possess significant cultural value for subsistence and sport hunting (Licona et al., 2011), commercial hunting, medicinal substances, clothing, tools, and for ritual objects (Santos-Fita et al., 2012). In Calakmul, most hunters do not rely on hunting as an economic practice or as their sole protein sources. Meat is purchased and/or livestock and poultry are raised, with hunted animals complementing their diet (Santos-Fita et al., 2012). Paca, white-tailed deer, and collared peccary are the most harvested species, after two bird species (the great curassow *Crax rubra* and the ocellated turkey *Meleagris ocellata*). Coatis, agouti, and brocket deer are also hunted but not to the same degree. Hunting in this region is most concentrated within 10km from the villages; however, there are frequently hunted sites as far as 20km from the villages (Santos-Fita et al., 2012). Hunting outside the reserve is highly unregulated, as are the sale of wild meat and the licensing of firearms. It is hypothesized that hunting is having an affect on the ranging patterns of forest ungulates in the CBR (Santos-Fita et al., 2012; Vester et al., 2007). Hunting may specifically impact larger species that occur at low densities, for example white-lipped peccary (Reyna-Hurtado, Naranjo, Chapman, & Tanner, 2010) as it is not known how many individuals are being harvested and if it is at a magnitude that is sustainable (Hoffmann et al., 2010;

Licona et al., 2011; Santos-Fita et al., 2012). It is known; however, that there have been significant reductions in the populations of hunted species documented over the past decade (Vester et al., 2007). While subsistence hunting generally is less impactful than commercial, both can equally exert pressure on large and medium prey species in particular (Santos-Fita et al., 2012). Excessive hunting pressure, especially when combined with other synergistic anthropogenic pressures can result in depletion of entire populations of species, which can have detrimental ecological impacts (Reyna-Hurtado & Tanner, 2007; Santos-Fita et al., 2012). Consequently, when humans and felids compete for the same prey, depletions of prey populations can impact the viability of cat populations and in-turn, ecosystem functioning (Novack et al., 2005).

Hunting in the Calakmul region has a seasonal influence with increased hunting rates in agricultural areas during the rainy season, especially during harvest of corn and other crops, due to the vulnerability of species such as collared peccary and white-tailed deer, which capitalize on these crops as a food source. During the dry season, forested areas are more often hunted due to better access to remote sites and the existence of fruit on the trees, correlating with an increased presence of frugivores. Brocket deer, pacas, coatis, and peccary are fruit eaters which may be more vulnerable during the dry season due to increased visibility (Ahumada et al., 2013; Hass & Valenzuela, 2002) and because they can be heard walking along the dry leaves (Santos-Fita et al., 2012).

As previously mentioned a significant disturbance that has also affected the ecological integrity of the CBR was the construction of a main road (Federal Highway 86) (Figure 2-2) that bisects the northern and southern parts of the reserve. Roads have the potential to negatively impact wildlife through acting as a barrier to movement, increasing human access to forests for hunting, logging and development, reduced connectivity, intensified human-wildlife conflict, and increased mortality through vehicular collisions (Colchero et al., 2011). The creation of a major road also opens the area to poaching and further disturbance (Khorozyan, Malkhasyan, & Abramov, 2008). Proximity to roads has been found to influence how jaguars (Conde et al., 2010) and pumas (Angelieri et al., 2016; Maehr, 2012) use habitat and it is thought that this road is now having noticeable effects on the ranging patterns of jaguar (Colchero et al., 2011).

Figure 2-2: Federal Highway 86 that bisects the northern and southern regions of Calakmul Biosphere Reserve, Mexico.

The current extent of knowledge on the status of jaguars, pumas, and their prey species in Campeche is quite limited. Recent research has revealed that genetic diversity of jaguars in the Yucatán Peninsula is some of the lowest reported for the species throughout their range, likely as a result of isolation and because the area is connected northward to areas that have the lowest densities reported as well (Roques et al., 2015). Loss of preferred habitat has also likely led to reported low populations of jaguar in the CBR (Vester et al., 2007). Some studies that have assessed the status of jaguars and pumas in the focal region include: general linear modeling for jaguars for a study area that encompassed part of the CBR (Conde et al., 2010); geographic ensemble risk models for jaguar and puma for all of Mexico (Zarco-González et al., 2013), and Bayesian movement models for behaviour of jaguars in the Mayan Forest, which included part of Campeche (Colchero et al., 2011). Petracca et al. (2013) conducted occupancy modeling for jaguars and the focal prey species in Sierra Madre Oriental, Mexico and relative abundance of ungulates was researched within the CBR (Reyna-Hurtado & Tanner, 2007). This research adjoins the handful of studies that model occupancy of jaguars, pumas, and the focal prey for this study in Mexico and it is also the first of its kind to incorporate latent occupancy of prey species as a covariate in occupancy models for these cats.

Chapter 3 Occupancy Modeling to Assess the Influence of Natural and Anthropogenic Landscape Variables on the Distribution of Focal Prey Species

3.1 Introduction

Global biodiversity has declined consistently over the past four decades, with notable decreases in the diversity of vertebrates and also in the extent of forests and many vertebrate species (Butchart et al., 2010). Tropical forests constitute only 6% to 7% of the Earth's surface, yet they contain more than half of all species richness, making them a significant reservoir for global biodiversity (Dirzo & Raven, 2003; Licona et al., 2011). Concurrently, tropical forests also have a high concentration of threatened species (Chazdon et al., 2009; Dirzo & Raven, 2003). Anthropogenic pressures are the primary cause of tropical biodiversity loss and particularly impactful activities include: deforestation (Wright & Muller-Landau, 2006); habitat fragmentation from development, agriculture, roads and trails (Zeilhofer et al., 2014); hunting and poaching (Hoffmann et al., 2010; Reyna-Hurtado & Tanner, 2007; Rodríguez-Soto et al., 2013), and human-wildlife conflict (Erb et al., 2012; Schuette et al., 2013). Tropical biodiversity is not restricted to reserves and parks; over 90% of the tropics lies beyond these borders and is therefore vulnerable to all of the aforementioned activities. At the same time, the interface between protected areas and unprotected ones is not definitive, as despite their protected status, parks and reserves are often directly and indirectly still negatively affected by anthropogenic pressures, threatening ecosystems within and beyond the borders (Chazdon et al., 2009).

Maintaining healthy populations of both predators and prey is crucial for supporting dynamic ecosystems and preserving biodiversity (Ripple et al., 2014). This importance is demonstrated by ungulate-felid interactions in tropical ecosystems. From a top-down ecological perspective, in the absence of sufficient numbers of felid predators, populations of ungulates will become hyperabundant, until limited by the carrying capacity of their environment. In the meantime; however, intense grazing reduces the quantity of palatable plant species and diversity, increases plant defenses, reduces plant recruitment, and lowers carrying capacity for consumers overall (Jorge et al., 2013; Ripple et al., 2014; Salo et al., 2010; Zanin et al., 2014).

Correspondingly, felids rely on ungulate populations as a food source and declines in prey availability can also have trophic cascade effects (Ripple et al., 2014). Ungulate populations, as well as other omnivores and herbivores, play a crucial role in the functioning of ecosystems by influencing forest structure and plant diversity through seed dispersal, seed predation and herbivory (Ahumada et al., 2013; Hass & Valenzuela, 2002; Licona et al., 2011). Declines in prey abundance may alter reproduction of felids by delaying the age of first reproduction, reducing litter sizes, and increasing offspring and adult mortality (Foster et al., 2010; Fuller & Sievert, 2001). Prey occupancy also can lead to an expansion of felid home ranges, as female cats will increase their home range in response to diminished prey availability and male felids will in turn expand their range to follow the females.

This results in a higher proportion of transient and dispersing individuals, which negatively influences viability (Conde et al., 2010; Fuller & Sievert, 2001; Stander et al., 1997).

Felid-prey interactions and consequently, the dynamics of the ecosystem and biodiversity, are all influenced by anthropogenic pressures (Butchart et al., 2010; Ripple et al., 2014; Terborgh et al., 2001; Vester et al., 2007). For example, in rural areas throughout the tropics various prey species, especially large game, are valued for subsistence and sport hunting due to their high nutritional content (Santos-Fita et al., 2012). Hunting in tropical areas is often poorly regulated and as such, it may directly impact larger species that occur at low densities as it is not known how many individuals are being harvested and if it is at a magnitude that is sustainable (Hoffmann et al., 2010; Licona et al., 2011; Santos-Fita et al., 2012); for example white-lipped peccary *Tayassu pecari* (Reyna-Hurtado et al., 2010) and in the case of poaching, jaguars *Panthera onca* (Silver et al., 2004). Other pressures can impact biodiversity in both positive and negative ways. The conversion of forest to agricultural land may drive some species to seek alternative habitat, whereas it may encourage others to occupy the area (Erb et al., 2012). Habitat fragmentation from development, agriculture, roads and trails, as well as increased interaction with humans and conflict can also impact wildlife by influencing how they occupy areas (Erb et al., 2012; Schuette et al., 2013).

In order to understand how anthropogenic pressures modify tropical ecosystems and impact wildlife; we need tools, such as ecological models, that describe how these factors influence the distribution of the species that reside there. They also are needed to facilitate an understanding of whether species distribution is influenced primarily by natural landscape variables, anthropogenic factors, or a combination of both. Hierarchical occupancy modeling that incorporates imperfect detection is one tool used to evaluate how natural and anthropogenic landscape variables determine occupancy of prey species, in order to identify crucial habitat for protection and/or restoration (Arroyo-Arce et al., 2014; Srivathsa et al., 2014).

In this chapter, my main objectives were to investigate if prey species are non-randomly distributed across a tropical region and how natural and anthropogenic landscape features are influential in shaping this distribution, through the use of hierarchical occupancy modeling. I focused on six representative focal species: white-lipped peccary; collared peccary *Pecari tajacu*; brocket deer *Mazama sp.*; white-tailed deer *Odocoileus virginianus*; lowland paca *Cuniculus paca*; Central American agouti *Dasyprocta punctate*, and white-nosed coati *Nasua narica*. These species were selected for modeling based on a priori knowledge of prey preferences of jaguar and puma *Puma concolor*, which are species of major conservation concern in the study area (Chapter 4) (de Azevedo & Murray, 2007; de Oliveira, 2002; Foster et al., 2010; Polisar et al., 2003). They were also selected as paca, white-tailed deer, and collared peccary are the most human harvested species, after two bird species (the great curassow *Crax rubra* and the ocellated turkey *Meleagris ocellata*), within the study area (Santos-Fita et al., 2012). Coatis, agouti, and brocket deer are also hunted but not to the same degree (Santos-Fita et al., 2012).

This study was conducted in the Calakmul Biosphere Reserve (CBR), which is located in the state of Campeche in Mexico. The reserve has become significant for the provision of some of the last remaining habitat for jaguars and pumas. It contains the greatest protected area of tropical forest (723,185 hectares) in Mexico and it also has the largest wild feline population in North America (Colchero et al., 2011; García-Frapolli et al., 2009). In this chapter, I modeled occupancy of selected prey species within the CBR as a function of landscape features and survey area. I focused on four variables that were hypothesized to influence occupancy of the focal species: distance to an aguada (m); total basal area (m2); tree species richness, and site, which encompassed each of the four survey areas as levels and represented different scales of anthropogenic disturbance (hunting in particular). Collared peccaries prefer areas of higher basal area and those close to water (Reyna-Hurtado & Tanner, 2007), white-lipped peccary avoid areas of high disturbance and the presence of hunting (Peres, 1996; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007), agoutis prefer higher tree species diversity, greater paca and brocket deer density occurs in areas proximal to a water source (Foster et al., 2010; Sollmann et al., 2012; Zeller et al., 2011), and white-tailed deer are largely habitat generalists (Petracca et al., 2013; Zeller et al., 2011). Despite its widespread usage, there is very little research on the occupancy of prey species in tropical Mexico. Petracca et al. (2013) conducted occupancy modeling for Sierra Madre Oriental, Mexico and relative abundance of ungulates was researched within the CBR (Reyna-Hurtado & Tanner, 2007).

Occupancy modeling is an effective tool for drawing inferences about prey species, such as: how anthropogenic and natural factors influence their distribution (Eaton, Hughes, Nichols, Morkill, & Anderson, 2011; Erb et al., 2012; Licona et al., 2011); how management designations influence occupancy of wildlife (Licona et al., 2011), and it is also used to monitor the status of populations (Ahumada et al., 2013; Petracca et al., 2013). My study will assist in identifying the factors that are influential in determining the distribution of valued prey species in the CBR, which has been otherwise lacking for these species and the region.

3.2 Methods

3.2.1 Survey Site

Four survey areas were used for my study: KM20; Zona Núcleo Sur; Mancolona, and Hormiguero (Figure 3-1) KM20 contains one of the few permanent aguadas in the reserve and is located in the south for research using transects in the core zone. Zona Núcleo Sur was accessed via vehicle from KM20 and is located in the southern core. Mancolona is the most northern research site. It is located on the outskirts of a village and is in the buffer zone. Hormiguero is located 7km from the community of Castellot and 1km from a Mayan ruin site. It also contains a large aguada and is situated in the buffer zone (Slater, 2014). Each survey area included four, approximately 2km long; transect lines (Figure 3 2). Along each transect (Figure 3 3) habitat survey plots were situated at 400m intervals, totaling 100 habitat plots in total. Each habitat plot consisted of a 20m x 20m marked parcel (Figure 3 4) adjacent to the transect line.

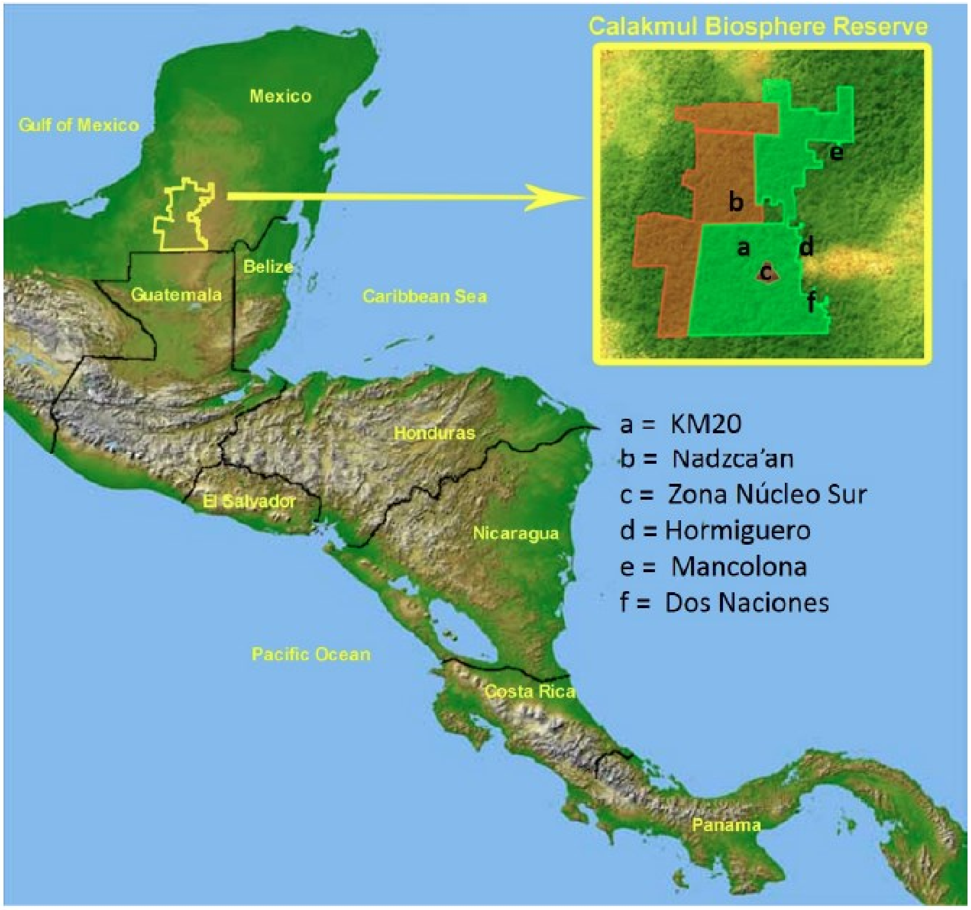


Figure 3-1: Calakmul Biosphere Reserve, Mexico, and the locations of the four field areas used (KM20, Mancolona, Hormiguero, and Zona Núcleo Sur), during the 2013 season (Slater, 2014).

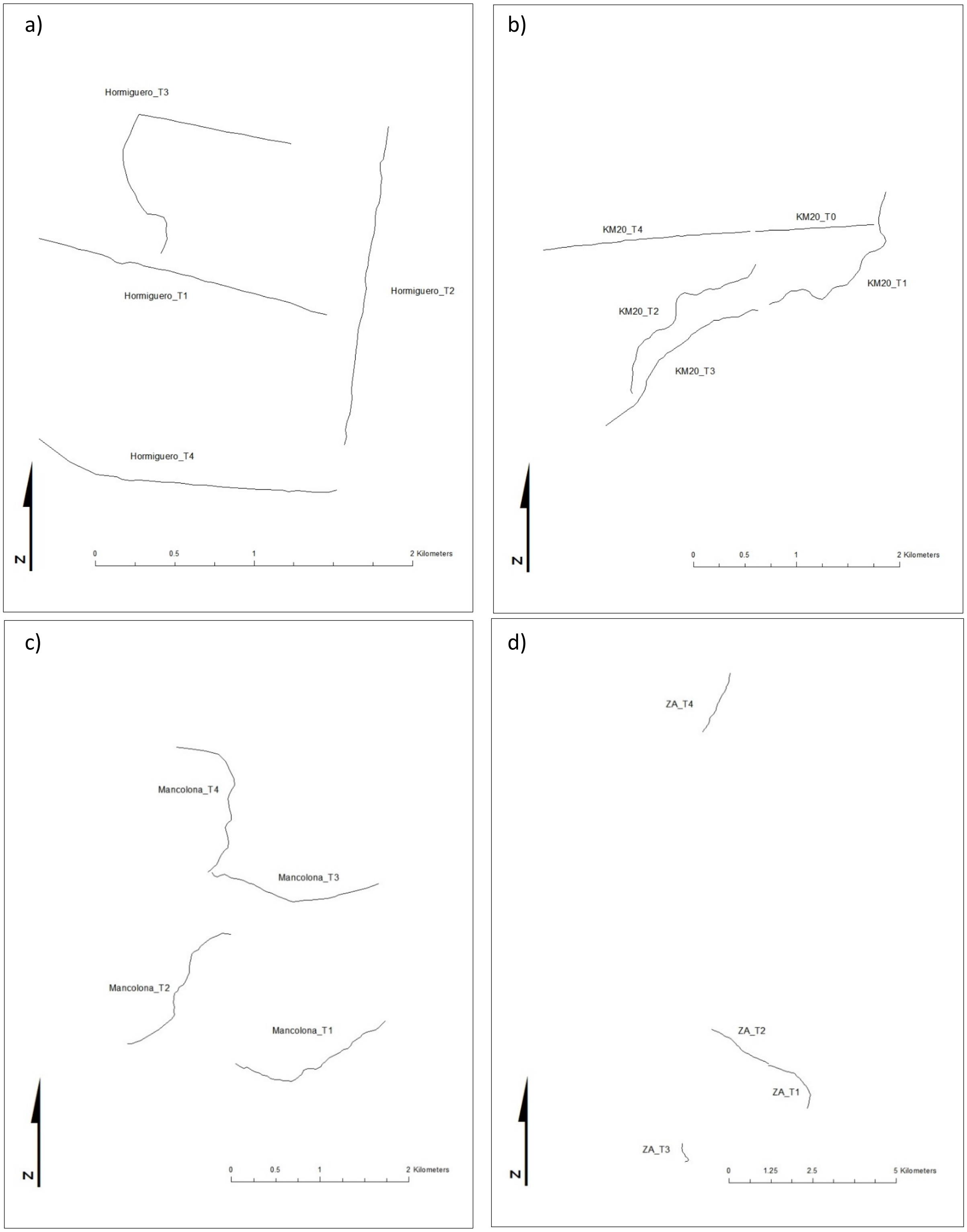


Figure 3-2: Location and length (km) of transects used for the 2013 field season in Calakmul Biosphere Reserve, Mexico (a) Hormiguero b) KM20 c) Mancolona d) Zona Núcleo Sur (Slater, 2014).

Figure 3-3: Transect 2 located in KM20 survey area in Calakmul Biosphere Reserve, Mexico.

Figure 3-4: 20m x 20m habitat survey plot located adjacent to transect 2 in KM20 survey area in Calakmul Biosphere Reserve, Mexico.

3.2.2 Line Transect Surveys

Data were collected by teams of students, led by university academics and local field guides, from June 25th to August 8th, 2013. Line-transect surveying and patch occupancy sampling methodology was based on the procedures presented by Peres (1999) and (Buckland et al., 2001). Surveys involved two to seven observers walking at speeds of 500-1000m/h the entire distance of the transect line beginning at 6:30am. Transects were surveyed for spoor (animal tracks or scat samples), and the identity of the species that produced it, and other variables (i.e. substrate) were recorded (Soto Navarro, Desniça, & Fernández, 2012). Each transect was surveyed at least four times totaling a distance of 160.2km of transects covered. To prevent double counting of the same track, sampling of each transect was completed with a minimum of 48 hours between sampling occasions for all but one survey of transect 2 in Mancolona, which was 24 hours (Funston et al., 2010). Observations for transect 2 in Mancolona were checked for duplicate recordings of the same track, with none found. Three transects were sampled repeatedly within approximately 48 hours and the rest were all resurveyed with at least three days between surveys. Finally, tracks were erased by disturbing the substrate after recordings were made of the width, length, age, leaf litter depth, distance along the transect and GPS coordinates (Keeping, 2014; Slater, 2014). If the source of spoor was ambiguous, the observation was not recorded. To minimize potential observer bias, observers were rotated for each survey between the different transects and lead observers worked with the teams to ensure that survey protocols and data collection methods were strictly maintained.

The observation or lack of observation of spoor indicated the presence or absence (detection-nondetection) of target prey species. Spoor detection has been used to survey prey species, such as ungulates (D'Eon, 2001), and was thus used in this study for focal prey species white-lipped peccary, collared peccary, brocket deer, white-tailed deer, lowland paca, Central American agouti, and white-nosed coati. The prey species chosen for modeling were selected based on a priori knowledge of prey preferences of jaguar and puma, which are species of major concern (see Chapter 4). Previous findings indicate that deer, peccary, agouti, coati, and paca were principle components of both cats' diets (de Azevedo & Murray, 2007; de Oliveira, 2002; Foster et al., 2010; Polisar et al., 2003).

Detection-nondetection data were compiled into detection histories for every 50m of the sampled transects to form individual sites (n). Each sample site (n) was designated with a 0 (absence/nondetection) or a 1 (presence/detection), of the target species for each sample period (T) (also know as a rep). For example, a detection history of 00000 would imply that the sample site was unoccupied by the target species, or else it was occupied, but the species was not detected during the sample periods. Detection histories were developed for each of the large prey species (brocket deer, white-tailed deer, collared peccary, and white-lipped peccary), for large prey combined (>15kg, included deer and peccary), for medium prey combined (2-15kg, included agouti, coati, and paca), and all the prey species together.

3.2.3 Habitat Surveys

Along each transect, habitat survey plots of 20m x 20m were situated at 400m intervals adjacent to the transect line. Data were collected on tree diversity (species and age), total basal area (m2), and measurement of understory vegetation, canopy cover, and leaf litter depth. During the surveys all trees within the plot having a circumference greater than 30cm were marked with tape, identified to species level and measurements were taken of the diameter at breast height (DBH), tree height, and health. DBH was measured with 50m tape measures. Suunto PM5 clinometers and tape measures were used to estimate tree height. Understory vegetation was measured by subdividing the plot into four quadrants with tape, and a 3m touch pole method was used every 1m along the dividing tape. A canopy scope was utilized for measuring the openness of the canopy. Measurements were taken from the centre of each of the quadrants and one from the centre of the overall 20m x 20m plot. Readings were taken by holding the scope 20cm from the eye, gazing upward into the canopy, and counting the number of dots that coincided with any gaps in the canopy cover to give an overall score out of 25. Five leaf litter depth measurements per plot were taken with a ruler: one in each quadrant and one in the centre of the plot. The distance of each plot to an aguada was also determined using GPS measurements (Slater, 2014).

3.2.4 Modeling Approach

Occupancy is simply the proportion of a study area that is occupied by the species of interest whereas; abundance is the total number of individuals in a population. Occupancy modeling is widely used globally as a surrogate to abundance and as an aid for informing conservation decision-making (Hines et al., 2010; Mackenzie et al., 2006; Welsh et al., 2013). Occupancy estimation sampling usually requires less effort than abundance surveys and is sometimes the only viable option for rare species (e.g. jaguar), where it would be essentially impossible to estimate abundance (Mackenzie et al., 2006; Zeller et al., 2011). Detection probability (ρ), which is the likelihood that an individual will be detected, is an important consideration when developing occupancy estimates as it cannot be explicitly known that all members of a species in the sample area will be sampled (Fiske & Chandler, 2011; Mackenzie et al., 2006). Because individuals may be present but not actually detected (imperfect detection), a naïve count will underestimate the true proportion of sites that are occupied (MacKenzie et al., 2002; Mackenzie et al., 2006). This can be overcome however, by the use of occupancy models. These models utilize a detection history to calculate a detection probability, which is then applied to adjust the naïve occupancy and to give an estimate of occupancy probability (φ). The occupancy probability can be interpreted as the probability of a site being occupied or as the proportion of the site that is likely occupied (Midlane et al., 2014).

Hierarchical occupancy modeling offers a unified framework for analysis that uses repeated presence-absence (detection/non-detection) data to model and adjust for the detection process (Kery, Chandler, & Royle, 2012; Welsh et al., 2013). It recognizes that two processes influence observations: the first is a state process, which determines occupancy at each site, while the second is a detection (observation) process, that yields observations that are provisional on the state process (Fiske & Chandler, 2011; Kery et al., 2012). A Bernoulli distribution describes both of these state processes by combining the canonical model for species occurrence and imperfect detection. Because the second is conditional on the first, the false positive errors are essentially negated (Kery et al., 2012).

The occupancy model for the state process is:

$$z_i \sim \mathit{Bernoulli}\ (\varphi)$$

The occupancy model for the detection process is:

$$y_{ij} \sim \mathit{Bernoulli}\ (z_i \rho_{ij})$$

The latent variable z_i represents the true state of occurrence at site i, φ is the expected value of z_i, y_{ij} is the observed value of occurrence at site i during survey j, and ρ_{ij} is the detection probability of the all individuals of a species at site i during survey j. The site-occupancy model can be interpreted as a hierarchical extension to a Bernoulli generalized linear model (GLM), logistic regression, or two linked GLMs (Kery et al., 2012). Five main assumptions were considered for occupancy modeling: population closure; no false positive errors; independent detections, homogeneity of detections, and that that the two Bernoulli distributions for occupancy and detection were a reasonable abstraction of reality (Kery et al., 2012; Mackenzie et al., 2006).

Occupancy modeling was completed in the 'unmarked' package in R (Fiske, Chandler, Miller, Royle, & Kery, 2014; R Development Core Team, 2010). This package fits hierarchical models of animal occupancy to data that incorporates imperfect detection (Fiske et al., 2014). The probability distribution of the observed data [$\Pr(x \mid \theta)$], where x denotes the data and θ denotes the parameters, can be viewed as a function of the parameters conditional on the data, which is the likelihood function [$L(\theta \mid x)$]. Maximum likelihood estimators (MLEs) are the values of the parameters that maximize the function, or make the data most likely given the underlying model (Mackenzie et al., 2006). The package 'unmarked' employs model-fitting functions that are specific to particular sampling methods and finds the MLEs of the parameters in the model (Fiske & Chandler, 2011). For this study a single-season site occupancy model (MacKenzie et al., 2002) that handles detection/non-detection data was used with the fitting function 'occu' (Fiske & Chandler, 2011).

3.2.5 Incorporating Covariates Into Occupancy Models

3.2.5.1 Modeling Occupancy as a Function of Covariates

Through a logit link function, occupancy models can be expressed as a function of site-level or observation-level covariates (Kery et al., 2012; Zeller et al., 2011). The logit link function converts linear combinations of covariate values into a value between 0 and 1 on a scale of probability (Mackenzie et al., 2006). The equation for the logit link function for variables related to occupancy is as follows:

$$\mathrm{logit}(\varphi_i) = x_i \beta$$

The variable x_i represents the values for the site-level or observation-level covariate of interest at the ith sampling unit, while β is the estimated regression coefficient representing the value of the covariates corresponding effects (Fiske & Chandler, 2011; Mackenzie et al., 2006). The equation for the logit link function for variables related to detection is as follows:

$$\text{logit}(\rho_{ij}) = v_{ij}\alpha$$

The variable v_{ij} represents the values for the observation-level covariates of interest at site i during survey j, while α is the estimated regression coefficient representing the value of the covariates corresponding effects (Fiske & Chandler, 2011).

For this study, only site-level covariates were included as the primary focus was on occupancy of target prey species as a function of habitat features, rather than on detection. Detection was held constant for all models, under the assumption that the covariates commonly modeled for detection would be found to have negligible influence. For example, the affect of observer on detection was not a concern as multiple observers were rotated for each survey between the different transects. The use of trained researchers and/or experienced volunteers within different observer groups has been shown to minimize variation of observations between surveys (Darwall & Dulvy, 1996; Edgar & Stuart-Smith, 2009). The pairing/grouping of observers together has also been found to minimize the effects of identification errors and improve accuracy of data through consultation and discussion of observations (Bernard et al., 2013). Also, several (>4) replicate surveys were completed for each transect, which reduced the problem of imperfect detection by minimizing the likelihood of not detecting a species despite the site being occupied (Guillera-Arroita et al., 2014). Finally, the detection process is accounted for in the inherent nature of a single-state site occupancy model through the incorporation of the canonical model for imperfect detection (Kery et al., 2012).

3.2.5.2 Covariates Selected for Study

The variable “site” was considered a categorical factor variable with each of the four survey areas: KM20 (km20); Zona Núcleo Sur (zns); Mancolona (man), and Hormiguero (horm) as the levels. Continuous site-level variables included distance to aguada (m), total basal area (m2), and tree species richness. These covariates were chosen, as they were hypothesized to influence prey habitat selection. Previous studies have found that collared peccaries prefer areas of higher basal area and those close to water, agoutis prefer higher tree species diversity, and greater paca density has been shown in areas proximal to a water source (Foster et al., 2010; Sollmann et al., 2012).

Standardization of continuous variables was completed to improve performance of the models and also to facilitate comparison of coefficients. Standardizing the variables essentially makes them unit less thus allowing for comparison based on relative size (Mackenzie, 2012; Sardy, 2008). The continuous covariates for this study were standardized using a z-transformation (Harihar & Pandav, 2012; Negroes et al., 2010) as follows:

$$\chi_i = \frac{\chi_i - a}{b}$$

The variable χ_i is the observed value for the covariate, a is the mean of the covariate values, and b is the standard deviation (Mackenzie, 2012). A summary of each of the covariates is shown in Table 3-2.

3.2.5.3 Data Exploration

Variance inflation factor (*VIF*) was used to check for collinearity between covariates. The *VIF* for a variable, *Xj* is the square root of the inverse of the R^2_j value of the regression of the variable *Xj* against all of the other explanatory variables (Zuur et al., 2010).

$$VIF_j = \sqrt{\frac{1}{(1 - R_j^2)}}$$

Collinearity was indicated by high *VIF* values, as this suggests that most of the variation in the variable can be explained by the other covariates. To resolve this issue, a preselected *VIF* threshold was chosen. I used a conservative value of <3. Variables with *VIF*s >3 were sequentially removed one at a time with the highest ones removed first and then the analysis repeated until only variables with a *VIF*<3 remained (Zuur et al., 2010). This was completed using source ("HighstatLib.R") and the function 'corvif' in R (R Development Core Team, 2010; Zuur et al., 2010). Variables not shown to be collinear were then included in global models for the target species.

Boxplots and Cleveland dotplots were created in R and utilized to visualize the spread of the data and inspect for outliers (R Development Core Team, 2010). Data were checked for errors when possible outliers were apparent.

3.2.6 Model Fitting and Selection

A global model was created for encompassing all possible covariates (Burnham & Anderson, 2002; Mackenzie et al., 2006) and is described below:

$$\rho(.)\psi(\text{site+aguada+rich+basal})$$

Because the global model was the most highly parameterized, if this model fit the data adequately then it would be inferred that any models that were less parameterized and thus more parsimonious would also fit the data (Burnham & Anderson, 2002; Cooch & White, 2002). Global models were evaluated for each species and species group for goodness-of-fit and to compute estimates of overdispersion. Goodness-of-fit was evaluated using methods developed by Mackenzie and Bailey (2004). The R package 'AICcmodavg' used the model and detection histories, along with a parametric bootstrap approach, (with 1000 bootstrap samples), to compute observed and expected values, the Pearson chi-square (X^2) test statistic and to estimate an overdispersion parameter (ĉ). Overdispersion was indicated if ĉ>1, underdisperison if ĉ <1, and lack-of fit demonstrated if ĉ>4 (Durso et al., 2011; Mackenzie & Bailey, 2004; Mazerolle, 2015). If ĉ for the global model was >1 then the value of ĉ was applied to all subsequent models derived from the global model. If ĉ <1 then the model was run without adding the overdispersion parameter and ĉ was fixed at one (Mazerolle, 2015).

Sixteen models were derived for each prey species and group of prey. These included one null model with constant occupancy and detection, with the remaining 15 being those that included occupancy as a function of the covariates (Table 3-1). Package 'unmarked' estimates occupancy and detection on the logit scale; therefore estimates were back-transformed to the original scale (Kery & Chandler, 2012). Akaike's Information Criterion (AIC) was used to evaluate goodness-of-fit of the data, as this method has become increasingly prevalent and beneficial for analyzing ecological data (Durso et al., 2011; Hines et al., 2010; Karanth et al., 2011; Mackenzie & Bailey, 2004). The most parsimonious models for the data were identified by minimizing the AIC values. Rather than selecting models based on the absolute magnitude of AIC value, the differences in AIC (ΔAIC) among the various models were evaluated (Mackenzie et al., 2006). For this study AICc, which is AIC with an adjustment for small sample size was used. Models with a ΔAICc <2 had substantial empirical support, those with values between 4 and 7 had substantially less support, and those with a difference >10 essentially had no support (Burnham & Anderson, 2002; Reed, 2011). AICc values also formed the basis for AICc weights (AICc*w*), which sum to one for all models of the set. Models and covariates were compared by AICc*w* to determine which ones had more support and relative goodness-of-fit (Arnold, 2010; Petracca et al., 2013; Tipton, Dreitz, & Doherty, 2008). Any with a value greater than 0.5 were considered to have the most statistical support (Burnham & Anderson, 2002; Erb et al., 2012; Wang, McShea, Wang, & Li, 2015).

If ĉ>1 was applied to the model, then a quasi-likelihood information criteria (QAICc) and QAICc*w* were used to evaluate models. This inflated the standard errors by a factor of $\sqrt{\hat{c}}$, added a parameter (K) to the model, and scaled the log-likelihood by ĉ (Mackenzie et al., 2006; Mazerolle, 2015). For models with ĉ<1, ĉ was fixed at one and AICc was used.

Rather than trying to identify the best model, the aim of the analysis was to produce a set of top ranking models that would best explain the data and could be used for multimodel inference via model averaging (Burnham & Anderson, 2002). Model averaging was conducted in the R package 'MuMin' (Barton, 2015) where the averaged coefficient estimate ($\widehat{\hat{\beta}}_\iota$) was calculated from the candidate models in which the parameter of interest appeared as follows (Symonds & Moussalli, 2011):

$$\widehat{\hat{\beta}}_\iota = \frac{\sum_{i=1}^{R} w_i \widehat{\hat{\beta}}_\iota}{\sum_{i=1}^{R} w_i}$$

Latent occurrence states for each prey species and groups of prey were derived from an estimate for z_i using function 'ranef' in R (Kéry & Royle, 2016; R Development Core Team, 2010). Function 'ranef' used empirical Bayes methods and incorporated the data, as well as the MLE's to estimate the posterior distribution of z_i (Fiske & Chandler, 2010). The Bayes estimate of the Probable Area Occupied (PAO) was derived from the empirical best-unbiased predictor (EBUP), which is the mean of the posterior distribution using the package 'lattice' in R (R Development Core Team, 2010). The PAO was compared to the population-level estimates of occupancy, as PAO represents the proportion of sample sites occupied, whereas occupancy is an estimate for an infinite number of sites

(Fiske & Chandler, 2010). The latent states were used subsequently in Chapter 4 for the analysis for jaguars and pumas where occupancy was modeled as a function of the estimates of latent occupancies of the prey species (Kery et al., 2012).

Table 3-1: Candidate set of 16 occupancy models for prey species for survey data from Calakmul Biosphere Reserve, Mexico. Models estimated with constant detection (ρ) and occupancy (ψ), and as a function of covariates: site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero); distance to an aguada (m); total basal area (m2), and tree species richness.

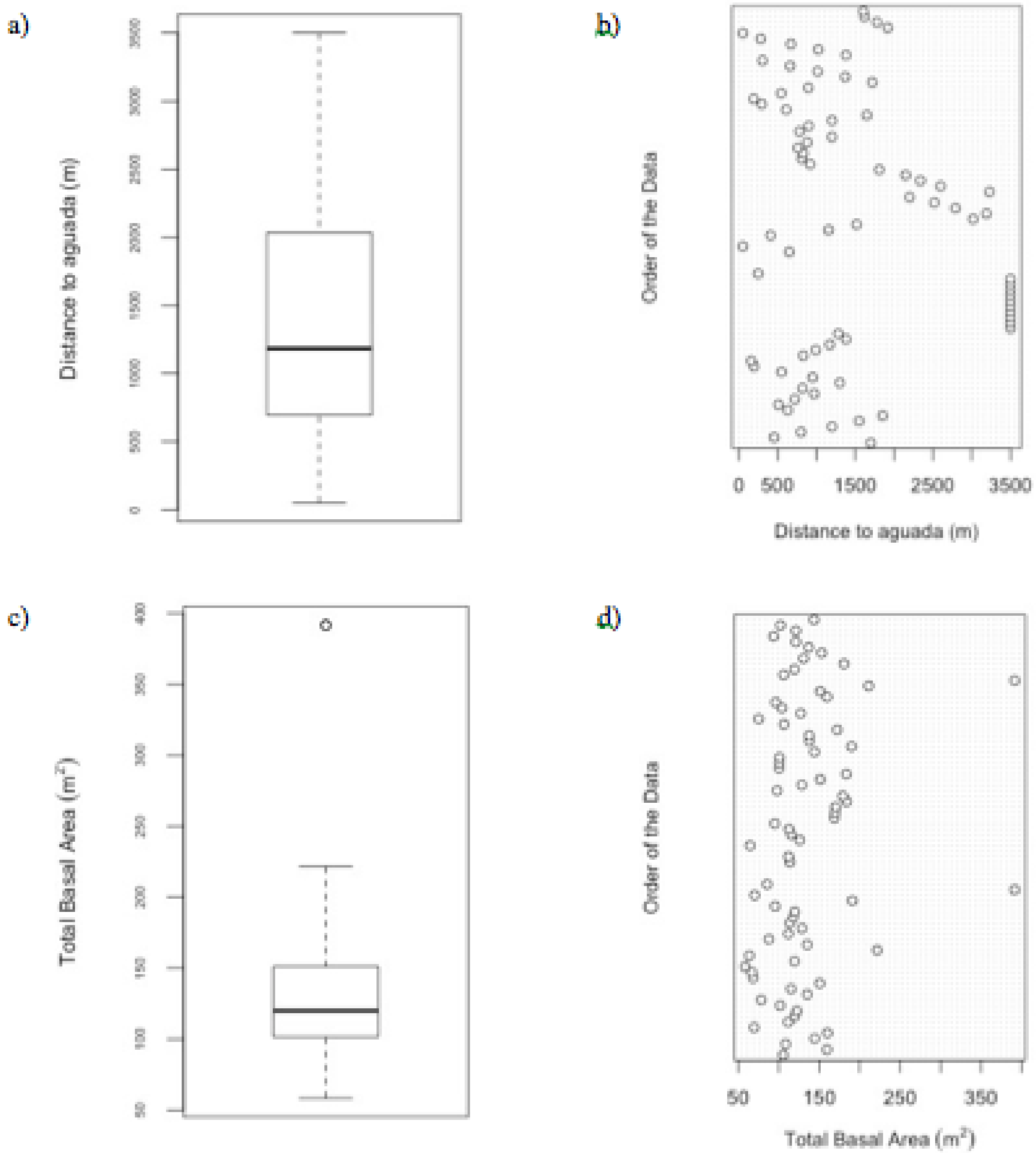
Model
ρ(.)ψ(.)
ρ(.)ψ(basal)
ρ(.)ψ(rich)
ρ(.)ψ(aguada)
ρ(.)ψ(site)
ρ(.)ψ(rich+basal)
ρ(.)ψ(aguada+rich)
ρ(.)ψ(aguada+basal)
ρ(.)ψ(aguada+rich+basal)
ρ(.)ψ(site+basal)
ρ(.)ψ(site+rich)
ρ(.)ψ(site+aguada)
ρ(.)ψ(site+basal+rich)
ρ(.)ψ(site+aguada+rich)
ρ(.)ψ(site+aguada+basal)
ρ(.)ψ(site+aguada+rich+basal)

3.3 Results

The four covariates were assessed for collinearity using *VIF* values (Table 3-2). Collinearity was not apparent as indicated by *VIF* values <3 (Zuur et al., 2010). All variables were then subsequently included in the global models. Boxplots and Cleveland dotplots for each covariate are displayed in Figure 3-5 (Note: data were ordered by site (Hormiguero, Zona Núcleo Sur, Mancolona, and KM20)). Outliers were not discovered and any points that appeared to be possible outliers were found to not likely be as a result of survey error.

Table 3-2: Variance inflation factors (*VIF*) for each of the four variables, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), included in the occupancy models for prey species from survey data from Calakmul Biosphere Reserve, Mexico.

Covariate	Abbreviation	Type	*VIF*
distance to an aguada	aguada	continuous site-level numeric	1.5954
tree species richness	rich	continuous site-level numeric	1.3662
site	site	categorical factor (4 levels)	2.0815
basal area	basal	continuous site-level numeric	1.0864


a)
Distance to aguada (m)
0
500
1000
1500
2000
2500
3000
3500
b)
Order of the Data
0
500
1500
2500
3500
Distance to aguada (m)
c)
Total Basal Area (m^2)
50
100
150
200
250
300
350
400
d)
Order of the Data
50
150
250
350
Total Basal Area (m^2)

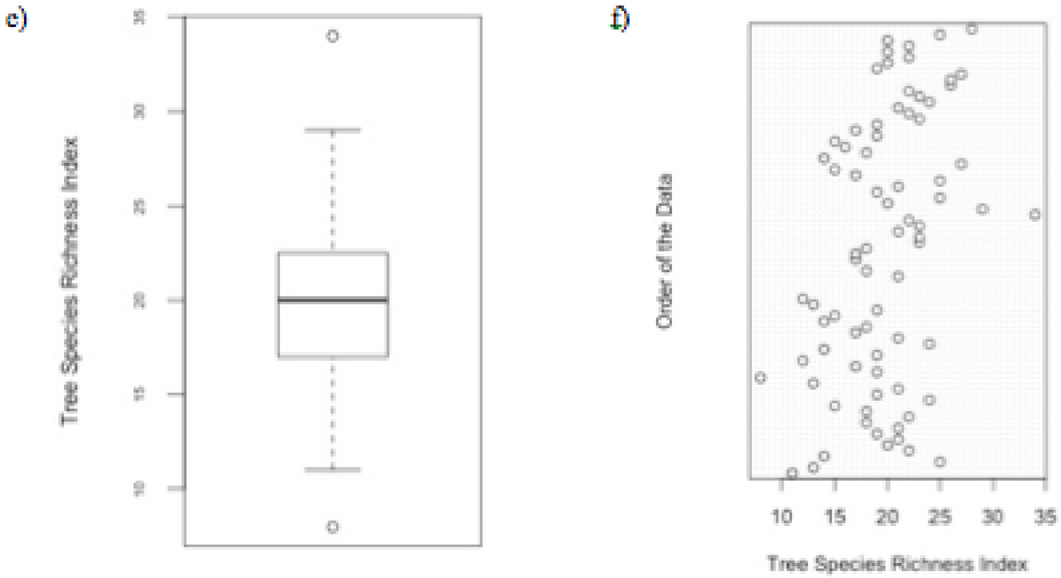


Figure 3-5: Boxplots and Cleveland dotplots for variables chosen for occupancy modeling from survey data from Calakmul Biosphere Reserve, Mexico a) Boxplot for distance to an aguada (m), b) Cleveland dotplot for distance to an aguada (m), c) boxplot for total basal area (m2), d) Cleveland dotplot for total basal area (m2), e) boxplot of tree species richness index, f) Cleveland dotplot for tree species richness index.

Results for the goodness-of-fit testing of the global models for each species and species group are shown in Table 3-3. The global models for each species and species group, except white-lipped peccary (ĉ =0.8705), indicated overdispersion of the model. All ĉ values were <4; however, demonstrating overdispersion, rather than lack-of-fit (Durso et al., 2011; Mackenzie & Bailey, 2004; Mazerolle, 2015). All subsequent models, except those for white-lipped peccary, were modeled with the ĉ applied.

Table 3-3: Pearson chi-square (X^2) test statistic, p-value, and overdispersion parameter (ĉ) for the global models of site occupancy estimates (ψ) for seven prey species (brocket deer, white-tailed deer, collared peccary, white-lipped peccary, lowland paca, Central American agouti, and coati) using survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m2), and tree species richness.

Binomial Name	Common Name	Functional Group	X^2	p	ĉ
Mazama sp	Brocket deer	large prey	27.600	0.009	2.0875
Odocoileus virginianus	White-tailed deer	large prey	17.583	0.204	1.2890
Pecari tajacu	Collared peccary	large prey	16.697	0.225	1.2368
Tayassu pecari	White-lipped peccary	large prey	12.105	0.533	0.8705
Cuniculus paca	Lowland paca	medium prey	29.013	0.007	2.1939
Dasyprocta punctate	Central American agouti				
Nasua narica	Coati				
		large prey	19.612	0.106	1.5081
		all prey	24.461	0.031	1.9368

A complete set of tables for top-performing models, as well as relative importance of each variable for each prey species and prey group, can be found in Appendix A. A summary of the most predictive models of site occupancy for each species, as well as each group of species is found in Table 3-4. For brocket deer, the null model was the only model with ΔQAICc value <2, indicating a lack of significant support for the influence of variables on the occupancy of brocket deer. This was reinforced by analysis of relative importance of variables, as the sum of each variable was <0.5.

The null model and $\rho(.)\psi(\text{basal})$ model were identified as top-performing models for white-tailed deer with ΔQAICc values of 0 and 1.798, respectively. The relative importance of basal area did not offer significant support for influence on occupancy, as the sum of QAICcw was 0.230.

Tree species richness was found to positively influence occupancy of collared peccary, with higher occupancy as tree diversity increased. The model $\rho(.)\psi(\text{rich})$, as well as the null model had ΔQAICc values of 1.564 and 0, respectively. The sum of QAICcw (0.311) for tree species richness did not indicate relative importance for the influence of this variable on occupancy of collared peccary.

The white-lipped peccary global model was the only global model with a $\hat{c}<1$ (0.8705). The $\hat{c}$ was therefore fixed at one and AICc utilized for model fitting. Five models were identified as top-performing models for white-lipped peccary. The null model had a ΔAICc value of 0, followed by $\rho(.)\psi(\text{rich})$, $\rho(.)\psi(\text{basal})$, $\rho(.)\psi(\text{aguada})$, then $\rho(.)\psi(\text{aguada+basal})$. Only the top three models were included as top-performing when included in the AICc*w* sum of 0.5. The relative importance for tree species richness, basal area, and distance to aguada were all <0.5, indicating that no one variable had greater influence on occupancy of white-lipped peccary.

Two models were identified as top-performing models for large prey grouped together (brocket deer, white-tailed deer, collared peccary, and white-lipped peccary). Delta QAICc for the null model was 0 and 0.005 for $\rho(.)\psi(\text{aguada})$. The relative difference between the two was quite small, indicating that both of these models must be considered for making inferences. Proximity to an aguada was identified as having a negative influence on occupancy with decreasing occupancy closer to water. It had a relative importance of 0.480.

Top-performing models for medium prey (lowland paca, Central American agouti, and coati) grouped together included the null and $\rho(.)\psi(\text{site})$. Model averaged occupancy for the site variable displayed higher β estimates for Zona Núcleo Sur and KM20. The relative importance of the site variable was <0.5 at (0.360).

The same two models were identified as top-performing models for all prey grouped together as large prey when grouped. The null model had a ΔQAICc of 0, while $\rho(.)\psi(\text{aguada})$ had a ΔQAICc of 0.447. Again, proximity to an aguada was identified as having a negative influence on occupancy with decreasing occupancy closer to water. It had a relative importance of 0.430.

Model averaged occupancy, (averaged over top-performing models only), was highest for large prey combined (0.963), followed by all seven prey species combined (0.962), brocket deer (0.865), white-tailed deer (0.843), collared peccary (0.842), medium prey combined (0.642), and finally white-lipped peccary (0.589) (Table 3-4). Estimated PAO differed from model averaged occupancy by more than 10% for medium prey (PAO was 11.2% >ψ), by more than 5% for white-tailed deer (PAO was 9.0% > ψ), and by less than 5% for all the rest of the species and species groups.

Table 3-4: Most predictive models of site occupancy estimates (ψ) for focal prey species as determined by delta Quasi Akaike's Information Criterion adjusted for small sample size (ΔQAICc) <2 for survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness. The Probable Area Occupied (PAO) is included for comparison to ψ and model averaged ψ.

Binomial Name	Common Name	Functional Group	Model	ΔQAICc	QAICc*w*	ψ	ψ(avg)	PAO
Mazama sp	Brocket deer	large prey	ρ(.)ψ(.)	0	0.398	0.865	0.865	0.865
Odocoileus virginianus	White-tailed deer	large prey	ρ(.)ψ(.)	0	0.310	0.933	0.843	0.933
			ρ(.)ψ(basal)	1.798	0.126	0.753		0.933
Pecari tajacu	Collared peccary	large prey	ρ(.)ψ(.)	0	0.323	0.838	0.842	0.838
			ρ(.)ψ(rich)	1.564	0.148	0.846		0.838
*Tayassu pecari**	White-lipped peccary	large prey	ρ(.)ψ(.)	0	0.236	0.587	0.589	0.587
			ρ(.)ψ(rich)	0.843	0.155	0.572		0.587
			ρ(.)ψ(basal)	1.073	0.138	0.587		0.587
			ρ(.)ψ(aguada)	1.702	0.101	0.589		0.587
			ρ(.)ψ(aguada+basal)	1.727	0.100	0.610		0.587
Cuniculus paca	Lowland paca	medium prey	ρ(.)ψ(.)	0	0.272	0.754	0.642	0.754
Dasyprocta punctate	Central American agouti		ρ(.)ψ(site)	1.223	0.147	0.530		0.754
Nasua narica	Coati							
		all large prey**	ρ(.)ψ(.)	0	0.236	0.951	0.963	0.951
			ρ(.)ψ(aguada)	0.005	0.236	0.975		0.951
		all prey	ρ(.)ψ(.)	0	0.276	0.949	0.962	0.949
			ρ(.)ψ(aguada)	0.447	0.221	0.974		0.949

**Tayassu pecari* modeled with ĉ =1 and AICc not QAICc **All large prey includes prey > 15kg (deer and peccary)

3.4 Discussion

Occupancy modeling has been widely used as an aid for informing conservation decision-making (Hines et al., 2010; Mackenzie et al., 2006; Welsh et al., 2013) and to facilitate an understanding of the major ecological factors influencing prey species distribution (Ahumada et al., 2013; Eaton et al., 2011; Erb et al., 2012; Licona et al., 2011; Petracca et al., 2013; Zeller et al., 2011). Despite its widespread usage, there is very little research on the occupancy of prey species in tropical Mexico. In this study, I use hierarchical occupancy modeling to identify the factors influencing the distribution of valued prey species in the CBR. My results suggest that distribution appears to be non-random for some prey species, and may in fact be influenced by natural and/or anthropogenic landscape features.

Occupancy models for brocket deer and white-tailed deer indicated that their distribution across the reserve was not influenced by the variables chosen for modeling in a meaningful way. This was expected as white-tailed deer are largely habitat generalists (Petracca et al., 2013; Zeller et al., 2011) and brocket deer are adaptable to a degree of habitat disturbance (Reyna-Hurtado & Tanner, 2007). Furthermore, the model averaged occupancies of brocket deer and white-tailed deer were quite high at 0.865 and 0.843, indicating that they are ubiquitous throughout the reserve. While brocket deer tend to prefer areas proximal to water (Zeller et al., 2011), this was not reflected in my study.

Higher occupancy of collared peccary was found to be weakly associated with increasing tree species richness; however, the relative importance of this variable (0.311), as determined by the sum of QAICc*w* did not offer significant support for its overall influence. The relative effects of tree diversity in determining distribution should not be ruled out entirely, since collared peccary eat both fruits and seeds; therefore, areas with higher tree species richness likely signify a larger variety of these food sources. Supporting previous research, (Peres, 1996; Reyna-Hurtado & Tanner, 2007) my results suggested that this species is highly adaptable to anthropogenic disturbance as indicated by a high model averaged site occupancy of 0.842, along with a lack of apparent effect of total basal area or site on distribution. Collared peccary prefer areas proximal to a permanent water source (Reyna-Hurtado et al., 2009; Zeller et al., 2011); however, this was not reflected in my study.

Model averaged occupancy of white-lipped peccary was 0.589, which is 30% lower than the occupancy of collared peccary. While there are no other data available on occupancy estimates for peccary in Mexico, Track Encounter Rates (mean number of tracks sighted in a kilometer of transect) for peccary in Calakmul were 72% higher for collared peccary than white-lipped peccary (Reyna-Hurtado & Tanner, 2007). My findings are concerning because white-lipped peccary have been found at lower abundance, (up to three times lower), in areas where hunting of this species occurs, and in the CBR, both peccary species are prized game choices for poorly regulated hunting (Reyna-Hurtado & Tanner, 2007). Unlike collared peccary though, white-lipped peccary are much less adaptable to habitat disturbance (Peres, 1996; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007). This was reflected in the CBR, as lower occupancy was associated with decreased tree species richness and diminished total basal area, which likely corresponds with disturbed habitat. White-lipped peccary tend to occupy areas with increased forest density as a means of protection, as hunting by humans mainly occurs in more open areas with less dense vegetation (Conde et al., 2010); therefore, dense habitats can provide safer refuge. It was hypothesized that occupancy of white-lipped peccary would be influenced by the covariate for site (which encompassed each of the four survey areas as levels), due to the species known susceptibility to hunting pressures (Petracca et al., 2014; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007). This was not supported by my study; however, suggesting that other factors, such as habitat disturbance, may be more influential in their distribution in the CBR. Subsequent research would be beneficial to determine the origin of the landscape variations and underlying causes of the reduction in habitat quality to evaluate why white-lipped peccary occupancy is lower in these areas. The species has also been found to have a high preference for water bodies (Reyna-Hurtado et al., 2009; Zeller et al., 2011); however, my results reiterate findings from Zeller et al. (2011) who found that water did not influence distribution of white-lipped peccary.

While the null model had the most support for large prey (deer and peccary) grouped together, the distribution of the collective group was found to possibly be non-random with decreased occupancy associated with proximity to water. This variable had weak support, as indicated by a relative importance <0.5 at 0.480. This variable was not found to be influential in the distribution of each species when modeled individually. Model averaged occupancy of the collective group of large prey (0.963) was almost identical to occupancy of all prey collectively (0.962), suggesting that the larger prey species likely determined occupancy of all prey when grouped together. More specifically, it is probable that the high occupancy and detections for both of the deer species, as well as collared peccary masked the effects of the other species in determining occupancy of all prey as a collective group, essentially making occupancy for both groups equal.

Occupancy models for medium prey indicated a possible influence from site (survey area), as the model incorporating this covariate was a top-performing model, secondary to the null model. However, the relative importance of this variable (0.360) necessitates careful interpretation of the implications of this result. Models exhibited higher β estimates for Zona Núcleo Sur and KM20, which are the two survey areas located in the core zone of the CBR, an area which is intended to be free of human settlement and disturbance (Ericson, 2006). This is an interesting finding as agoutis and pacas are habitat generalists (Zeller et al., 2011), while coatis adapt well to anthropogenic disturbance (Novack et al., 2005). Supporting previous research (Novack et al., 2005; Zeller et al., 2011), my results suggest that distribution for these species was not influenced to a significant degree by landscape variables. Pacas are highly prized by hunters in the buffer zones of the CBR, while agouti and coatis are hunted but not to the same degree. Furthermore, hunting around the CBR is primarily concentrated to within 10km from villages (Santos-Fita et al., 2012). Because models for medium prey species did not indicate an influence of landscape variables on distribution but did exhibit higher occupancy in the core of the reserve, this could suggest that hunting pressures are influencing their distribution. This conclusion cannot be drawn from these results alone, and therefore, further research is required to support this. The model averaged occupancy for medium prey of 0.642, may indicate that these species are not abundant overall and/or that they are concentrated more in the core of the reserve in response to human presence/settlement in the buffer zones.

In the core and buffer zones of the CBR, the probability of any site being occupied by one of the large focal species is 0.963, it is 0.642 for medium prey, and for any of the focal species is 0.962. Brocket deer, white-tailed deer, and collared peccary are the most ubiquitous throughout the reserve with model average occupancies of 0.865, 0.843, and 0.842, respectively. Ungulate populations are crucial for the functioning of healthy ecosystems and felid-prey interactions in the tropics (Ahumada et al., 2013; Licona et al., 2011) and my results suggest that brocket deer and white-tailed deer, and possibly collared peccary are occupying both undisturbed and disturbed areas essentially equally. Prioritizing protection and/or restoration of forest with high tree species diversity may help to ensure that collared peccary have access to a variety of fruits and seeds, as is their dietary preference (Ahumada et al., 2013); however, these species are known to be highly adaptable to disturbance over all (Reyna-Hurtado & Tanner, 2007).

In contrast to the deer species and collared peccary, my results indicate some concern for white-lipped peccary and medium prey in the CBR. Three significant findings from this study were as follows: 1) model averaged occupancy of white-lipped peccary was 0.589, which is 30% lower than the occupancy of collared peccary; 2) distribution of white-lipped peccary appears to be non-random with lower occupancy associated with areas that may coincide with increased habitat disturbance (decreased tree species richness and diminished total basal area), and 3) medium prey occupancy models suggest that these prey species may not be abundant overall and/or their distribution is concentrated more in the core of the reserve possibly in response to human presence in the buffer zones. It is already known that populations of white-lipped peccary are declining in Mexico and globally, mean group sizes in the CBR are smaller than groups in other areas in their range, likely due to hunting pressures (Reyna-Hurtado et al., 2010), and that the estimated total population for the southern area of Calakmul is only a maximum of 1,500 individuals (Reyna-Hurtado et al., 2010). Furthermore, if local populations of white-lipped peccary can no longer adapt to anthropogenic pressures, (hunting in particular), extirpation is likely, as has happened with other populations throughout their geographical range (Peres, 1996; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007). Currently, 70% of remaining habitat for this species is subject to hunting pressures and habitat disturbance (Altrichter et al., 2012); therefore, prioritizing protection and restoration of large areas (>100km2) of primary, dense, continuous, and diverse forests in the CBR would help ensure that this species has access to the habitats and foods that they prefer and large enough home ranges (Reyna-Hurtado et al., 2010).

Detailed data from multiple years and during both the dry and wet seasons are required on the ranging patterns of white-lipped peccary in the CBR to support my results and to determine specifically which areas may need to be prioritized for conservation and/or restoration (Altrichter et al., 2012; Reyna-Hurtado et al., 2009). Furthermore, limitation and/or better regulation of both subsistence and sport hunting of this species is necessary in the CBR region to prevent further declines in white-lipped peccary populations (Altrichter et al., 2012; Reyna-Hurtado et al., 2010). According to Reyna-Hurtado et al. (2010), hunting of white-lipped peccary in Calakmul has already impacted the species, reducing group sizes and even eliminating some groups completely. In order to develop a sustainable conservation strategy, consultation is needed to work with subsistence hunters to ensure that they are still able to meet their needs, while local populations of white-lipped peccary are not jeopardized (Reyna-Hurtado et al., 2010). This species is not only meaningful culturally to the people of the rural tropics (Reyna-Hurtado et al., 2009); it also plays a significant part in the functioning of Neotropical ecosystems, such as the CBR, through their frugivorous habits, and as a primary prey source for jaguars and pumas (Altrichter et al., 2012). The ecological and cultural values that this species possesses warrants the necessity for further investigation of their status in the reserve and into conservation of remaining populations or the long-term presence of white-lipped peccary in the CBR cannot be guaranteed.

In regards to the third significant finding, my results suggest that medium prey may not be abundant overall and/or their distribution is concentrated more in the core of the reserve. Further research is required to establish why medium prey occupancy is higher in undisturbed/unoccupied habitat to determine if there is a relationship between human occupation, and specifically hunting, and this distribution. A thorough evaluation of the hunting practices of around the reserve should be completed nonetheless, as currently, hunting in Calakmul is poorly regulated and it is not truly known how many individuals of the focal species are being harvested (Santos-Fita et al., 2012; Slater, 2014). It is however; known that pacas are highly prized by hunters in the buffer zones (Santos-Fita et al., 2012) and that there have been significant reductions in the populations of several hunted species documented over the past decade in the southern Yucatán (Vester et al., 2007). The implementation of a community-based conservation strategy that utilizes adaptive co-management and a interdisciplinary framework would be beneficial, as drawing upon multiple sources of knowledge about the wildlife and the humans residing in Calakmul could result in better outcomes for the viability of the reserve and the well-being of its human inhabitants (Armitage, De Loë, & Plummer, 2012; Chazdon et al., 2009; Folke, Hahn, Olsson, & Norberg, 2005; Lemos & Agrawal, 2006). It is not known from this study how the variable for site (survey area) is influencing the distribution of each of the three of the focal medium prey species (paca, agouti, and coati) individually; further investigation and modeling each species independently would be beneficial to determine this. Model averaged occupancy was also 33.3% lower for medium prey species compared to large ones. Additional research to evaluate abundance of medium prey would aid in comprehending if these results were due to actual lower abundance of medium species overall, if they are simply more difficult to detect using spoor sampling, or if they are abundant, but simply concentrated in specific areas throughout the reserve.

There are many other significant anthropogenic pressures that need to be considered to gain a full perspective on the factors influencing the distribution of the focal species in the CBR. Further sampling and investigation should occur to gather data for modeling occupancy as a function of the following factors: proximity to roads, settlements (ejidos), agriculture, livestock, and core zone (Negroes et al., 2010; Petracca et al., 2014; Zeller et al., 2011); number of settlements (Zeller et al., 2011); hunting rates of each species; recent forest disturbance (e.g. burns/cuts of forest in a given time period) (Poley et al., 2014); and proportion of open areas (Zeller et al., 2011). Expanding the sampling area to include areas beyond the reserve would also aid in evaluating the degree to which these factors are influencing the distribution of focal prey, as it would provide a diverse range of levels of disturbance from very minimal (core zone) to quite high (outside the reserve).

3.5 Conclusions

In this chapter, my main objective was to use hierarchical occupancy modeling to investigate if prey species are non-randomly distributed across a tropical region and how natural and anthropogenic landscape features are influential in shaping this distribution. I found that distribution appears to be random for brocket and white-tailed deer species, is largely random for collared peccary, and non-random for white-lipped peccary, large prey as a group, and medium prey species collectively. While this study provides much needed insight into how both natural and anthropogenic landscape features are influential in shaping the distribution of valued prey in Campeche, and in the CBR, there is still deficient knowledge about the status of these species. Reserves such as the CBR provide an opportunity for critical protection of global and local biodiversity (Chazdon et al., 2009; Smardon & Faust, 2006), as well as focal prey species and large carnivores, which are fundamental for supporting dynamic tropical ecosystems (Ripple et al., 2014). As such, the value of further research in the CBR and the need to conserve and restore critical habitat for keystone species such as the white-lipped peccary cannot be ignored.

Chapter 4 Occupancy Modeling to Assess the Influence of Prey Occupancy and Natural and Anthropogenic Landscape Variables on the Distribution of Jaguar *Panthera onca* and Puma *Puma concolor*

4.1 Introduction

In the past four decades, both biodiversity and individual populations of numerous species in the tropics have consistently declined (Butchart et al., 2010). Large carnivores have been particularly affected, with 17% of species listed as threatened, including 20% of all felid species (Zarco-González et al., 2013, 2012). The troubled status of wild cats can be attributed to many factors including: deforestation, especially of tropical forests (Wright & Muller-Landau, 2006); habitat fragmentation from development, agriculture, roads and trails (Zeilhofer et al., 2014); hunting and poaching (Hoffmann et al., 2010; Reyna-Hurtado & Tanner, 2007; Rodríguez-Soto et al., 2013), and human-wildlife conflict (Erb et al., 2012; Schuette et al., 2013). Populations of large cats are vulnerable to anthropogenic pressures as they occur at relatively low densities, and they require sizeable home ranges, which are often fragmented by human-modified landscapes (Hoffmann et al., 2010; Srivathsa et al., 2014; Zanin et al., 2014). Perceptions that they pose a threat to human livelihood and life also put large felids at risk for conflict with people (Inskip & Zimmermann, 2009; Schuette et al., 2013; Zeller, 2007).

Maintaining healthy populations of both felids and prey is crucial for supporting dynamic ecosystems, as the loss of felid predators can have trophic cascade effects (Angelieri, Adams-Hosking, Ferraz, de Souza, & McAlpine, 2016; Ripple et al., 2014). Changes in the status of wild cat populations can have trophic effects on pollination and pollinators, seed dispersal, seed predators, folivores, mesopredators, woody plant recruitment, bird abundance, and soil carbon/nitrogen ratios (Jorge et al., 2013; Ripple et al., 2014; Salo et al., 2010). Prey abundance conversely impacts felids, for example by influencing reproduction by delaying the age of first reproduction, reducing litter sizes, and increasing mortality of offspring and adults (Foster et al., 2010; Fuller & Sievert, 2001). Prey occupancy also can lead to an expansion of felid home ranges, as female cats will increase their home range in response to diminished prey availability and male felids will in turn expand their range to follow the females. This results in a higher proportion of transient and dispersing individuals, which negatively influences viability (Conde et al., 2010; Fuller & Sievert, 2001; Stander et al., 1997). Other factors such as habitat disturbance or conflict with humans may also play a role in influencing distribution of wild cats in some circumstances (Woodroffe, 2001). In order to identify crucial felid habitat for protection and/or restoration and to understand how each of these factors, (anthropogenic pressures, landscape features, and prey availability), impact wild cats, we need tools, such as ecological models, that describe how these elements influence felid distribution. Hierarchical occupancy modeling that incorporates imperfect detection is one method used to evaluate how these variables determine occupancy of felid species (Arroyo-Arce et al., 2014; Fiske et al., 2014; Srivathsa et al., 2014).

As the Neotropics' largest and second largest top predators, jaguars *Panthera onca* and pumas *Puma concolor* are critical for maintaining ecosystem functioning and dynamics (Jorge et al., 2013). In this chapter my objective was to investigate if jaguars and pumas are non-randomly distributed across a tropical region and how natural and anthropogenic landscape features, as well as prey occupancy, are influential in shaping this distribution. It was hypothesized that prey occupancy will have a greater effect on the occupancy of jaguars and pumas than landscape characteristics do because felid distribution is thought to largely depend on prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Stander et al., 1997). Jaguars and pumas are sympatric species throughout most of Central and South America (Novack et al., 2005). Jaguars are the third largest cat in the world and the largest in the Americas; however, there is an overall lack of knowledge of the status of this Near Threatened species (Caso et al., 2015; Zeller, 2007). While pumas are listed by the IUCN as a Species of Least Concern, they are classified as Near Threatened in Brazil and as Vulnerable outside the Amazon Basin. Like the jaguar, little is known about the status of pumas (Negroes et al., 2010; Nielsen et al., 2015).

This study was conducted in the Calakmul Biosphere Reserve (CBR), which is located in the state of Campeche in Mexico. The reserve has become significant for the provision of some of the last remaining habitat for jaguars and pumas. It contains the greatest protected area of tropical forest (723,185 hectares) in Mexico and also has the largest wild feline population in North America (Colchero et al., 2011; García-Frapolli et al., 2009). In this chapter, I used hierarchical occupancy modeling to assess the relative influence of landscape variables and prey occupancy in determining the distribution of jaguars and pumas within the CBR. The prey species chosen for modeling were selected based on a priori knowledge that they are principle components of both cats' diets in tropical regions (de Azevedo & Murray, 2007; de Oliveira, 2002; Foster et al., 2010; Polisar et al., 2003). Prey species included: white-lipped peccary *Tayassu pecari*; collared peccary *Pecari tajacu*; brocket deer [the red *Mazama americana* and gray *M. Pandora* brocket deer (referred to as brocket deer *Mazama sp.* hereafter)], white-tailed deer *Odocoileus virginianus*; lowland paca *Cuniculus paca*; Central American agouti *Dasyprocta punctate*, and white-nosed coati *Nasua narica*. I focused on four variables that were hypothesized to influence occupancy of the focal species: distance to aguada (m); total basal area (m2); tree species richness, and site, which encompassed each of the four survey areas as levels and represented different scales of anthropogenic disturbance (hunting in particular) (Foster et al., 2010; Peres, 1996; Petracca et al., 2013; Reyna-Hurtado et al., 2010; Reyna-Hurtado & Tanner, 2007; Sollmann et al., 2012; Zeller et al., 2011). Jaguar probability of occurrence increases with closer proximity to a water source, whereas pumas are largely habitat generalists, with no overall strong habitat preference (Sollmann et al., 2012; Zeilhofer et al., 2014).

Occupancy modeling is an effective method for acquiring valuable information on the influence of landscape variables on large carnivore distribution (Harmsen et al., 2009; Reed, 2011; Stander, 1998). Specifically, density and occupancy studies for jaguars and pumas have been done throughout Central and South America (Ahumada et al., 2013; Negroes et al., 2010; Núñez-Pérez, 2011; Petracca et al., 2013; Rosas-Rosas & Bender, 2012; Silver et al., 2004; Sollmann et al., 2012; Zanin et al., 2015; Zeller et al., 2011). Despite the widespread usage of occupancy modeling, there is very little research on how prey occupancy is influential in shaping the distribution of large carnivores. When prey variables are incorporated into modeling it is often done using indices such as overall prey biomass or density (Karanth et al., 2011; Midlane et al., 2014; Negroes et al., 2010; Robinson et al., 2014), general presence or absence of prey (Alexander et al., 2015; Harihar & Pandav, 2012; Petracca et al., 2013), photo-trap rates (Sunarto et al., 2015), or prey richness (Negroes et al., 2010; Zanin et al., 2015). My study provides insight into how both natural and anthropogenic landscape features, and prey occupancy, are influential in shaping distribution of jaguars and pumas within Mexico. The current extent of knowledge on distribution patterns for these cats in Campeche includes general linear modeling for jaguars for a study area that encompassed part of the CBR (Conde et al., 2010), geographic ensemble risk models for jaguar and puma for all of Mexico (Zarco-González et al., 2013), and Bayesian movement models for behaviour of jaguars in the Mayan Forest, which included part of Campeche (Colchero et al., 2011). My research adjoins the handful of studies that model occupancy of jaguars and pumas in Mexico and it is also the first of its kind to incorporate latent occupancy of prey species as a covariate in occupancy models for these cats.

4.2 Methods

4.2.1 Survey Site

Refer to section 3.2.1 for study area information.

4.2.2 Survey Design

Refer to sections 3.2.2 for detailed methods on line transect and habitat surveys. Transects were surveyed for spoor (animal tracks or scat samples), and the identity of the species that produced it, and other variables (i.e. substrate) were recorded (Soto Navarro et al., 2012). Each transect was surveyed at least four times totaling a distance of 160.2km of transects covered. To prevent double counting of the same track, sampling of each transect was completed with a minimum of 48 hours between sampling occasions for all but one survey of transect 2 in Mancolona, which was 24 hours (Funston et al., 2010). Observations for transect 2 in Mancolona were checked for duplicate recordings of the same track, with none found. Three transects were sampled repeatedly within approximately 48 hours and the rest were all resurveyed with at least three days between surveys. Finally, tracks were erased by disturbing the substrate after recordings were made of the width, length, age, leaf litter depth, distance along the transect and GPS coordinates (Keeping, 2014; Slater, 2014). If the source of spoor was ambiguous, the observation was not recorded. To minimize potential observer bias, observers were rotated for each survey between the different transects and lead observers worked with the teams to ensure that survey protocols and data collection methods were strictly maintained.

The observation or lack of observation of spoor indicated the presence or absence (detection-nondetection) of target species. Spoor detection has been used to survey prey species, such as ungulates (D’Eon, 2001), and was thus used in this study for white-lipped peccary, collared peccary, brocket deer, white-tailed deer, lowland paca, Central American agouti, and white-nosed coati. The prey species chosen for modeling were selected based on a priori knowledge of prey preferences of jaguar and puma. Previous findings indicate that deer, peccary, agouti, coati, and paca were principle components of both cats' diets (de Azevedo & Murray, 2007; de Oliveira, 2002; Foster et al., 2010; Polisar et al., 2003). Spoor detection has also been used to survey for large felids, such as leopards, lions, tigers, and cheetahs (Funston et al., 2010; Hines et al., 2010; Houser, Somers, & Boast, 2009; Stander, 1998) and was used in this study for jaguars and pumas.

Detection-nondetection data were compiled into detection histories for every 50m of the sampled transects to form individual sites (n). Each sample site (n) was designated with a 0 (absence/nondetection) or a 1 (presence/detection), of the target species for each sample period (T) (also know as a rep). For example, a detection history of 00000 would imply that the sample site was unoccupied by the target species, or else it was occupied, but the species was not detected during the sample periods. Detection histories were developed for each of the large prey species (brocket deer, white-tailed deer, collared peccary, and white-lipped peccary), for large prey combined (>15kg, included deer and peccary), for medium prey combined (2-15kg, included agouti, coati, and paca), and all the prey species together. Due to scarce detections for jaguar and puma, the detection histories of both were merged into one archetypal "species" of interest, referred to henceforth as "predator" (Ahumada et al., 2013; Alldredge, Pollock, Simons, & Shriner, 2007; Dunstan, Foster, & Darnell, 2011; Picard, Mortier, Rossi, & Gourlet-Fleury, 2010). In order for models to converge, a minimum number of detections (recaptures or observations) are required, due to adjustments for imperfect detection (Banks-Leite et al., 2014). The decision to pool jaguar and puma data together was based on low detection frequency, the presumed need for comparable management strategies (Novack et al., 2005), shared prey preferences (de Oliveira, 2002; Foster et al., 2010) and habitat preferences (Foster et al., 2010; Harmsen et al., 2009). Also, differentiating between the tracks of jaguars and pumas is extremely difficult; it can be reliably done if at least one of each the hind and front foot is present, and both idiosyncratic features and quantitative measurements taken (Rosas-Rosas & Bender, 2012). As this protocol was not followed for this study, differentiation could not have been reliably guaranteed, which further supports the decision to merge the detection histories for these species.

4.2.3 Modeling Approach

Occupancy is simply the proportion of a study area that is occupied by the species of interest whereas; abundance is the total number of individuals in a population. Occupancy modeling is widely used globally as a surrogate to abundance and as an aid for informing conservation decision-making (Hines et al., 2010; Mackenzie et al., 2006; Welsh et al., 2013). Occupancy estimation sampling usually requires less effort than abundance surveys and is sometimes the only viable option for rare species (e.g. jaguar), where it would be essentially impossible to estimate abundance (Mackenzie et al., 2006; Zeller et al., 2011). Detection probability (ρ), which is the likelihood that an individual will be detected, is an important consideration when developing occupancy estimates as it cannot be explicitly known that all members of a species in the sample area will be sampled (Fiske & Chandler, 2011; Mackenzie et al., 2006). Because individuals may be present but not actually detected (imperfect detection), a naïve count will underestimate the true proportion of sites that are occupied (MacKenzie et al., 2002; Mackenzie et al., 2006). This can be overcome however, by the use of occupancy models. These models utilize a detection history to calculate a detection probability, which is then applied to adjust the naïve occupancy and to give an estimate of occupancy probability (φ). The occupancy probability can be interpreted as the probability of a site being occupied or as the proportion of the site that is likely occupied (Midlane et al., 2014).

Hierarchical occupancy modeling offers a unified framework for analysis that uses repeated presence-absence (detection/non-detection) data to model and adjust for the detection process (Kery et al., 2012; Welsh et al., 2013). It recognizes that two processes influence observations: the first is a state process, which determines occupancy at each site, while the second is a detection (observation) process, that yields observations that are provisional on the state process (Fiske & Chandler, 2011; Kery et al., 2012). A Bernoulli distribution describes both of these state processes by combining the canonical model for species occurrence and imperfect detection. Because the second is conditional on the first, the false positive errors are essentially negated (Kery et al., 2012).

The occupancy model for the state process is:

$$z_i \sim \mathit{Bernoulli}\ (\varphi)$$

The occupancy model for the detection process is:

$$y_{ij} \sim \mathit{Bernoulli}\ (z_i \rho_{ij})$$

The latent variable z_i represents the true state of occurrence at site i, φ is the expected value of z_i, y_{ij} is the observed value of occurrence at site i during survey j, and ρ_{ij} is the detection probability of the all individuals of a species at site i during survey j. The site-occupancy model can be interpreted as a hierarchical extension to a Bernoulli generalized linear model (GLM), logistic regression, or two linked GLMs (Kery et al., 2012). Five main assumptions were considered for occupancy modeling: population closure; no false positive errors; independent detections, homogeneity of detections, and that that the two Bernoulli distributions for occupancy and detection were a reasonable abstraction of reality (Kery et al., 2012; Mackenzie et al., 2006).

Occupancy modeling was completed in the 'unmarked' package in R (Fiske et al., 2015; R Development Core Team, 2010). This package fits hierarchical models of animal occupancy to data that incorporates imperfect detection (Fiske et al., 2014). The probability distribution of the observed data [Pr(x | θ)], where x denotes the data and θ denotes the parameters, can be viewed as a function of the parameters conditional on the data, which is the likelihood function [L(θ | x)]. Maximum likelihood estimators (MLEs) are the values of the parameters that maximize the function, or make the data most likely given the underlying model (Mackenzie et al., 2006). The package 'unmarked' employs model-fitting functions that are specific to particular sampling methods and finds the MLEs of the parameters in the model (Fiske & Chandler, 2011). For this study a single-season site occupancy model (MacKenzie et al., 2002) that handles detection/non-detection data was used with the fitting function 'occu' (Fiske & Chandler, 2011).

4.2.4 Incorporating Covariates Into Occupancy Models

4.2.4.1 Modeling Occupancy as a Function of Covariate

Refer to section 3.2.5.1 for a detailed description of the facilitation of modeling occupancy as a function of covariates through a logit link function. For this study, only site-level covariates were included as the primary focus was on occupancy of jaguar and puma as a function of habitat features and prey occupancy, rather than on detection. Refer to Table 4-1 for a summary of each covariate. Detection was held constant for all models, under the assumption that the covariates commonly modeled for detection would be found to have negligible influence. For example, the affect of observer on detection was not a concern as multiple observers were rotated for each survey between the different transects. The use of trained researchers and/or experienced volunteers within different observer groups has been shown to minimize variation of observations between surveys (Darwall & Dulvy, 1996; Edgar & Stuart-Smith, 2009). The pairing/grouping of observers together has also been found to minimize the effects of identification errors and improve accuracy of data through consultation and discussion of observations (Bernard et al., 2013). Also, several (>4) replicate surveys were completed for each transect, which reduced the problem of imperfect detection by minimizing the likelihood of not detecting a species despite the site being occupied (Guillera-Arroita et al., 2014). Finally, the detection process is accounted for in the inherent nature of a single-state site occupancy model through the incorporation of the canonical model for imperfect detection (Kery et al., 2012).

4.2.4.2 Covariates Selected for Study

The variable "site" was considered a categorical factor variable with each of the four survey areas: KM20 (km20); Zona Núcleo Sur (zns); Mancolona (man), and Hormiguero (horm) as the levels. Continuous site-level variables included distance to aguada (m), total basal area (m2), tree species richness, large (>15kg) prey latent occurrence state (z) (peccary and deer); medium (2-15kg) prey z (pacas, agouti, and coati), all prey z, and finally individual large prey species z (brocket deer, white-tailed deer, collared peccary, and white-lipped peccary. Latent occurrence states for each prey species and groups of prey were derived from an estimate for z using function 'ranef' in R (Kéry & Royle, 2016; R Development Core Team, 2010). Function 'ranef' used empirical Bayes methods and incorporated the data, as well as the MLE's to estimate the posterior distribution of z (Fiske & Chandler, 2010). Occupancy of predator was then modeled as a function of the estimates of z for the prey species, thereby incorporating occupancy of prey as a covariate (Kery et al., 2012).

The covariates chosen for modeling were selected based on a priori knowledge of prey and habitat preferences of jaguar and puma. Previous studies have found that deer, peccary, agouti, coati, and paca were principle components of both cats' diets (de Oliveira, 2002; Foster et al., 2010; Polisar et al., 2003). Collared peccaries prefer areas of higher basal area, agoutis prefer higher tree species diversity, and greater paca density has been shown in areas proximal to a water source (Foster et al., 2010; Sollmann et al., 2012). Jaguar occurrence has also been found to be positively influenced by proximity to a water source, whereas pumas have been found to be generalists, with no overall strong habitat preference (Sollmann et al., 2012; Zeilhofer et al., 2014).

Standardization of continuous variables was completed to improve performance of the models and also to facilitate comparison of coefficients. Standardizing the variables essentially makes them unit less thus allowing for comparison based on relative size (Mackenzie, 2012; Sardy, 2008). The continuous covariates (distance to aguada (m), total basal area (m2), and tree species richness) were standardized using a z-transformation (Harihar & Pandav, 2012; Negroes et al., 2010) as follows:

$$\chi_i = \frac{\chi_i - a}{b}$$

The variable χ_i is the observed value for the covariate, a is the mean of the covariate values, and b is the standard deviation (Mackenzie, 2012).

4.2.4.3 Data Exploration

Variance inflation factor (*VIF*) was used to check for collinearity between variables. The *VIF* for a variable, *Xj* is the square root of the inverse of the R^2_j value of the regression of the variable *Xj* against all of the other explanatory variables (Zuur et al., 2010).

$$VIF_j = \sqrt{\frac{1}{(1 - R_j^2)}}$$

Collinearity was indicated by high *VIF* values, as this suggests that most of the variation in the variable can be explained by the other covariates. To resolve this issue, a preselected *VIF* threshold was chosen. I used a conservative value of <3. Variables with *VIF*s >3 were sequentially removed one at a time with the highest ones removed first and then the analysis repeated until only variables with a *VIF*<3 remained (Zuur et al., 2010). This was completed using source ("HighstatLib.R") and the function 'corvif' in R (R Development Core Team, 2010; Zuur et al., 2010). Variables not shown to be collinear were then included in global models for the target species.

Boxplots and Cleveland dotplots were created in R and utilized to visualize the spread of the data and inspect for outliers (R Development Core Team, 2010). Data were checked for errors when possible outliers were apparent.

4.2.5 Model Fitting and Selection

A global model was created encompassing all possible covariates (Burnham & Anderson, 2002; Mackenzie et al., 2006). Because the global model was the most highly parameterized, if this model fit the data adequately then it would be inferred that any models that were less parameterized and thus more parsimonious would also fit the data (Burnham & Anderson, 2002; Cooch & White, 2002). The global model was used to compute estimates of overdispersion and evaluated for goodness-of-fit using methods developed by Mackenzie and Bailey (2004). The R package 'AICcmodavg' incorporated the model and detection histories, along with a parametric bootstrap approach, (with 1000 bootstrap samples), to compute observed and expected values, the Pearson chi-square (X^2) test statistic and to estimate an overdispersion parameter (ĉ). Overdispersion was indicated if ĉ>1, underdisperison if ĉ <1, and lack-of fit demonstrated if ĉ>4 (Durso et al., 2011; Mackenzie & Bailey, 2004; Mazerolle, 2015). If ĉ for the global model was >1 then the value of ĉ was applied to all subsequent models derived from the global model. If ĉ <1 then the model was run without adding the overdispersion parameter and ĉ was fixed at one (Mazerolle, 2015).

Models included constant occupancy and detection and also incorporated occupancy as a function of the covariates. To choose the models that best fit the data, Akaike's Information Criterion (AIC) was used, as this method has become increasingly prevalent and beneficial for analyzing ecological data (Durso et al., 2011; Hines et al., 2010; Karanth et al., 2011; Mackenzie & Bailey, 2004). The most parsimonious models for the data were identified by minimizing the AIC values. Rather than selecting models based on the absolute magnitude of AIC value, the differences in AIC (ΔAIC) among the various models were evaluated (Mackenzie et al., 2006). For this study AICc, which is AIC with an adjustment for small sample size, was used. Models with a delta AICc (ΔAICc) <2 had substantial empirical support, those with values between 4 and 7 had substantially less support, and those with a difference >10 essentially had no support (Burnham & Anderson, 2002; Reed, 2011). AICc values also form the basis for AICc weights (AICc*w*), which sum to 1 for all models of the set. These were used again to assess models and covariates to determine which ones had more support and relative goodness-of-fit (Petracca et al., 2013).

Modeling was done with a hierarchical approach. Models incorporating occupancy as a function of habitat covariates were first modeled separately from those that incorporated prey z. Models with AICc*w* that summed to 90% and/or had a ΔAICc <2 were selected for further analysis, eliminating any with uninformative parameters (Arnold, 2010; Harihar & Pandav, 2012). A final set of models was created using the chosen top-performing models from the previous analyses that incorporated both habitat covariates and latent occurrences. For example ρ(.)ψ(brock+med+aguada). Models were ranked by AICc and AICc*w* and top-performing models identified by a ΔAICc <2. The relative importance of each covariate was evaluated by comparing the sum of the AICc*w* of each variable. Those with a value greater than 0.5 were considered to have the most statistical support (Burnham & Anderson, 2002; Erb et al., 2012; Wang et al., 2015).

Rather than trying to identify the best model, the aim of the analysis was to produce a set of top ranking models that would best explain the data and could be used for multimodel inference via model averaging (Burnham & Anderson, 2002). Model averaging was conducted from the models with an AICc*w*~90% in the R package 'MuMin' (Barton, 2015) where the averaged coefficient estimate ($\hat{\hat{\beta}}_\imath$) was calculated from the candidate models in which the parameter of interest appeared as follows (Symonds & Moussalli, 2011):

$$\hat{\hat{\beta}}_\imath = \frac{\sum_{i=1}^{R} w_i \hat{\hat{\beta}}_\imath}{\sum_{i=1}^{R} w_i}$$

The Bayes estimate of the Probable Area Occupied (PAO) was derived from the empirical best-unbiased predictor (EBUP) using the top-performing model, which is the mean of the posterior distribution using the package ‘lattice’ in R (R Development Core Team, 2010). The PAO was compared to the population-level estimates of occupancy, as PAO represents the proportion of sample sites occupied, whereas occupancy is an estimate for an infinite number of sites (Fiske & Chandler, 2010).

4.3 Results

Eleven covariates were assessed for collinearity using *VIF* values. Correlation with the variable for “all prey *z*” (the latent occurrence of all prey grouped together) was found to be too high for the function to work. In Chapter 3 I found that occupancy estimates for the target prey species were significantly higher for large prey (>30% greater) compared to medium prey, thus I concluded that occupancy of the group “all prey” was likely primarily influenced by occupancy of large prey. Furthermore, occupancy of the groups “large prey” and “all prey” were essentially the same. Due to the aforementioned reasons, it was decided that the variable “all prey *z*” could be eliminated from further analysis. The covariate for site had a *VIF* of 3.6724, and was thus eliminated and the calculation of *VIF* for the remaining variables completed again. Once the variable for site was removed, all remaining covariates had a *VIF* <3 (Table 4-1). The global model was created from the remaining covariates:

$$\rho(.)\psi(\text{aguada+rich+basal+brock+whit+col+lip+med+lg})$$

Boxplots and Cleveland dotplots for each covariate are displayed in Chapter 3.3 Figure 3-5. (Note: data were ordered by site (Hormiguero, Zona Núcleo Sur, Mancolona, and KM20)). Outliers were not discovered and any points that appeared to be possible outliers were found to not likely be as a result of survey error.

Results for goodness-of-fit testing of the global model showed underdisperison with a ĉ of 0.8025 (Table 4-2). Subsequent models derived from the global model were run without adding an overdispersion parameter and ĉ was fixed at one (Mazerolle, 2015).

Table 4-1: Variance inflation factors (*VIF*) for each variable, [site, distance to an aguada (m), total basal area (m^2), tree species richness, brocket deer latent occurrence (*z*), white-tailed deer *z*, collared peccary *z*, white-lipped peccary *z*, medium prey (lowland paca, Central American agouti, and coati combined) *z*, and large prey (deer and peccary species) *z*], included in the occupancy models for predator (jaguar and puma combined) from survey data from Calakmul Biosphere Reserve, Mexico.

Covariate	Abbreviation	Type	VIF_1	VIF_2
distance to an aguada	aguada	continuous site-level numeric	1.6789	1.1372
tree species richness	rich	continuous site-level numeric	1.4600	1.0886
basal area	basal	continuous site-level numeric	1.1357	1.1054
brocket deer	brock	continuous site-level numeric	1.9838	1.9628
white-tailed deer	whit	continuous site-level numeric	1.8338	1.6188
collared peccary	col	continuous site-level numeric	1.6052	1.4853
white-lipped peccary	lip	continuous site-level numeric	1.2095	1.1910
medium prey	med	continuous site-level numeric	1.8536	1.4787
large prey	lg	continuous site-level numeric	2.2067	1.8571
site	site	categorical factor (4 levels)	3.6724	

Table 4-2: Pearson chi-square (X^2) test statistic, p-value, and overdispersion parameter (ĉ) for the global model of site occupancy estimates (ψ) for predator (jaguar and puma combined) using survey data from Calakmul Biosphere Reserve, Mexico. Model estimated as a function of distance to an aguada (m), total basal area (m^2), tree species richness, and latent occurrence states (*z*) for brocket deer, white-tailed deer, collared peccary, white-lipped peccary, medium prey (lowland paca, Central American agouti, and coati), and large prey (deer and peccary species).

Binomial Name	Common Name	Functional Group	X^2	p	ĉ
Panthera onca	jaguar	predator	10.7798	0.674	0.8025
Puma concolor	puma				

Six models from the first candidate set of models for occupancy as a function of habitat characteristics all had a ΔAICc<2 and also summed to a total AICc*w* of ~90%; therefore, these were included in further modeling (Table 4-3).

Of the models that incorporated prey *z* as variables (Table 4-4), the AICc*w* for models containing brocket deer, white-tailed deer, and medium prey summed to 90%; however, white-tailed deer had a ΔAICc>2. To confirm the decision to exclude this variable from further models, AICc*w* of each variable was assessed. The AICc*w* for white-tailed deer *z* was 0.07, indicating a lack of importance for this variable influencing occupancy of predator; therefore, the covariate was excluded. The AICc*w*s for large prey, collared peccary, and white-lipped peccary *z* showed lack of substantial influence on occupancy of predator as well with values of 0.05, 0.04, and <0.01, respectively.

A final candidate set of 27 models was created that incorporated both habitat features and *z* estimates together, as well as separately. Twelve models had a cumulative AICc*w* of ~90%, with six having a ΔAICc <2 (Table 4-5). The relative importance values and β estimates for each variable were calculated from the 12 models in Table 4-5. Three of the five covariates had AICc*w*>0.5: brocket deer *z* (0.92), medium prey *z* (0.78), and distance to aguada (0.51) (Table 4-6). Latent occurrence of both brocket deer and medium prey had a positive influence on occupancy of predator. Proximity to an aguada had a negative influence with lower occupancy of predator at closer proximities to water.

A summary of the most predictive models (ΔAICc<2) is displayed in Table 4-7. Occupancy of predator in the reserve was estimated at a minimum of 0.0190 and a maximum of 0.0363. The model averaged occupancy was 0.0292, which was substantially lower than the PAO of 0.6635.

Table 4-3: First candidate set of occupancy models for predator (jaguar and puma combined) using survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant occupancy (ψ) and detection (ρ), and habitat characteristics (distance to aguada (m), total basal area (m^2), and tree species richness). Model criterion includes Akaike's Information Criterion adjusted for small sample size (AICc), delta AICc (ΔAICc), AICc weights (AICc*w*), twice the negative log-likelihood value (-2log(LL)), and the number of parameters (*K*).

Model	AICc	ΔAICc	AICc*w*	-2 log(LL)	*K*
ρ(.)ψ(.)	320.89	0	0.256	316.72	2
ρ(.)ψ(aguada)	321.26	0.373	0.213	314.93	3
ρ(.)ψ(rich)	322.16	1.275	0.136	315.83	3
ρ(.)ψ(aguada+rich)	322.74	1.853	0.102	314.18	4
ρ(.)ψ(aguada+basal)	322.77	1.881	0.100	314.20	4
ρ(.)ψ(basal)	322.83	1.948	0.097	316.50	3
ρ(.)ψ(rich+basal)*	324.15	3.260	0.050	315.58	4
ρ(.)ψ(aguada+rich+basal)*	324.31	3.419	0.046	313.45	5

*Models excluded from further consideration due to ΔAICc>2

Table 4-4: Second candidate set of occupancy models for predator (jaguar and puma combined) using survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant occupancy (ψ) and detection (ρ), latent occurrence states (*z*) for individual prey species (brocket deer, white-tailed deer, collared peccary, white-lipped peccary), medium prey combined (lowland paca, Central American agouti, and coati), and large prey combined (deer and peccary species). Model criterion includes Akaike's Information Criterion adjusted for small sample size (AICc), delta AICc (ΔAICc), AICc weights (AICc*w*), twice the negative log-likelihood value (-2log(LL)), and the number of parameters (*K*).

Model	AICc	ΔAICc	AICc*w*	-2 log(LL)	*K*
ρ(.)ψ(brock)	311.49	0	0.647	305.16	3
ρ(.)ψ(med)	314.00	2.511	0.184	307.67	3
ρ(.)ψ(whit)*	316.05	4.557	0.066	309.71	3
ρ(.)ψ(lg)*	316.59	5.106	0.050	310.26	3
ρ(.)ψ(col)*	317.00	5.506	0.041	310.66	3
ρ(.)ψ(.)	320.89	9.397	0.006	316.72	2
ρ(.)ψ(lip)*	321.53	10.044	0.004	315.20	3

***Models excluded from further consideration due to ΔAICc>2**

Table 4-5: Final candidate set of occupancy models for predator (jaguar and puma combined) using survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of habitat characteristics (distance to aguada (m), total basal area (m^2), and tree species richness), and latent occurrence states (*z*) for brocket deer and medium prey species combined (lowland paca, Central American agouti, and coati). Model criterion includes AICc, delta AICc (ΔAICc), AICc weights (AICc*w*), twice the negative log-likelihood (-2log(LL)), and the number of parameters (*K*). Only models totalling to a cumulative AICc*w* of ~90% are shown.

Model	AICc	ΔAICc	AICc*w*	-2 log(LL)	*K*
ρ(.)ψ(brock+med)	309.45	0	0.163	300.89	4
ρ(.)ψ(brock+med+aguada)	309.46	0.009	0.162	298.60	5
ρ(.)ψ(brock+med+aguada+basal)	309.99	0.537	0.124	296.77	6
ρ(.)ψ(brock+med+aguada+rich)	310.67	1.219	0.089	297.45	6
ρ(.)ψ(brock+med+rich)	310.84	1.391	0.081	299.98	5
ρ(.)ψ(brock+med+basal)	311.44	1.987	0.060	300.58	5
ρ(.)ψ(brock)	311.49	2.041	0.059	305.16	3
ρ(.)ψ(brock+aguada)	311.80	2.351	0.050	303.24	4
ρ(.)ψ(brock+med+rich+basal)	312.83	3.378	0.030	299.61	6
ρ(.)ψ(brock+rich)	312.90	3.456	0.029	304.34	4
ρ(.)ψ(brock+aguada+basal)	313.18	3.736	0.025	302.33	5
ρ(.)ψ(brock+basal)	313.58	4.129	0.021	305.01	4

Table 4-6: Relative importance (sum of AICc*w*), model averaged β estimates with standard error, and direction of influence (+ve or –ve) for each variable, [latent occurrence states (*z*) for brocket deer and medium prey species (lowland paca, Central American agouti, and coati combined), distance to an aguada (m), total basal area (m^2), and tree species richness], derived from the top-performing models (AICc*w*~90%) of the final candidate set of occupancy models for predator (jaguar and puma combined).

Covariate	Relative Importance	β estimate	Unconditional SE
brocket deer *z*	0.92	3.199	1.442
medium prey *z*	0.78	2.201	1.158
distance to an aguada	0.51	0.820	0.663
basal area	0.29	-0.412	0.459
tree species richness	0.28	-0.452	0.512

Table 4-7: Most predictive models of site occupancy estimates (ψ) of predator (jaguar and puma combined) as determined by delta Akaike's Information Criterion adjusted for small sample size (ΔAICc) <2 for survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of distance to an aguada (m), total basal area (m^2), tree species richness, and latent occurrence states (*z*) for brocket deer and medium prey combined (lowland paca, Central American agouti, and coati). The Probable Area Occupied (PAO) is included for comparison to ψ and model averaged ψ.

Model	ΔAICc	AICc*w*	ψ	SE(ψ)	ψ(avg)	PAO
ρ(.)ψ(brock+med)	0	0.163	0.0363	0.0472	0.0292	0.6635
ρ(.)ψ(brock+med+aguada)	0.009	0.162	0.0290	0.0412		
ρ(.)ψ(brock+med+aguada+basal)	0.537	0.124	0.0190	0.0322		
ρ(.)ψ(brock+med+aguada+rich)	1.219	0.089	0.0219	0.0362		
ρ(.)ψ(brock+med+rich)	1.391	0.081	0.0332	0.0455		
ρ(.)ψ(brock+med+basal)	1.987	0.060	0.0356	0.0470		

4.4 Discussion

Despite the widespread usage of occupancy modeling for jaguars and pumas throughout Central and South America (Ahumada et al., 2013; Negroes et al., 2010; Núñez-Pérez, 2011; Petracca et al., 2013; Rosas-Rosas & Bender, 2012; Silver et al., 2004; Sollmann et al., 2012; Zanin et al., 2015; Zeller et al., 2011), there is very little research on how prey occupancy explicitly influences the distribution of these carnivores within Mexico. In this study, I assessed the relative influence of landscape variables, as well as prey occupancy, in determining the distribution of jaguars and pumas within the CBR, through the use of hierarchical occupancy modeling. My results suggest that distribution in the CBR for jaguars and pumas as a pair is primarily influenced by the latent occupancy of brocket deer and medium prey species. Lower occupancy was found at sites closer to an aguada, suggesting that proximity to water may have a slight influence as well. As mentioned previously, due to scarce detections for jaguars and pumas, the detection histories of both were merged into one archetypal "species" of interest, referred to henceforth as "predator" (Alldredge et al., 2007; Dunstan et al., 2011; Picard et al., 2010).

I hypothesized that prey occupancy would have a greater effect on the occupancy of predator than landscape characteristics because felid distribution is thought to largely depend on prey availability (Bled et al., 2015; Fuller & Sievert, 2001; Stander et al., 1997). This hypothesis was supported by my results as predator occupancy was most influenced by latent occupancy of brocket deer (AICcw=0.92) and medium prey (AICcw= 0.78). While the diets of jaguars are highly variable their preferred prey species include paca, deer (white-tailed and brocket), peccary (white-lipped and collared), and coatis (Foster et al., 2010; Novack et al., 2005; Slater, 2014; Weckel et al., 2006). Brocket deer have been found to dominate the diets of pumas regularly and jaguars to a lesser degree (Foster, 2010; Novack et al., 2005). In order to maximize energy gain, jaguars and pumas will select prey with the largest body size that also has the least risk in hunting, or they will be opportunistic and take prey that is vulnerable and abundant, even if it is not substantially large in body size (Gómez-Ortiz & Monroy-Vilchis, 2013; Polisar et al., 2003). Occupancy modeling of focal prey species in Chapter 3 determined that model averaged occupancy was 0.865 for brocket deer, 0.843 for white-tailed deer, 0.842 for collared peccary, 0.642 for medium prey, and lowest for white-lipped peccary at 0.589. While white-tailed deer occupancy was similar to brocket deer, the larger body size of the white-tailed deer may actually be discouraging felid consumption. In hot humid tropical forests, such as in the CBR, decomposition of large prey items after a kill may limit selection of larger prey, as spoilage may inhibit maximizing energy gain (Foster et al., 2010). Collared peccary were found to essentially be as ubiquitous as deer; however, the costs of selecting them as prey may outweigh the energy benefits. Collared peccary live in groups and possess canine teeth that are almost as large as and as sharp as those of the jaguar (Polisar et al., 2003), which makes the potential for injury high when preying upon them (de Azevedo & Murray, 2007). These factors may be limiting the selection of white-tailed deer and collared peccary as a prey source, compared to the more ubiquitous, vulnerable, and fairly large sized brocket deer. In Chapter 3 it was determined that brocket deer were randomly distributed; because distribution of predator was found to be significantly affected by the latent occupancy of brocket deer it would be worthwhile to conduct two-species modeling detailed by

MacKenzie & Nichols (2004). This would allow for evaluation and quantification of the level of interaction between brocket deer and predator and to determine whether detection of one depends upon the presence of the other (Mackenzie et al., 2006, 2004).

While large prey provide the most caloric energy, medium prey that has the least risk associated with predation is often equally beneficial to supplement the diets of jaguars and as a primary food source for pumas (Novack et al., 2005; Polisar et al., 2003). This is supported by my results as the model incorporating medium prey as a covariate was a top-performing model; the relative importance of latent occupancy of medium prey of 0.78 further suggests that medium prey are quite influential in the distribution of jaguars and/or pumas in the CBR. This is not surprising for pumas as medium-sized mammals make up a substantial portion of their diets, especially when pumas are sympatric with jaguars (Foster et al., 2010; Gómez-Ortiz & Monroy-Vilchis, 2013). In the Cookscomb Basin Wildlife Sanctuary in Belize, jaguars took smaller prey and less variety of species in buffer zones where hunters likely had depleted the area of larger game species such as deer and white-lipped peccary (Foster et al., 2010). Furthermore, in areas where larger prey (white-lipped peccary and deer) is depleted from human hunting, medium prey species may contribute greatly to sustaining jaguar populations (Foster et al., 2010).

The distribution of predator was also possibly influenced by proximity to water with decreasing occupancy closer to aguadas. The relative importance of this variable (AICc*w*= 0.51) was just above the level at which it is considered relevant (AICc*w*=>0.5) (Burnham & Anderson, 2002). This result was surprising as higher occupancy of jaguars has been found with closer proximity to a water source due to increased prey presence (de Azevedo & Murray, 2007; Sollmann et al., 2012; Zeilhofer et al., 2014). Pumas are largely habitat generalists; however, the species can display a tendency to occupy drier areas, possibly because they are deterred by the higher jaguar presence around water (Angelieri et al., 2016; Sollmann et al., 2012). It is possible that by combining jaguar and puma detections into one detection history, the expected outcome of a selection for habitat with water by jaguars could have been masked by puma preference for drier areas. Additional data are needed to model each species independently to confirm this, as detections were too low for both species to be modeled separately.

Model averaged occupancy of predator was quite low at 0.0292, especially compared to the PAO of 0.6635. The PAO represents the proportion of sample sites occupied, whereas occupancy is an estimate for an infinite number of sites (Fiske & Chandler, 2010). While there are no other data available on occupancy estimates specifically for jaguars and pumas in Mexico it has been estimated at (0.156) for both species together in Emas National Park (ENP) in Brazil (Sollmann et al., 2012). Because tropical humid forests, such as those in Mexico, often have a richer diversity of medium and large-sized prey species compared to other types of tropical forest, higher density of jaguars and pumas may be expected (Núñez-Pérez, 2011). Several density studies in Mexico have determined that jaguar density in particular is on the high end of estimates for their home range overall (Núñez-Pérez, 2011); therefore, I would expect that occupancy estimates for jaguar and puma in the CBR would also be higher than, for example ENP in Brazil; however, this was not reflected in my study. Density estimates for jaguar in ENP were 0.3 to 0.6 individuals/100km2 (Sollmann et al., 2012), compared to estimates in Calakmul of 3.3 to 6.7 individuals/100km2 (Ceballos et al., 2002). A significant difference between the two reserves is that the ENP is ~1320km2 (Sollmann et al., 2012) whereas the CBR is ~7225km2 (Vester et al., 2007), providing substantially more area for the large home range requirements of jaguars and pumas (Hoffmann et al., 2010). As the main objective for this study was to investigate how jaguars and pumas are distributed across a tropical region, this wide disparity between the model averaged occupancy and the PAO was not considered further for this study. It would however, be worthwhile to investigate, as when species occupancy is low, actual and predicted abundances may not coincide (Khorozyan et al., 2008; Tosh, Reyers, & Jaarsveld, 2004). Furthermore, low occupancy estimates could be indicative of decreased abundance; however, it could also result from low detections. To maximize detection probability, the total sampling area in the CBR could be expanded in subsequent research from 16 transects (totaling 32km sampled) in this study, to 55 transects (55km sampled) (Licona et al., 2011) or even 90 transects (206km sampled) (Reyna-Hurtado & Tanner, 2007), reflecting the sample area found in similar spoor surveys for large mammals in the tropics.

Although necessary for this study, amalgamation of detection histories for jaguars and pumas into one archetypal "species" of interest (Ahumada et al., 2013; Alldredge et al., 2007; Dunstan et al., 2011; Picard et al., 2010) may be a limitation of this research. Because these cats can demonstrate dietary and habitat overlap to some degree (Foster et al., 2010; Novack et al., 2005), it makes it difficult to distinguish if the factors influencing distribution of the pair is affecting either or both species individually. Furthermore, whether the occupancy estimate for predator is influenced primarily by jaguar or by puma occupancy, cannot be determined without additional data. A long-term survey expanding on the methods used in this study over the course of at least a year is recommended to maximize detections of each species individually to allow for independent modeling (Karanth et al., 2011; Mackenzie et al., 2006), as non-invasive spoor sampling is especially useful for studying elusive and wide-ranging species, such as jaguars and pumas (Long, Donovan, MacKay, Zielinski, & Buzas, 2011; Reed, 2011; Stanley & Royle, 2005). Ceballos et al. (2002) conducted long-term camera trapping of jaguars from 1997 to 1999 to study population ecology in the CBR; this method could also be used alone or in conjunction with spoor sampling (Rosas-Rosas & Bender, 2012) to maximize detections for evaluating populations and occupancy in the study area for both jaguars and pumas (Arroyo-Arce et al., 2014; Harmsen et al., 2009; Negroes et al., 2010; Silver et al., 2004; Sollmann et al., 2012).

As data on the feeding ecology and predatory patterns of felids in the tropics are scarce (Novack et al., 2005), further research is needed to support my occupancy results and to gain a better understanding of how jaguars and pumas function as sympatric predators and individually in the CBR. In particular, exploration of the feeding ecology of jaguars and pumas in the study area would be beneficial for evaluating food habits of these cats in great detail. Genetic scat analysis of a sample size of around 100 samples would be a reliable method to describe the diets of both cats (Foster et al., 2010; Novack et al., 2005). Because large felids will demonstrate more selective diet choices when prey is abundant and less selective choices when prey is plentiful, feeding ecology studies can reflect relative scarcity or abundance of prey (Polisar et al., 2003). This would aid in the understanding of human-cat conflict in the CBR, as frequency of livestock predation is in part inversely related to availability of wild prey (Petracca et al., 2014; Polisar et al., 2003).

Currently, hunting in Calakmul is poorly regulated and it is not truly known how many individuals of prey species are being harvested (Santos-Fita et al., 2012; Slater, 2014). It is known however, that there have been significant reductions in the populations of hunted species documented over the past decade in the southern Yucatán (Vester et al., 2007), yet there is little understanding of how competition with human hunters for prey is impacting jaguars and pumas in the tropics (Novack et al., 2005). Model averaged occupancy of white-lipped peccary in the CBR was 0.589, which is 30% lower than the occupancy of collared peccary (Chapter 3). While there are no other data available on occupancy estimates for peccary in Mexico, Track Encounter Rates (mean number of tracks sighted in a kilometer of transect) for peccary in Calakmul were 72% higher for collared peccary than white-lipped peccary (Reyna-Hurtado & Tanner, 2007). The lower occupancy could be the results of human hunting as hunting pressure on white-lipped peccary in Calakmul has already impacted the species, reducing group sizes and even eliminating some groups completely (Reyna-Hurtado et al., 2010). Because white-lipped peccary are a primary prey source for jaguars and pumas (Altrichter et al., 2012), their lower status in the CBR is of concern as there is an increased prevalence of livestock depredation in areas where white-lipped peccary have declined (Cavalcanti & Gese, 2010; de Azevedo & Conforti, 2008). Seventy percent of all cattle depredation in the Mayan Forest is from male jaguars (Conde et al., 2010) and is thought that illegal poaching may be the biggest threat to their survival (Zarco-González et al., 2013). Gaining a better understanding of human-wildlife conflict in the study area is therefore critical for persistence of jaguars in the CBR (Conde et al., 2010). Data on the severity of the conflict with pumas in Mexico are scarce; therefore, further research on this would benefit conservation of puma greatly as well (Zarco-González et al., 2013). Identifying areas where conflict with humans and livestock depredation has already occurred, or is likely to occur in Calakmul is also necessary to understand why conflict is occurring and to prevent poaching of these cats from retaliation or from perceived threat (Conde et al., 2010). If these areas are isolated, preventive management techniques can be implemented to protect livestock, including: inhibiting livestock from entering the forest; installing electric fences around maternity pastures; moving livestock out of areas that are prone to flooding in the wet season to avoid crowding and isolation; limiting or eliminating forest clearing to provide a reservoir for prey, and finally, excavation of water retention ponds for prey species to elevate prey populations and potentially focus felid attention away from livestock (Polisar et al., 2003).

While jaguar and puma occupancy is largely influenced by prey availability, there are other variables that should be considered for further evaluation in the CBR to advance understanding of their distribution and to identify key areas for protection and/or restoration. Despite limitations on human disturbance in the core zone and much of the buffer zone, the ecosystems within and beyond the borders of these zones are still directly and indirectly affected by anthropogenic pressures (Chazdon et al., 2009). Subsequent research to build on the results of this study should incorporate additional spatial factors into models, such as: proximity to roads (Angelieri et al., 2016; Conde et al., 2010; Maehr, 2012), settlements (ejidos), agriculture, and livestock (Negroes et al., 2010; Petracca et al., 2014; Zeller et al., 2011); number of settlements (Zeller et al., 2011); recent forest disturbance (e.g. burns/cuts of forest in a given time period) (Poley et al., 2014), and proportion of open areas (Zeller et al., 2011).

4.5 Overall Conclusions and Recommendations

In this study, I assessed the relative influence of landscape variables (distance to aguada (m), total basal area (m2), tree species richness, and site, which encompassed each of the four survey areas as levels and represented different scales of disturbance) in determining the occupancy of jaguars, pumas (predator), and valued prey species (brocket deer, white-tailed deer, collared peccary, white-lipped peccary, paca, agouti, and coati) in the Calakmul Biosphere Reserve in Campeche, Mexico. I also incorporated latent occupancy estimates for focal prey into occupancy models for jaguars and pumas to evaluate the relative influence of prey occupancy on the distribution of these felids.

Occupancy models for brocket deer and white-tailed deer indicated that the variables selected for modeling were not influential in their distribution in the CBR. Collared peccary were largely randomly distributed; however, the distribution was weakly associated with increasing tree species richness. Model averaged occupancy of white-lipped peccary was 0.589, which is 30% lower than the occupancy of collared peccary, and lower occupancy was associated with decreased tree species richness and diminished total basal area, which could correspond to disturbed habitat. Follow up research would be beneficial to determine the origin of the landscape variations and the underlying causes of the reduction in habitat quality to evaluate why white-lipped peccary occupancy is lower in these areas. It is also recommended that long-term studies be conducted on the ranging patterns of white-lipped peccary in the CBR to support my results and to determine specifically which areas to prioritize for protection and/or restoration, if needed. And finally, a thorough evaluation of the hunting practices around the reserve should be completed, as currently, it is not known how many individuals of the focal species are being harvested (Santos-Fita et al., 2012; Slater, 2014).

Occupancy models for medium prey (paca, agouti, and coati) collectively suggest that they may not be abundant overall and/or their distribution is concentrated more in the core of the reserve. Further research is required to establish why medium prey occupancy is higher in undisturbed/unoccupied habitat to determine if there is a relationship between human occupation, and specifically hunting, and this distribution. Additional investigation and modeling of each species independently would aid in determining how the variable for site (survey area) is influencing each of the focal medium prey species individually. Model averaged occupancy was also 33.3% lower for medium prey compared to large prey. Additional research to evaluate the abundance of medium prey would aid in comprehending if these results were due to actual lower abundance of medium species overall, if they are simply more difficult to detect using spoor sampling, or if they are abundant, yet simply concentrated in specific areas throughout the reserve.

Higher occupancy of predator was associated with increased latent occupancies of brocket deer and medium prey. Subsequent research using two-species modeling detailed by Mackenzie, Bailey, & Nichols (2004) would be beneficial for evaluating and quantifying the level of interaction between brocket deer and jaguar/puma and medium prey and jaguar/puma to determine whether detection and occupancy of one depends upon the presence of the other (Mackenzie et al., 2006, 2004). Lower occupancy for predator was found at sites closer to an aguada, suggesting that proximity to water may have a slight negative influence as well. It is possible that by combining jaguar and puma detections into one detection history, the expected outcome of a selection for habitat with water by jaguars could have been masked by puma preference for drier areas. Additional data are needed to model each species independently to confirm this, as detections were too low for either species to be reliably modeled separately. Model averaged occupancy of predator was quite low at 0.0292, especially compared to the PAO of 0.6635. Low occupancy estimates could be indicative of decreased abundance; however, it could also result from low detections. To maximize detection probability, the total sampling area in the CBR should be expanded in subsequent research, reflecting the sample area found in similar spoor surveys for large mammals in the tropics (Licona et al., 2011; Reyna-Hurtado & Tanner, 2007). A long-term survey expanding on the methods used in this study over the course of at least a year is also recommended to maximize detections of each species, allowing for independent modeling (Karanth et al., 2011; Mackenzie et al., 2006).

Due to the association between reduced prey availability and an increased frequency of livestock depredation and human-wildlife conflict (Petracca et al., 2014; Polisar et al., 2003) and the known risk for human-wildlife conflict for jaguars and pumas (Conde et al., 2010), I propose the necessity for additional research on the feeding ecology and predatory patterns of felids in Calakmul. There are limited data on the severity of conflict with these cats in Calakmul; therefore, identifying areas where conflict with humans and livestock depredation has already occurred, or is likely to occur in also important for comprehending why conflict is occurring and to prevent poaching of these cats from retaliation or from perceived threat (Conde et al., 2010).

Subsequent research to build on the results of this study, to increase the validity of the models, and to evaluate anthropogenic pressures specifically should incorporate additional spatial factors into models for all focal species, such as: proximity to roads (Angelieri et al., 2016; Conde et al., 2010; Maehr, 2012), settlements (ejidos), agriculture, and livestock (Negroes et al., 2010; Petracca et al., 2014; Zeller et al., 2011); number of settlements (Zeller et al., 2011); recent forest disturbance (e.g. burns/cuts of forest in a given time period) (Poley et al., 2014), and proportion of open areas (Zeller et al., 2011). Expanding the sampling area to include areas beyond the reserve would also aid in evaluating the degree to which these factors are influencing the distribution of focal prey, as it would provide a diverse range of levels of disturbance from very minimal (core zone) to quite high (outside the reserve). While the use of AIC to evaluate the goodness-of-fit of models is widely used and beneficial in occupancy modeling (Burnham & Anderson, 2002; Hines et al., 2010; Karanth et al., 2011; Mackenzie et al., 2009), additional cross validation of the models developed in this study could lend further support to their validity (Colchero et al., 2011; Conde et al., 2010).

While this study provides much needed insight into the factors that are influential in shaping distribution of jaguars, pumas, and valued prey species in Campeche, and in the CBR, there is still much to learn about the status of these species. This research adjoins only a handful of studies that model occupancy of jaguars, pumas, and focal prey in Mexico and it is the first to incorporate latent occupancy of prey species as a covariate in occupancy models for these cats. My research highlights the need for further understanding of the status of wildlife populations in this important geographic region. Tropical forests are reservoirs for global and local biodiversity; reserves, such as the CBR constitute less than 10% of the tropics overall (Chazdon et al., 2009; Dirzo & Raven, 2003; Licona et al., 2011); therefore, the fate of biodiversity and of threatened species like jaguar, puma, and white-lipped peccary depends on both ecological reserves and the human-modified landscapes that surround them (Chazdon et al., 2009; Negroes et al., 2010; Reyna-Hurtado & Tanner, 2007). As the Neotropics' largest and second largest top predators (Jorge et al., 2013), healthy populations of jaguars and pumas, as well as a diversity of prey are vital for supporting dynamic ecosystems, as the loss of large felid predators and/or prey populations can have trophic cascade effects (Angelieri et al., 2016; Ripple et al., 2014; Salo et al., 2010). As such, expanding our knowledge about the statuses of these species in the CBR would be invaluable to the conservation of jaguars, pumas, white-lipped peccary, the socio-ecological systems of the region and for biodiversity overall (Núñez-Pérez, 2011; Rodríguez-Soto et al., 2013).

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Appendix A

Table A- 1: Occupancy models for brocket deer fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter ĉ =2.0875). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (QAICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	191.77	0	0.398	185.43	3
ρ(.)ψ(basal)	193.86	2.097	0.140	185.30	4
ρ(.)ψ(aguada)	193.92	2.156	0.136	185.36	4
ρ(.)ψ(rich)	193.95	2.178	0.134	185.38	4
ρ(.)ψ(aguada+basal)	196.04	4.268	0.047	185.18	5
ρ(.)ψ(rich+basal)	196.11	4.346	0.045	185.26	5
ρ(.)ψ(aguada+rich)	196.16	4.389	0.044	185.30	5
ρ(.)ψ(site)	197.92	6.150	0.018	184.70	6
ρ(.)ψ(aguada+rich+basal)	198.35	6.578	0.015	185.13	6
ρ(.)ψ(site+basal)	200.12	8.353	0.006	184.47	7
ρ(.)ψ(site+aguada)	200.29	8.527	0.006	184.65	7
ρ(.)ψ(site+rich)	200.33	8.558	0.006	184.68	7
ρ(.)ψ(site+basal+rich)	202.60	10.834	0.002	184.45	8
ρ(.)ψ(site+aguada+rich)	202.79	11.021	0.002	184.64	8
ρ(.)ψ(site+aguada+basal)	202.98	11.213	0.001	184.83	8
ρ(.)ψ(site+aguada+rich+basal)	205.16	13.395	0.000	184.44	9

Table A- 2: Relative importance (sum of QAICc*w*), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =2.0875), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for brocket deer.

Covariate	Relative Importance	β estimate	Unconditional SE
basal area	0.257	-0.045	0.171
distance to an aguada	0.251	0.035	0.201
tree species richness	0.248	-0.027	0.177
site	0.041	0.057 (horm)	0.303
		0.133 (zns)	0.763
		0.076 (man)	0.392
		0.075 (km20)	0.388

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 3: Occupancy models for white-tailed deer fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter ĉ =1.289). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (QAICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	310.64	0	0.310	304.31	3
ρ(.)ψ(basal)	312.44	1.798	0.126	303.88	4
ρ(.)ψ(rich)	312.77	2.126	0.107	304.21	4
ρ(.)ψ(aguada)	312.80	2.158	0.105	304.24	4
ρ(.)ψ(site)	313.07	2.431	0.092	299.86	6
ρ(.)ψ(site+rich)	314.13	3.482	0.054	298.48	7
ρ(.)ψ(site+aguada)	314.71	4.066	0.041	299.06	7
ρ(.)ψ(rich+basal)	314.71	4.066	0.041	303.85	5
ρ(.)ψ(aguada+rich)	314.92	4.278	0.036	304.06	5
ρ(.)ψ(site+basal)	315.48	4.837	0.028	299.83	7
ρ(.)ψ(site+aguada+rich)	315.64	5.002	0.025	297.50	8
ρ(.)ψ(site+basal+rich)	316.60	5.958	0.016	298.45	8
ρ(.)ψ(site+aguada+basal)	317.05	6.407	0.013	298.90	8
ρ(.)ψ(site+aguada+rich+basal)	318.22	7.579	0.007	297.49	9
ρ(.)ψ(aguada+basal)**	307.74	n/a	0.48	296.88	5
ρ(.)ψ(aguada+rich+basal)**	310.05	n/a	0.15	296.84	6

Table A- 4: Relative importance (sum of QAICc*w*), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =1.289), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for white-tailed deer.

Covariate	Relative Importance	β estimate	Unconditional SE
tree species richness	0.286	-0.073	0.624
site	0.275	0.283 (horm)	0.619
		0.381 (zns)	0.895
		2.947 (man)	41.411
		2.335 (km20)	53.025
basal area	0.230	0.116	0.565
distance to an aguada	0.227	-0.117	0.657

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 5: Occupancy models for collared peccary fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter $\hat{c}$ =1.2368). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (QAICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	299.42	0	0.323	293.09	3
ρ(.)ψ(rich)	300.98	1.564	0.148	292.42	4
ρ(.)ψ(aguada)	301.65	2.230	0.106	293.09	4
ρ(.)ψ(basal)	301.65	2.230	0.106	293.09	4
ρ(.)ψ(site)	302.59	3.166	0.066	289.37	6
ρ(.)ψ(aguada+rich)	303.10	3.681	0.051	292.24	5
ρ(.)ψ(rich+basal)	303.27	3.853	0.047	292.42	5
ρ(.)ψ(aguada+basal)	303.94	4.523	0.034	293.09	5
ρ(.)ψ(site+rich)	304.25	4.834	0.029	288.61	7
ρ(.)ψ(site+basal)	304.47	5.049	0.026	288.82	7
ρ(.)ψ(site+aguada)	305.02	5.596	0.020	289.37	7
ρ(.)ψ(aguada+rich+basal)	305.46	6.040	0.016	292.24	6
ρ(.)ψ(site+basal+rich)	306.29	6.868	0.010	288.14	8
ρ(.)ψ(site+aguada+basal)	306.50	7.080	0.009	288.35	8
ρ(.)ψ(site+aguada+rich)	306.75	7.333	0.008	288.60	8
ρ(.)ψ(site+aguada+rich+basal)	309.30	9.876	0.002	288.57	9

Table A- 6: Relative importance (sum of QAICcw), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =1.2368), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m2), and tree species richness), derived from the candidate set of occupancy models for collared peccary.

Covariate	Relative Importance	β estimate	Unconditional SE
tree species richness	0.311	0.155	0.393
basal area	0.250	-0.079	0.527
distance to an aguada	0.246	0.011	0.315
site	0.171	0.779 (horm)	76.104
		1.081 (zns)	20.331
		0.098 (man)	0.400
		1.548 (km20)	81.461

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 7: Occupancy models for white-lipped peccary fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness. Model criterion includes Akaike's Information Criterion adjusted for small sample size (AICc), delta AICc (ΔAICc), AICc weights (AICc*w*), twice the negative log-likelihood value (-2log(LL)), and the number of parameters (*K*).

Model	AICc	ΔAICc	AICc*w*	-2 log(LL)	*K*
ρ(.)ψ(.)	225.37	0	0.236	221.20	2
ρ(.)ψ(rich)	226.22	0.843	0.155	219.88	3
ρ(.)ψ(basal)	226.45	1.073	0.138	220.12	3
ρ(.)ψ(aguada)	227.07	1.702	0.101	220.74	3
ρ(.)ψ(aguada+basal)	227.10	1.727	0.100	218.54	4
ρ(.)ψ(rich+basal)	227.39	2.022	0.086	218.84	4
ρ(.)ψ(aguada+rich)	227.84	2.463	0.069	219.28	4
ρ(.)ψ(aguada+rich+basal)	227.85	2.474	0.069	216.98	5
ρ(.)ψ(site)	230.90	5.528	0.015	220.04	5
ρ(.)ψ(site+basal)	232.00	6.626	0.009	218.78	6
ρ(.)ψ(site+rich)	232.77	7.394	0.006	219.54	6
ρ(.)ψ(site+aguada)	233.09	7.719	0.005	219.88	6
ρ(.)ψ(site+aguada+basal)	233.59	8.214	0.004	217.94	7
ρ(.)ψ(site+basal+rich)	233.96	8.583	0.003	218.30	7
ρ(.)ψ(site+aguada+rich)	234.78	9.405	0.002	219.14	7
ρ(.)ψ(site+aguada+rich+basal)	235.12	9.746	0.002	216.96	8

Table A- 8: Relative importance (sum of AICc*w*) and model averaged β estimates and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for white-lipped peccary.

Covariate	Relative Importance	β estimate	Unconditional SE
basal area	0.411	0.536	0.507
tree species richness	0.392	0.381	0.338
distance to an aguada	0.352	-0.403	0.439
site	0.046	0.351(horm)	0.853
		-0.239(zns)	0.899
		0.584(man)	0.940
		0.605(km20)	1.017

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 9: Occupancy models for large prey (brocket deer, white-tailed deer, collared peccary, white-lipped peccary) fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter ĉ =1.5081). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (QAICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	237.09	0	0.236	230.75	3
ρ(.)ψ(aguada)	237.09	0.005	0.236	228.53	4
ρ(.)ψ(aguada+basal)	239.10	2.014	0.086	228.24	5
ρ(.)ψ(aguada+rich)	239.22	2.129	0.082	228.36	5
ρ(.)ψ(rich)	239.25	2.160	0.080	230.68	4
ρ(.)ψ(basal)	239.31	2.218	0.078	230.74	4
ρ(.)ψ(site)	239.83	2.743	0.060	226.61	6
ρ(.)ψ(aguada+rich+basal)	241.34	4.249	0.028	228.12	6
ρ(.)ψ(site+aguada)	241.40	4.311	0.027	225.75	7
ρ(.)ψ(rich+basal)	241.53	4.445	0.026	230.68	5
ρ(.)ψ(site+rich)	242.12	5.031	0.019	226.47	7
ρ(.)ψ(site+basal)	242.26	5.177	0.018	226.62	7
ρ(.)ψ(site+aguada+rich)	243.81	6.719	0.008	225.66	8
ρ(.)ψ(site+aguada+basal)	243.86	6.774	0.008	225.71	8
ρ(.)ψ(site+basal+rich)	244.62	7.531	0.005	226.47	8
ρ(.)ψ(site+aguada+rich+basal)	246.33	9.242	0.002	225.60	9

Table A- 10: Relative importance (sum of QAICc*w*), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =1.5081), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for large prey (brocket deer, white-tailed deer, collared peccary, white-lipped peccary).

Covariate	Relative Importance	β estimate	Unconditional SE
distance to an aguada	0.480	0.763	1.136
basal area	0.250	-0.048	0.270
tree species richness	0.250	-0.040	0.332
site	0.150	0.488 (horm)	1.269
		1.577 (zns)	26.110
		1.555 (man)	17.540
		0.290 (km20)	0.779

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 11: Occupancy models for medium prey (lowland paca, Central American agouti, and coati) fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter ĉ =2.1939). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (AICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	181.29	0	0.272	174.96	3
ρ(.)ψ(site)	182.52	1.223	0.147	169.30	6
ρ(.)ψ(basal)	183.46	2.166	0.092	174.90	4
ρ(.)ψ(rich)	183.50	2.203	0.090	174.93	4
ρ(.)ψ(aguada)	183.52	2.228	0.089	174.96	4
ρ(.)ψ(site+aguada)	184.26	2.967	0.062	168.62	7
ρ(.)ψ(site+rich)	184.79	3.498	0.047	169.15	7
ρ(.)ψ(site+basal)	184.82	3.520	0.047	169.17	7
ρ(.)ψ(rich+basal)	185.72	4.429	0.030	174.87	5
ρ(.)ψ(aguada+basal)	185.75	4.460	0.029	174.90	5
ρ(.)ψ(aguada+rich)	185.79	4.494	0.029	174.93	5
ρ(.)ψ(site+aguada+basal)	186.61	5.310	0.019	168.46	8
ρ(.)ψ(site+aguada+rich)	186.73	5.439	0.018	168.58	8
ρ(.)ψ(site+basal+rich)	187.15	5.851	0.015	169.00	8
ρ(.)ψ(aguada+rich+basal)	188.08	6.789	0.009	174.87	6
ρ(.)ψ(site+aguada+rich+basal)	189.12	7.827	0.005	168.39	9

Table A- 12: Relative importance (sum of QAICc*w*), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =2.1939), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for medium prey (lowland paca, Central American agouti, and coati).

Covariate	Relative Importance	β estimate	Unconditional SE
site	0.360	0.011 (horm)	0.320
		2.263 (zns)	26.702
		0.227 (man)	0.445
		0.808 (km20)	1.263
distance to an aguada	0.260	-0.065	0.295
basal area	0.250	0.042	0.218
tree species richness	0.240	-0.026	0.162

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)

Table A- 13: Occupancy models for seven prey species (brocket deer, white-tailed deer, collared peccary, white-lipped peccary, lowland paca, Central American agouti, and coati) fit to survey data from Calakmul Biosphere Reserve, Mexico. Models estimated as a function of constant detection (ρ) and occupancy (ψ), site surveyed (KM20, Zona Núcleo Sur, Mancolona, and Hormiguero), distance to an aguada (m), total basal area (m^2), and tree species richness (modeled with overdispersion parameter ĉ =1.9368). Model criterion includes Quasi Akaike's Information Criterion adjusted for small sample size (QAICc), delta QAICc (ΔQAICc), QAICc weights (QAICc*w*), twice the negative log-likelihood value (-2log(QLL)), and the number of parameters (*K*).

Model	QAICc	ΔQAICc	QAICc*w*	-2 log(QLL)	*K*
ρ(.)ψ(.)	167.44	0	0.276	161.10	3
ρ(.)ψ(aguada)	167.88	0.447	0.221	159.32	4
ρ(.)ψ(rich)	169.61	2.173	0.093	161.04	4
ρ(.)ψ(basal)	169.66	2.220	0.091	161.09	4
ρ(.)ψ(aguada+basal)	169.95	2.517	0.078	159.09	5
ρ(.)ψ(aguada+rich)	170.04	2.608	0.075	159.19	5
ρ(.)ψ(site)	171.02	3.583	0.046	157.80	6
ρ(.)ψ(rich+basal)	171.89	4.460	0.030	161.04	5
ρ(.)ψ(aguada+rich+basal)	172.21	4.779	0.025	159.00	6
ρ(.)ψ(site+aguada)	172.77	5.336	0.019	157.12	7
ρ(.)ψ(site+rich)	173.35	5.910	0.014	157.70	7
ρ(.)ψ(site+basal)	173.45	6.012	0.014	157.80	7
ρ(.)ψ(site+aguada+rich)	175.20	7.764	0.006	157.05	8
ρ(.)ψ(site+aguada+basal)	175.24	7.802	0.006	157.09	8
ρ(.)ψ(site+basal+rich)	175.85	8.410	0.004	157.70	8
ρ(.)ψ(site+aguada+rich+basal)	177.73	10.299	0.002	157.01	9

Table A- 14: Relative importance (sum of QAICc*w*), model averaged β estimates and standard error (modeled with overdispersion parameter ĉ =1.9368), and direction of influence (+ve or –ve) for each variable, (site, distance to an aguada (m), total basal area (m^2), and tree species richness), derived from the candidate set of occupancy models for seven species of prey (brocket deer, white-tailed deer, collared peccary, white-lipped peccary, lowland paca, Central American agouti, and coati).

Covariate	Relative Importance	β estimate	Unconditional SE
distance to an aguada	0.430	0.688	1.091
basal area	0.250	-0.045	0.264
tree species richness	0.250	-0.043	0.316
site	0.110	0.356 (horm)	1.090
		1.206 (zns)	67.183
		1.205 (man)	19.172
		0.213 (km20)	0.673

*(horm=Hormiguero camp, zns= Zona Núcleo Sur camp, man=Mancolona camp, km20=KM20 camp)