The influence of habitat features and co-occurring species on puma (*Puma concolor*) occupancy across eight sites in Belize, Central America

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Christopher B. Rowe

Abstract (Academic)

Large carnivores play many vital biological, economic, and conservation roles, however, their biological traits (low population densities, cryptic behavior) make them difficult to monitor. Pumas have been particularly difficult to study because the lack of distinctive markings on their coats prevents individual identification, precluding mark-recapture and other similar analyses. Further, compared to temperate areas, research on the interspecific interactions of Central American felids is particularly lacking. I used single- and multi-season, single-species occupancy models and two-species co-occurrence models to analyze camera trapping and habitat data collected at eight study sites across Belize. Puma occupancy was positively influenced by jaguar trap success, understory density, canopy cover, and human trap success, and negatively influenced by stream density. Jaguar trap success was the best predictor of where pumas occurred, while prey species were not found to influence puma occupancy. Mean occupancy was 0.740 (0.013) and ranged from 0.587 (0.042) to 0.924 (0.030). Over time, puma occupancy rates were generally high (> 0.90) and stable. Puma occupancy was higher in logged areas, suggesting that current levels of natural resource extraction at those sites were not detrimental to the species. Co-occurrence modeling showed little evidence for interactions between the carnivores, suggesting that jaguars may be acting as an umbrella species and that conservation efforts directed at jaguars are likely to benefit the other carnivores, including pumas. Overall, these findings are positive for puma conservation, but human-induced land use change is expanding and further monitoring will give us insight into how pumas respond to human encroachment.

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Christopher B. Rowe

Abstract (Public)

Large carnivores play many vital biological, economic, and conservation roles, however, their biological traits (low population densities, cryptic behavior) make them difficult to monitor. Pumas have been particularly difficult to study because they lack distinctive markings on their coats, making it difficult to identify individuals. Further, compared to temperate areas, there is little research on how cat species in Central American interact. To learn more about the habitat that pumas prefer and how they interact with other carnivores, I used single- and multi-season, single-species occupancy models and two-species co-occurrence models to analyze camera trapping and habitat data collected at eight study sites over multiple years across Belize. Puma distribution across the landscape was positively influenced by jaguar activity levels, understory density, canopy cover, and human activity levels, and negatively influenced by how wet sites were. Jaguar activity level was the best predictor of where pumas occurred, while prey species did not influence puma occupancy. Over time, these puma occupancy rates were generally high and stable. Puma occurrence was higher in logged areas, suggesting that current levels of natural resource extraction at those sites were not detrimental to the species. There was little evidence of interactions between the carnivores, suggesting that jaguars could act as an umbrella species and that conservation efforts directed at jaguars are also likely to benefit pumas. Overall, these findings are good news for puma conservation, but human-induced land use change is expanding and further monitoring will give us insight into how pumas respond to human encroachment.

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mean understory density to 1.0 m in height, within 100 m of each site. The number at the end of each model refers to the model type and is explained in Table 3.2. K is the number of parameters in each model. ΔAIC is the difference between the AIC of each model and the top model. AIC weight is the proportion of evidence that each model draws from the data.

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Figure Captions

Figure 1.1. Historic range of the puma (*Puma concolor*) showing the six subspecies identified by genetic analysis. Reprinted from Culver et al. (2000).

Figure 1.2. Present range of the puma (*Puma concolor*). Pumas are known to be extant in the orange areas. They are possibly extant in the purple area (adapted from the IUCN Red List of Threatened Species).

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Figure 2.1. The eight study sites in Belize used in this analysis. Each dot represents one camera location as of 2015, except Chiquibul (2008), Cockscomb (2008), and Fireburn (2009). Protected areas are shown in gray. Surveyed protected areas are shown in dark gray.

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Figure 3.1. The eight study sites in Belize used in this analysis. Each dot represents one camera location in 2015, except Chiquibul (2008), Cockscomb (2008), and Fireburn (2009). Protected areas are shown in gray. Surveyed protected areas are shown in dark gray.

Figure 3.2. Schematic diagram of the microhabitat survey conducted at each camera station. Tree data were collected at the camera station and at 50 meters and 100 meters along each of the three major transects (shown as open or closed circles). Understory data were collected every 2 meters along six 40 m transects that ran perpendicular to the three main transects at 50 meters and 100 meters from the cameras.

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I. Introduction

Puma Taxonomy, Distribution, and Habitat Associations

The puma is the largest member of the subfamily Felinae and the fourth largest felid in the world. It is the largest member of its genus and the most studied felid in North America, however, there have been fewer studies of the species in Central and South America and those focus mostly on central and southern South America. As recently as the 1980s, researchers suggested there were as many as 32 subspecies, but genetic analysis by Culver et al. (2000) found support for only six subspecies (Fig. 1.1). One subspecies, *Puma concolor cougar*, is the only subspecies in North America and northern Central America, including Belize. The other five subspecies all occur in Central and South America. Although the Florida panther, *Puma concolor coryii*, is often listed as a separate subspecies in the literature, its status is currently unresolved (Culver et al. 2000, Wilson and Reeder 2005).

The puma has the largest geographic range of any terrestrial mammal in the Western Hemisphere (Fig. 1.2), ranging from British Columbia to southern Chile (Iriarte et al. 1990). Its range covers approximately 110° of latitude, the greatest of any non-migratory land animal (Iriarte et al. 1990). Its historic range previously covered all of the continental United States and much of southern Canada, but by the 1890s, it had been extirpated from the east, except for a small population in Florida (Sunquist and Sunquist 2002).

Weights of adult pumas vary widely over their geographic range (Iriarte et al. 1990) with pumas from Canada and Chile (the northern and southern extremes of their range) weighing roughly twice as much as tropical pumas (Sunquist and Sunquist 2002). The smallest adult males recorded were in Peru and weighed 28-30 kg (Emmons 1987). Those in Canada and Chile are typically 65-85 kg (Sunquist and Sunquist 2002).

The puma occurs in a wide range of habitats and can be found from sea level to 5800 m elevation (Sunquist and Sunquist 2002). Pumas appear to prefer habitat that provides stalking cover, however, given their wide geographic distribution, that cover takes many forms throughout their range, including rocks, cliffs, sagebrush, and dense understory (Sunquist and Sunquist 2002). The ability to adapt to a wide range of habitats and variable prey makes the puma one of the most adaptable and generalist mammalian carnivores (Iriarte et al. 1990).

Sunquist and Sunquist (2002) report that the puma has a social system common among felids in which female home ranges are largely exclusive and are determined by prey availability, while male home ranges overlap several female home ranges. Social and territorial constraints are thought to keep puma populations below a level set by prey densities (Seidensticker et al. 1973).

Feeding Behavior

Pumas typically stalk their prey, but they are also strong runners (Sunquist and Sunquist 2002). They appear to hunt by opportunistic encounter (Emmons 1987). Most successful attacks are launched from 2.5-10 m (Sunquist and Sunquist 2002), potentially explaining their affinity for dense understory and other stalking cover. Pumas vary their method of killing depending on prey size; small prey are usually killed by a bite to the back of neck, while larger prey are killed by suffocation (Branch 1995). Pumas generally launch themselves at prey, knocking the target off balance, then holding the prey with their claws, biting the neck or throat (Sunquist and Sunquist 2002). A good example of this hunting strategy can be seen in this short (~1min) video https://www.youtube.com/watch?v=B85Hi4djjZk&feature=youtu.be. Prey are usually cached and may be fed upon for up to 19 days (Seidensticker et al. 1973), although this time is reduced to as little as two days in the tropics because of increased spoilage rates (Núñez et al. 2000). Prey size ranges from small rodents to moose (*Alces alces*) and varies with latitude (Iriarte et al. 1990).

In temperate regions, pumas target larger prey, including prey larger than themselves. Pumas are morphologically adapted to kill large prey, but will freely switch to small- and medium-sized prey if they are locally abundant and if large prey are not available or vulnerable (Iriarte et al. 1990). In Southern Chile, pumas increased predation on guanacos (*Lama guanicoe*), a large prey species, during birthing and juvenile expulsion (the time when territorial males expel the previous year's juveniles from family groups) when the animals were more vulnerable to predation (Iriarte et al. 1990). Deer (*Odocoileus* spp.) are especially important to pumas, making up 60-80% of the diet in North America (Ackerman et al. 1984, Iriarte et al. 1990, Sunquist and Sunquist 2002). Temperate pumas eat larger prey than tropical pumas and specialize on a smaller number of prey taxa. Medium-sized prey (1-15 kg) become more important in the tropics (Núñez et al. 2000, Sunquist and Sunquist 2002), where pumas are smaller and tend to focus on prey less than half their weight (Iriarte et al. 1990), but this may merely reflect prey availability. Dietary breadth also increases in the tropics (Iriarte et al. 1990). The mean weight of vertebrate prey consumed (MWVP) is positively correlated with puma body weight and inversely correlated with food niche breadth across the Americas (Iriarte et al. 1990). In general, MWVP is lower closer to the equator, possibly influenced by smaller puma body size, prey availability and vulnerability, habitat characteristics, and competition with jaguars (*Panthera onca*) (Iriarte et al. 1990). One proposed explanation is that the closed, forested habitat typical of much of the tropics reduces encounter rates with large prey and so favors smaller pumas better able to exploit smaller prey. A second possible explanation is character displacement to avoid competition with the jaguar, the largest felid in the Americas (Iriarte et al. 1990).

Pumas are opportunistic predators and will switch prey depending on availability (Leopold and Krausman 1991). In a long-term study in Chile, the proportion of guanacos consumed tracked changes in guanaco abundance (Iriarte et al. 1991). European hares (*Lepus europaeus*) became more important in the pumas' diet when guanaco abundance was low (Iriarte et al. 1991). Learning also seems to be important in prey selection, as young pumas have been seen to ignore potential prey species until having consumed them (Sunquist and Sunquist 2002).

Niche Partitioning

Although the puma is the most studied felid in North America, there is less known about pumas in Central or South America. Additionally, the ecological and behavioral factors that allow puma and jaguar coexistence remain unclear (Scognamillo et al. 2003) because there is a general lack of knowledge about the predatory patterns of large felids living in the neotropics (Weber and Rabinowitz 1996). Diet studies have shown a large degree of dietary overlap across their ranges, making them potential competitors (Harmsen et al. 2009). Although direct aggression between felid species has rarely been observed in the neotropics, this may be a result of the dense habitat and difficulty in observing interactions directly, rather than a lack of aggression. Núñez et al. (2000) found an ocelot that had been killed, but not consumed by a puma in their study in Mexico. At one of our study sites (La Milpa 2014), the staff of a research station found a puma that they believe was killed by a jaguar, based on the crushed skull typical of jaguar kills. Additionally, Claudia Wultsch found ocelot claws in a jaguar scat in Belize, although the ocelot may have been scavenged (Marcella Kelly, personal communication).

Some studies in the neotropics have found considerable dietary overlap and minimal prey partitioning between pumas and jaguars (Emmons 1987, Iriarte et al. 1991, Taber et al. 1997, Farrell et al. 2000, Núñez et al. 2000) and that, where available, medium- and large-sized species are the preferred prey of both species (Emmons 1987, Iriarte et al. 1991, Taber et al. 1997, Núñez et al. 2000). Núñez et al. (2000) found that both felids fed mainly upon mammalian species, especially white-tailed deer (*Odocoileus virginianus*) in Jalisco, Mexico. They also found that both felids had relatively high MWVP (12.74 kg for pumas and 15.60 kg for jaguars) and a high degree of dietary overlap, but that the puma had a broader prey niche. Taber et al. (1997) suggest that this similarity in diet suggests that either pumas and jaguars both occur at densities too low to produce competition or that habitat structure influences prey selection.

Other studies have found evidence of diet partitioning between pumas and jaguars (Novack et al. 2005, De Azevedo 2008, Foster et al. 2010). Surprisingly, Novack et al. (2005) found that larger prey were more important in the diet of pumas than jaguars in Guatemala. De Azevedo (2008) found that jaguars largely consumed medium- and large-sized prey while pumas consumed mostly medium-sized prey in southern Brazil. It should be noted that only Farrell et al. (2000), Novack et al. (2005), and Foster et al. (2010) used genetic analysis to identify the source of the scat they collected. The other studies relied on identifying tracks observed near the scat at the time of collection. This seems potentially problematic given the large degree of overlap in the size of jaguars and pumas and recent work noting high misidentification rates that occur when using scat morphology alone to identify carnivore species from scat (Davison et al. 2002, Reed et al. 2004, Harrington et al. 2010, Lonsinger et al. 2015, Morin et al. 2016).

A third, smaller predator in this system, the ocelot (*Leopardis pardalis*) also overlaps with pumas and jaguars across much of their ranges. Moreno et al. (2006) found considerable overlap in diet between pumas and ocelots in Panama. Ocelots typically rely on small prey (< 1 kg), which is < 10% of their body weight (Sunquist and Sunquist 2002). This is consistent with the energetic model of Carbone et al. (1999) of carnivore diet, which suggests that predators

> 21.5 kg (e.g., pumas and jaguars) focus on prey > 45% of their body mass (e.g., deer and peccaries), whereas predators < 21.5 kg focus on smaller prey.

Few studies focusing on gray foxes (*Urocyon cinereoargenteus*) in Central America exist, but at 1.8-3.6 kg, they are smaller than any of the felid species (Reid, 2009). They are common and widespread in deciduous and semideciduous forests, less common in evergreen forests and are not found in lowland, wet forests (Reid 2009). They are omnivorous, eating large quantities of fruit, but specialize on small mammals and insects (Reid 2009). Novaro et al. (1995) found that their diet consisted mainly of fruit and arthropods, some birds, small rodents, with other vertebrates also taken during the dry season in Belize.

There has been mixed evidence that tropical felids show temporal niche partitioning. Harmsen et al. (2011) and Foster et al. (2013) found that pumas and jaguars are most active at the same times as their main prey species and show no signs of minimizing encounters with each other. Foster et al. (2013) found pumas and jaguars to be nocturnal and crepuscular, while Hernández-Saintmartín et al. (2013) found them to be cathemeral and found that jaguar activity overlapped that of their main prey species, but pumas did not, perhaps because they were displaced by the larger jaguar. Di Bitetti et al. (2010) found that the six felid species of Brazil (five of which also occur in Belize) were all cathemeral, except for the diurnal jaguarundi (*Puma yagouaroundi*), and that they alternated peaks of activity.

The evidence for spatial avoidance is also mixed, with several studies finding no spatial avoidance (Crawshaw and Quigley 1991, Scognamillo et al. 2003, Noss et al. 2006 reviewed in Harmsen et al. 2009), while others found that pumas avoid areas favored by jaguars, such as waterside habitats and dense forests (Schaller and Crawshaw 1980, Emmons 1987). While

Harmsen et al. (2009) found that pumas and jaguars had similar activity patterns and habitat use in Belize, they were not seen at the same time and place.

Núñez et al. (2000) warn that we should be cautious about making evolutionary inferences based on recent dietary data because of human-induced changes to habitat that disrupt predator-prey assemblages. Human impacts have severely disrupted natural predator-prey assemblages in much of the world (Weber and Rabinowitz 1996). Pumas and jaguars are both sensitive to human disturbance, with both species showing a high dependence on native forests and low tolerance to anthropogenic change, but jaguars seem more sensitive to these changes (De Angelo et al. 2011). Although they have a high degree of dietary overlap, De Angelo et al. (2011) found that the puma's higher tolerance of disturbance meant more patches in their study site were suitable for the species. Núñez et al. (2000) found that the puma's ability to exploit smaller prey gave it an advantage over the jaguar in areas with human-induced habitat changes.

Not surprisingly, puma population densities are highest in protected areas and lowest in areas with the most poaching and logging, most likely because of decreased prey availability. In northern Arizona, pumas were rarely found in areas that had been clear cut within the last six years and those that were seen were young dispersers (Van Dyke et al. 1986). As well as competition for space, humans and pumas also compete directly for food, with both species tending to favor the same prey species (e.g., deer and peccaries). Pumas respond to this conflict by becoming more nocturnal or crepuscular in areas with human disturbance (Van Dyke et al. 1986, Paviolo et al. 2009). Foster et al. (2010) found that jaguar and puma dietary breadth was lower in protected areas and showed little overlap, with jaguars favoring armadillos (*Dasypus novemcinctus*) and white-lipped peccaries (*Tayassu pecari*), while pumas relied mainly on agoutis (*Dasyprocta punctata*) and red brocket deer (*Mazama americana*). Outside of protected areas, jaguars took mostly medium-sized prey and cattle and pumas were not present (Foster et al. 2010). Ackerman et al. (1984) found that pumas in Utah had < 1% cattle in their diet and suggested that preventing overhunting of prey species and good husbandry practices can potentially reduce human-felid conflicts.

De Azevedo (2008) found that high hunting pressure on prey lowered jaguar MWVP, but that pumas did not show this trend. Novack et al. (2005) found no differences between the diets of pumas in areas with or without hunting even though prey availability differed.

It is likely that the predatory activities of large cats play an important role in maintaining biodiversity and structural integrity of tropical forest systems (Terborgh et al. 1999). The complete loss of predators in an area can result in “ecological meltdown” (Terborgh et al. 2001), but a partial loss can still result in dramatic ecological changes. Lower trophic level species may increase in density or change behavior when released from competition or predation (Moreno et al. 2006). Competitive release should theoretically allow a mesopredator to expand its niche in the absence of a larger competitor (Brown and Wilson 1956), but this has not been well documented in the literature for larger vertebrates (Moreno et al. 2006). One documented case comes from Barro Colorado Island (BCI) in Panama. At two sites, one on the island and one on the mainland nearby, in the absence of jaguars, ocelots at both sites consumed larger prey than elsewhere in their range, suggesting competitive release; pumas on BCI consumed more peccaries and deer (i.e., larger prey) than in other populations, but showed no difference in prey selection between the mainland and the island (Moreno et al. 2006).

The paucity of evidence supporting competitive release in tropical carnivores is surprising given that most carnivores have flexible and opportunistic diets (Gittleman 1985). These results are alarming because it may indicate that any niche left vacant by the removal of a carnivore may remain empty, which is especially troubling given that > 40% of carnivore species worldwide are considered to be at risk (Moreno et al. 2006).

Single-season, single-species occupancy models

Presence/absence data have long been used to infer ecological processes, but there are few instances where species are certain to be detected, even when present. These false absences lead to biased parameter estimates (Moore and Swihart 2005) and the consequences of this non-detection error are more severe if associated with site-specific covariates (Gu and Swihart 2004). Several efforts have been made to divide this count statistic (presence/absence counts) by some estimated detection probability (Seber 1982 reviewed in MacKenzie et al. 2002), but this detection probability may vary with site characteristics, time, or environmental variables (MacKenzie et al. 2002). MacKenzie et al. (2002) developed a method analogous to a closed-population, mark-recapture model, with an additional parameter ψ, the probability that a site is occupied by the species. Closed-population capture-recapture models attempt to estimate the number of individuals never encountered, based on the information from individuals that are encountered at least once. In occupancy modeling, the sites are analogous to the individuals in capture-recapture models, except that sites with all-zero encounter histories are known. This means that the total number of sites is known, so the objective is to estimate the proportion that are actually occupied. This method uses patterns of detection and non-detection of a species over multiple visits to each site to estimate detection probabilities (p) and the proportion of sites occupied (ψ). Sites must be “closed” to changes in occupancy (i.e., no new sites are occupied and no sites are abandoned) during the sampling period. Using a logit-transformation on occupancy and/or detection probability allows us to incorporate covariates on these parameters. Because sampling is designed to keep ψ constant within surveys, covariates for site occupancy are constant across occasions, but can vary by site; detection probability can vary by both occasion and site. These models can also account for missing observations. In simulations, MacKenzie et al. (2002) found that parameter estimates were generally unbiased if detection was greater than 0.3.

Occupancy analysis was used in this study, rather than estimating abundance, because most of the species in this analysis were not identifiable to individual. In the absence of some marking process, occupancy is likely the most appropriate method for analyzing camera trap data for unmarked species. It should be noted that for larger species, occupancy is analogous to site-use, rather than a true occupancy analysis, because these larger species likely had home ranges that included > 1 camera location. This likely exacerbated the problem of spatial autocorrelation. When ordinary logistic regression is used to model spatial patterns of species presence/absence, locations closer together in space are likely to exhibit more similar attributes than those that are farther apart (Moore and Swihart 2005). This results in a violation of independence assumptions, resulting in artificially narrow confidence intervals for parameter estimates and erroneous conclusions about the importance of predictor variables (Legendre 1993).

Multi-season, single-species occupancy models

Models of how occurrence changes in patchy habitat through the processes of colonization and local extinction (or alternatively, patch persistence) have become well known in the ecological literature under the name “metapopulation models” (Hanski 1998). However, these models do not account for imperfect detection. For this reason, MacKenzie et al. (2003) generalized their single-season occupancy model to account for changes in the occupancy state of sites by introducing parameters for local extinction and colonization probabilities. These models, also called dynamic occupancy models, allow inference about the occurrence of a species at a collection of sites and how changes in occurrence are driven by colonization and local extinction while accounting for imperfect detection (Kéry and Chandler 2012). The use of the logit link or other suitable link functions allows all parameters to be modeled as functions of covariates (Kéry and Chandler 2012). Multi-season occupancy models have four parameters: occupancy in the initial season, site colonization rate, site extinction rate, and detection rate. Occupancy in subsequent seasons is a derived parameter calculated from occupancy in the initial season adjusted by the extinction and colonization rates. This requires that sites be in the same location from season to season.

Two-species co-occurrence models

Imperfect detection is also an issue when comparing the occupancy rates of multiple species occurring simultaneously (Nichols et al. 1998, Cam et al. 2000). Early approaches used nested subsets of species present at one location that were also present at another location. They considered only species richness and could not be used for a small number of species (i.e., they could be used for species assemblages, but they could not be used to examine the interactions between pairs of species). Mackenzie et al. (2004) extended their previous single-species occupancy models to examine the co-occurrence of multiple species simultaneously. They recommended examining < 4 species at a time because the number of parameters expands exponentially with each additional species. This model deals with both non-detection and possible habitat preference (Mackenzie et al. 2004) and can be used to address questions about the importance of interspecific interactions such as competition and predator-prey relationships. Likelihood ratio tests can be used to test for the independence of species with respect to detection or occupancy or the Akaike Information Criterion (AIC) can be used to rank models (Mackenzie et al. 2004). The magnitude of interaction between species can be estimated from the parameter estimates of the full model with an estimate called the species interaction factor (Φ), which gives a meaningful interpretation of the strength of a covariate relationship on the non-independence of two species (Mackenzie et al. 2004). If $\Phi < 1$, then the two species occur together less often than would be expected by chance alone. If $\Phi > 1$, the two species occur together more often than expected by chance. If the confidence interval for Φ includes 1, then there is insufficient evidence to conclude that there is an interaction between the two species. It is not possible to infer from this analysis what causal relationship the two species have, only that they occur together more or less often than should happen by chance alone (Richmond et al. 2010).

Richmond et al. (2010) developed a second parameterization of the two-species occupancy model using only conditional probabilities as parameters. As a result, this conditional two-species occupancy model is more numerically stable when covariates are used. This model estimates the probability of occupancy for a subdominant species conditional upon the presence of a dominant species. The original two-species occupancy model developed by Mackenzie et al. (2004) did not consider directionality of effects between the two species. In the second parameterization, dominant and subdominant mean only that the occupancy of one species (dominant) affects occupancy of a second species (subdominant). It does not imply any particular behavioral interaction. These models can also be used to test whether the detection of either species differs when one or both species are present, and whether the detection of the subdominant species depends on detection of the dominant species when both are present (Richmond et al. 2010). Two-species co-occurrence models have been used to examine the interactions of different rail species (Richmond et al. 2010), several salamander species (Mackenzie et al. 2004), felid species in Sumatra (Sunarto et al. 2015), carnivore and primate species in Madagascar (Farris et al. 2014), and jaguar-puma co-occurrence in Brazil (Sollmann et al. 2012, Astete et al. 2017).

If the occupancy of the subdominant species is the same in the presence or absence of the dominant species and there are no covariates in the best-supported model, this suggests that there is no interaction between the two species and that none of the measured covariates explain the occupancy of the subdominant species. If a similar model, with covariates, is the best supported model, this suggests that there is no interaction between the two species and that the occupancy of the subdominant species is best explained by the habitat. If the occupancy of the subdominant species differs in the presence or absence of the dominant species and there are no covariates in the best supported model, this suggests that the interaction between the two species is sufficient to explain the occupancy of the subdominant species. If a similar model, with covariates, is the best supported model, this suggests that there is an interaction between the two species that changes across the landscape. The same is true for the effects of the dominant species on the detection of the subdominant species.

The second parameterization of two-species occupancy models has eight parameters, as follows (note the capitalization of the superscripts indicates occupied or detected for the particular species denoted as A or B):

Ψ^{A}: probability that the area is occupied by species A
Ψ^{BA}: probability that the area is occupied by species B, given that species A is present
Ψ^{Ba}: probability that the area is occupied by species B, given that species A is not present
p^{A}: probability of detecting species A, given species B is not present
p^{B}: probability of detecting species B, given species A is not present
r^{A}: probability of detecting species A, given that both are present
r^{BA}: probability of detecting species B, given that both are present and species A was detected

r^{Ba}: probability of detecting species B, given that both are present and species A was not detected

In each case, species A is the dominant species and species B is the subdominant species. From these parameters we can derive the species interaction factor (Φ) from the following formula:

$$\Phi = \frac{\psi^{A}\psi^{BA}}{\psi^{A}(\psi^{A}\psi^{BA} + (1-\psi^{A})\psi^{Ba})}$$

Study site

Belize is a small country (22,963 km^2) approximately the size of Massachusetts lying on the eastern coast of the Yucatan Peninsula in Central America at 17° 15' N latitude and 88° 45' W longitude. Most of the country lies within La Selva Maya (the Mayan Forest), which also includes northern Guatemala and Mexico's Yucatan Peninsula. At 13.3 million hectares, the Mayan Forest is the second largest tropical rainforest in the Americas, after the Amazon rainforest. Despite its small size, Belize offers a diversity of habitats including broadleaf moist subtropical forest, mountainous pine forest, lowland pine savanna, and wetlands (Fig. 1.3). Elevation ranges from sea level to 1160 m, and the area is considered a biodiversity hotspot (Conservation International 2011). I used camera trapping data from eight study sites located throughout Belize as described below (Fig. 1.4).

Chiquibul Forest Reserve and National Park (CFRNP): These two areas (reserve and national park) occupy 1,670 km^2 of mainly lowland broadleaf moist forest in mid-western Belize. Elevation is approximately 500 m; annual rainfall averages about 1,500 mm with a wet season from June to January. Three surveys were conducted here between 2006 and 2008, with a microhabitat survey in 2008. The area is highly disturbed by illegal extraction of natural resources (e.g., timber, xate and other non-timber forest products). Poaching of wildlife is thought to be relatively high.

Cockscomb Basin Wildlife Sanctuary (CBWS): This jaguar preserve encompasses 437 km^2 of dense secondary growth sub-tropical rainforest. Elevation ranges from 50 to 1,120 m and annual rainfall averages around 2,700 mm with a wet season from June to December. One survey was conducted here in 2008.

Fireburn Reserve: 736 ha of lowland moist forest, wetland, and savanna at the southern end of Shipstern Lagoon in northeastern Belize. The study site includes the reserve and the surrounding area. One survey was conducted here in 2009.

Gallon Jug Estate and Yalbac Ranch and Cattle Corporation: two privately-owned timber companies comprising 530 km^2 and 650 km^2, respectively. Gallon Jug Estate is south of and contiguous with the La Milpa section of the RBCMA. The area consists of subtropical broadleaf forest with one village of ~ 150 people and 12 km^2 of agriculture for the production of coffee, cacao, and cattle. This survey site was established in 2013 and is surveyed annually; a microhabitat survey was conducted in 2013. Yalbac Ranch and Cattle Corporation is south of and contiguous with Gallon Jug Estate. This area consists of subtropical broadleaf forest and also is subject to logging. The area was extensively damaged by a hurricane and wildfires and features an especially dense understory. Only nine sites were established in the first year of this study (2014), therefore this study site was treated as an extension of the Gallon Jug study site for some analyses.

Hill Bank: the eastern portion of the Rio Bravo Conservation and Management Area (RBCMA), a privately-owned protected area consisting of 1,050 km^2 of subtropical moist broadleaf forest, wetland, and lowland savanna in northwestern Belize. Elevation in the park ranges from 40 m to

160 m and annual rainfall averages from 1,550 to 1,600 mm per year, with a wet season from May through December. Hill Bank is located on the low-lying coastal plain. Selective logging is conducted here to fund the RBMCA. Surveys have been conducted here since 2009, with microhabitat surveys in 2010 and 2015.

La Milpa: the western portion of the RBMCA located in the higher elevation Bravo Hills. No logging is permitted in the core area of La Milpa. A survey was conducted here in 2008 and annually since 2010, with microhabitat surveys in 2008 and 2013.

Mountain Pine Ridge Forest Reserve (MPR): 430 km^2 of lowland and submontane pine forest with some broadleaf moist forest interspersed. Elevation ranges from 120 to 1,016 m and annual rainfall averages from 1,550 to 2,100 mm with a wet season between June and December. Surveys have been conducted here since 2003 and are still being conducted annually; microhabitat surveys were conducted in 2007 and 2011.

Current study

In this study, I used occupancy analysis on data collected from a long-term, remote camera trapping study to examine the factors that determine where pumas occur across eight study sites in Belize and what effects potential prey species have on puma occupancy, the effects that sympatric carnivores have on the occupancy of other carnivores in the same region. I used single-species, single-season occupancy analysis to examine puma habitat preferences. I used single-species, multi-season occupancy to examine changes in puma occupancy over time. I used two-species occupancy to test the effects that potential prey species had on puma occupancy, as well as the effects that larger carnivores had on smaller carnivores for four sympatric carnivores: jaguars, pumas, ocelots, and gray foxes. My research fills an important knowledge gap because pumas are little-studied in Central America. These pumas are considerably smaller and seem to favor smaller prey than their better-studied temperate counterparts. These differences in size and diet are likely to cause differences in the ecological role that this felid plays in this ecosystem. My research also directly examines the effects that sympatric carnivores have on one another, an area of research that is particularly lacking in Central America. My thesis work consists of two primary objectives: 1) Examine the factors affecting puma occupancy across eight study sites, including landscape characteristics, microhabitat features, and trapping rates of jaguars and potential prey species using single-season and multi-season occupancy models, and 2) Examine the effects of potential prey species on pumas and the effects that four sympatric carnivores have on one another using two-species co-occurrence models.

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Figure 1.1. Historic range of the puma (*Puma concolor*) showing the six subspecies identified by genetic analysis. Reprinted from Culver et al. (2000).

Figure 1.2. Present range of the puma (*Puma concolor*). Pumas are known to be extant in the orange areas. They are possibly extant in the purple area (adapted from the IUCN Red List of Threatened Species).

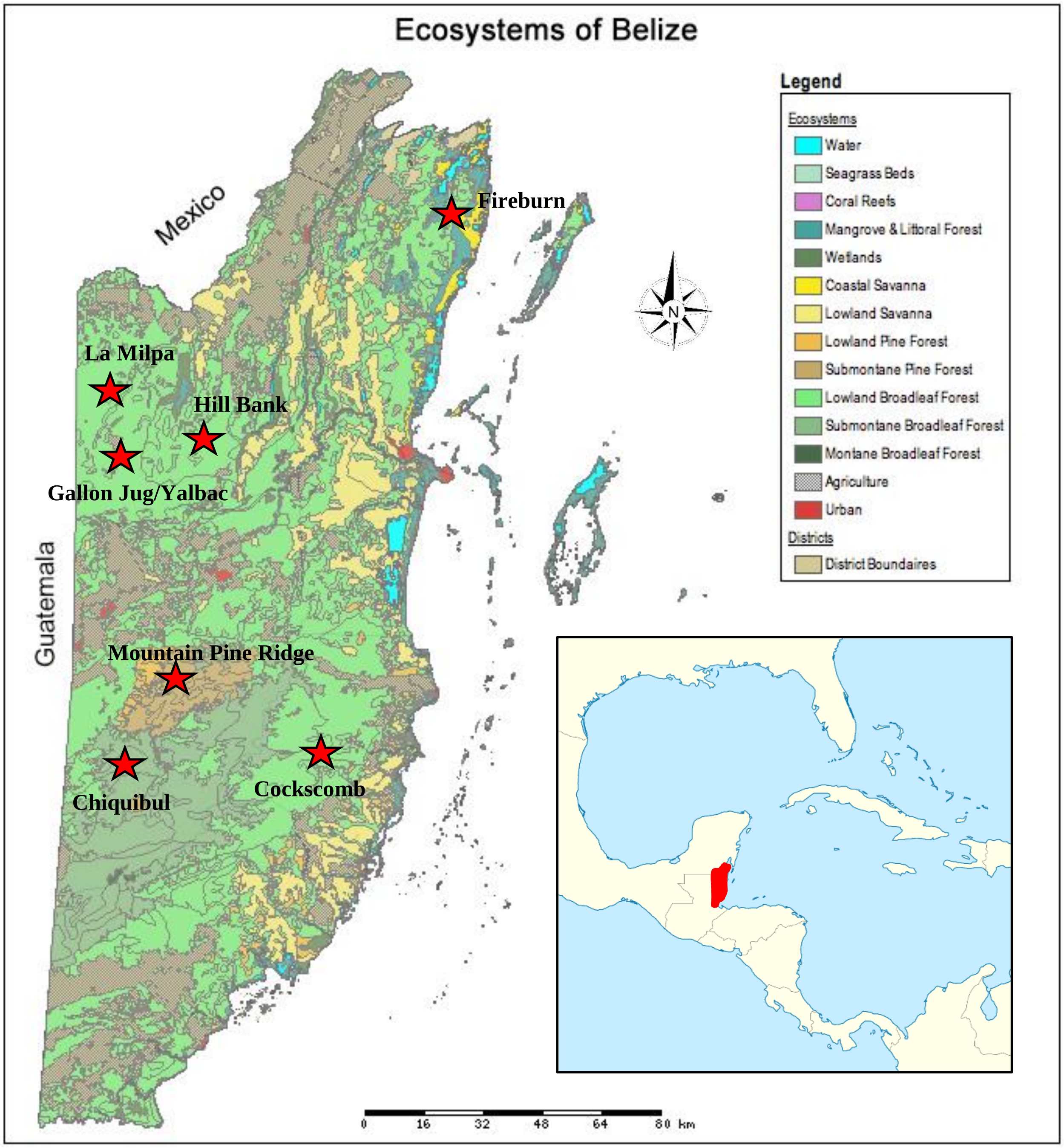

Figure 1.3. Ecosystems of Belize, with eight study sites shown. Belize map adapted from <http://www.iwlearn.net/belize>. Inset map adapted from Wikimedia Commons <https://creativecommons.org/licenses/by-sa/3.0>.

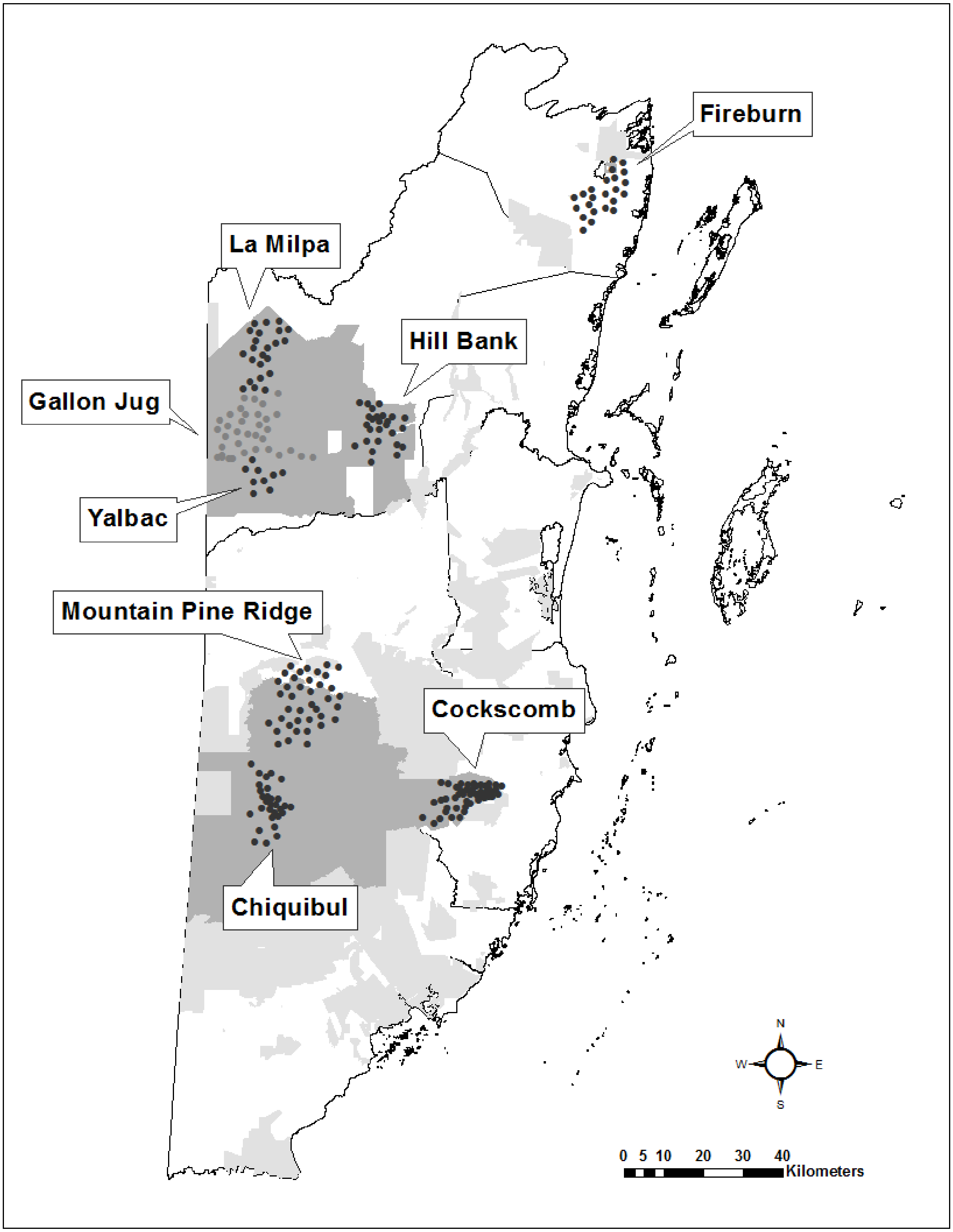

Figure 1.4. The eight study sites in Belize used in this analysis. Each dot represents one camera location in 2015, except Chiquibul (2008), Cockscomb (2008), and Fireburn (2009). Protected areas are shown in gray. Surveyed protected areas are shown in dark gray.

II. *Puma occupancy across 8 study sites in Belize, Central America: effects of habitat, prey, and other predators*

Abstract

Although pumas are well-studied in North and South America, few studies focus on pumas in Central America. To address this knowledge gap, I used single-season and dynamic occupancy models to analyze camera trapping and habitat data (17,011 trap nights at 277 sites) collected at eight study sites over multiple years across Belize. Puma occupancy was strongly positively influenced by jaguar trap success and understory density, with some support for the positive influence of canopy cover, weak positive influence of human trap success, and weak negative influence of stream density. Jaguar trap success was the best predictor of where pumas occurred. Prey species were not found to influence puma occupancy. Mean occupancy across all sites combined was 0.740 (0.013) and ranged from 0.587 (0.042) to 0.924 (0.030). Puma occupancy was higher in logged areas, suggesting that current levels of natural resource extraction at those sites are not detrimental to the species. Over time, puma occupancy rates were generally high (> 0.90) and stable. They were lower in Mountain Pine Ridge, but steadily increased over six years, starting ~ 0.55 and increasing to > 0.75. The positive influence of jaguar activity on puma occupancy suggests that jaguars act as an umbrella species and conservation efforts directed toward them are also likely to benefit pumas. While puma occupancy appeared stable in the areas surveyed, widespread land use changes are taking place across Belize and throughout Central America, warranting further study of the responses of pumas and other large carnivores to human-induced landscape change.

Key words: Belize, camera-trapping, dynamic occupancy, predator-prey dynamics, puma, single-season occupancy

Introduction

Pumas (*Puma concolor*) are the most-studied felid in North America and are generally well-studied in southern South America as well. However, few studies focus on pumas in Central America. The puma has the largest latitudinal distribution of any non-migratory land animal (Iriarte et al. 1990), ranging from British Columbia to Patagonia. Because their range is so extensive, pumas occur in a wide variety of habitats, including tropical rainforest, seasonally flooded savannas, semi-arid scrub, high mountains, dense fir forests, open pine forests, canyon land with stands of mixed conifers, hardwood hammocks, pine flatwoods, cypress swamps, and cabbage palm woodland (Seidensticker et al. 1973, Belden et al. 1988, Maehr et al. 1990, Laing and Lindzey 1991, Sunquist and Sunquist 2002). The characteristics of puma habitat vary widely across their range, but stalking cover appears to be one essential component that is consistent across habitat types (Sunquist and Sunquist 2002). Pumas depend on stalking cover because most successful attacks against prey are launched from < 10 m, however, given their wide geographic distribution, this cover takes many forms throughout their range, including rocks, cliffs, sagebrush, and dense understory (Sunquist and Sunquist 2002). In Belize, this stalking cover mostly takes the form of dense understory. While pumas occur in a wide range of habitats, they have been found to avoid grasslands (Logan and Irwin 1985), agricultural lands, and open meadows, most likely because these areas lack stalking cover (Sunquist and Sunquist 2002). Puma habitat choice may be driven by competition, but the evidence is equivocal (Sunquist and Sunquist 2002). There is some evidence that pumas avoid waterside habitats and dense forest, areas that are favored by jaguars (Schaller and Crawshaw 1980, Emmons 1987, Sollmann et al. 2012).

Because of their extensive distribution, pumas show dramatic variation in size and prey preference across their range. Pumas in the tropics generally weigh half as much as their temperate counterparts. Temperate pumas rely on prey larger than themselves, with deer (*Odocoileus* spp.) composing 60-80% of their diet in North America (Anderson 1983 reviewed in Sunquist and Sunquist 2002). This demonstrates that pumas are morphologically adapted to kill large prey (Iriarte et al. 1990), however, they are opportunistic predators and will switch prey depending on availability (Leopold and Krausman 1991). Medium-sized mammalian prey (1-15 kg) have been found to be the most important prey type for pumas in the tropics (Emmons 1987, Sunquist and Sunquist 2002, De Azevedo 2008, Foster et al. 2010). These differences suggest that studies of pumas in North and South America may not adequately describe Central American pumas. Weber and Rabinowitz (1996) lamented the general lack of knowledge about the predatory patterns of large felids living in the neotropics. While this knowledge gap has been filled somewhat in the last two decades, studies on puma occurrence and population density have lagged behind, especially compared to studies on jaguars (Sunquist and Sunquist 2002, Silver 2004, Weckel et al. 2006a, 2006b, Harmsen et al. 2009, 2011, Foster et al. 2010, 2013, Kelly et al. 2012, Wultsch et al. 2014).(Silver 2004, Weckel et al. 2006a, 2006b, Harmsen et al. 2009, 2011, Foster et al. 2010, Kelly et al. 2012, Wultsch et al. 2014)(Silver 2004, Weckel et al. 2006a, 2006b, Harmsen et al. 2009, 2011, Foster et al. 2010, Kelly et al. 2012, Wultsch et al. 2014) Given this deficiency of knowledge and a trend of population declines (IUCN 2017), pumas in Central America warrant further study. An extensive camera trapping project begun in 2001 and conducted across Belize afforded me the opportunity to contribute to filling this knowledge gap.

My aim was to provide valuable insight on the habitat, prey species, and interspecific competition factors that affect where pumas occur in Belize. To achieve this goal my objectives were to 1) determine the microhabitat and landscape characteristics that influence puma occupancy, 2) examine the effects of human disturbance on puma occupancy, 3) determine the influence of prey species on puma occupancy, 4) examine the effects that jaguars, a larger sympatric carnivore, has on puma occupancy, and 5) examine how puma occupancy has changed over six years. To achieve my objectives, I conducted single-season and dynamic occupancy analyses using microhabitat data and camera trapping data that were collected at eight study sites throughout Belize and landscape habitat data from available geographic information system layers. I used occupancy analysis, rather than estimating abundance, because pumas and most of the other species in this analysis, were not easily identifiable to individual. In the absence of some marking process, occupancy is likely the most appropriate method for analyzing the habitat associations for an unmarked species camera trap data and it give us insight into the species' distribution across the landscape while accounting for imperfect detection. I predicted that puma occupancy would be positively correlated with denser understory because of their affinity for stalking cover. I further predicted that pumas would avoid wetter areas in order to avoid jaguars, which favor those areas (Harmsen et al. 2010, Tobler and Powell 2013). I also predicted that puma occupancy would be higher in areas with higher prey availability, as measured by presence and trap success, especially for medium-sized mammalian prey, and that it would be lower in areas with higher jaguar activity.

Materials and methods

Study site

Belize is a small country (22,963 km^2) approximately the size of Massachusetts lying on the eastern coast of the Yucatan Peninsula in Central America at 17° 15' N latitude and 88° 45' W longitude. Most of the country lies within La Selva Maya (the Mayan Forest), which also includes northern Guatemala and Mexico’s Yucatan Peninsula (Fig. 1.3; Chapter1). At 13.3 million hectares, the Mayan Forest is the second largest tropical rainforest in the Americas, after the Amazon rainforest. Despite its small size, Belize offers a diversity of habitats including broadleaf moist subtropical forest, mountainous pine forest, lowland pine savanna, and wetlands, with elevations ranging from sea level to 1160 m, and is considered a biodiversity hotspot (Conservation International 2011).

I used multiple years of camera trapping data from eight study sites located throughout Belize in this analysis (Fig. 2.1). The study sites included five protected areas (Chiquibul Forest Reserve and National Park, Cockscomb Basin Wildlife Sanctuary, Fireburn Reserve, La Milpa (the western portion of Rio Bravo Conservation and Management Area (RBCMA), and Mountain Pine Ridge Forest Reserve, one protected area with selective logging (Hill Bank, the eastern portion of RBCMA), and two privately-owned timber companies (Gallon Jug Estate and Yalbac Ranch and Cattle Corporation). Yalbac had only nine camera locations in its first year, so it was generally treated as an extension of the contiguous Gallon Jug. However, in some analyses, I treat Yalbac separately because microhabitat data for these two study sites were collected in different years.

Camera Trapping

The dataset used in single-season occupancy analysis is a subset of camera trapping data collected from 2001 to the present and includes only the years in which microhabitat data were collected. Three of the eight study sites each had two years of microhabitat data resulting in a dataset with 11 study site-year combinations with a total of 17,011 trap nights (Table 2.1). Four study sites had a sufficient number of camera locations and years of data to include in the multi-season occupancy analysis. This resulted in four datasets with a total of 34,781 total trap nights (Table 2.2).

Camera trapping techniques followed Silver et al. (2004), modified by experience in the field. The original study was designed to produce jaguar population density estimates, but pumas are similar in size and habits, so the study design is likely appropriate for pumas as well (Harmsen et al. 2009), but the spacing of camera locations may cause problems with spatial autocorrelation in an occupancy analysis. At each study site, a grid was established that consisted of motion-activated cameras placed ~ 2-3 km apart. At each camera location, a pair of cameras was placed ~ 30-40 cm above the ground on either side of a road, active or disused logging road, or human or game trail.

Cameras were only placed on trails and roads because jaguars, pumas, and other large carnivores are so wide-ranging and occur at such low densities that obtaining an adequate number of captures is of paramount importance in obtaining precise density estimates (Tobler and Powell 2013). Cameras placed off trails in early years of this project had capture probabilities of ~ 0 for target species (Marcella Kelly, personal communication).

Each survey was conducted for ~ 2 to 3 months to maximize the number of captures while attempting to meet demographic and geographic closure assumptions. Cameras were checked every ~ 10 days because of high failure rates caused by excessive moisture. The spacing between camera locations was chosen based on the smallest reported home range size for jaguars in this region (10 km^2: Rabinowitz and Nottingham 1986) to ensure that no home range could be located entirely between cameras.

Each photographic image was stamped with the time and date and all encountered animals were recorded. Mammals (except for bats and some smaller rodent species) and many birds (especially ground birds) were identified to species. On any day that both cameras at one location were inoperative, that day was removed from analysis. I collapsed the capture histories to 7-day periods. Because this often resulted in a partial week remaining, 1-6 days were dropped as necessary from the beginning or end of the survey. Periods with inoperative cameras did not necessarily match the 7-day capture occasions, so any capture occasion that was missing > 3 days was considered a missing capture occasion.

Landscape covariates

To examine the landscape effects of habitat on puma occupancy, I plotted camera locations in ArcMap 10.3 (ESRI 2011) using pre-existing geographic information system (GIS) layers available online from the Biodiversity and Environmental Resources Data System of Belize (BERDS) website, which serves as a clearinghouse for GIS data for Belize (Meerman and Clabaugh 2015). I used these GIS layers to estimate the distance from each camera location to the nearest water source, the nearest road, the nearest human settlement, and the nearest agricultural field. All distances were rounded to the nearest 10 m. Shipstern Lagoon was excluded as a water source in the Fireburn study site because it is brackish water. Only roads that are still in use and that carry regular traffic were included. The Roads and Tracks GIS layer is highly detailed and includes many disused roads and abandoned logging roads, therefore, I chose which roads to include based on our experience in the field. This made little difference in most of our study sites, as they generally have few roads, but the Mountain Pine Ridge is covered by a grid of little used, old logging roads. I also calculated the length of roads within 1000 m of each camera location as a measure of the level of human disturbance. This was also done for streams as a measure of how wet an area was. I also calculated the proportion of area within 1000 m of each camera location that was occupied by water bodies, but most values were 0, so this covariate was dropped.

Microhabitat covariates

Microhabitat data were collected at each camera location when it was established and at five-year intervals for longer running sites. Three 100 m transects were laid out at each camera location at 0^0, 120^0, and 240^0 (Fig. 2.2). Any transect that ran directly down a road was adjusted 10^0 to the right or left so that it measured vegetative features and structure. At every 10 meters along each transect, the presence or absence of canopy cover in the crosshairs of a scope was recorded. These points were averaged to produce an estimate of mean canopy cover within 100 m of each camera location. At the center of the camera location and at 50 m and 100 m along each transect, the diameter at breast height (DBH) of the nearest tree in each of four quadrants (NE, SE, SW, NW) and the distances to those trees were measured. The Point-Centered Quarter Method detailed in Pollard (1971) was then used to estimate tree density at each camera location, using the correction factor developed by Warde and Petranka (1981) for any plots that did not contain a tree of sufficient size (≥ 5 cm DBH) within 50 meters of the central point. From these data, I calculated the basal area of trees within 100 meters of each camera location. At 50 meters and 100 meters along each transect, a 40 m transect was laid perpendicular to the 100 m transects and the understory cover was measured every 2 meters. This resulted in 20 samples along each of six transects. A 2 m pole, held vertically, was dropped randomly beside the transect and any vegetation (live or dead) that contacted the pole at three height intervals, 0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m was recorded. I did not differentiate between live and dead vegetation because I did not think that it would have an impact on the effectiveness of the understory to serve as stalking cover and because the difference between live and dead vegetation was not always readily apparent in areas of dense woody vines, lianas, and treefalls. I calculated two habitat covariates for each camera location from the understory data: mean understory density ≤ 1 m in height and the coefficient of variation (CV) of the understory ≤ 1 m in height. This height seemed the most reasonable as a measure of stalking cover, given puma size. To calculate the mean understory density, I averaged the score for 0-0.5 m and 0.5-1 m at each sample and then found the average of the 120 samples for each camera location. To calculate the CV of the understory, I calculated the standard deviation of the mean understory density of the six transects and divided this by the mean understory density. Table 2.3 gives a full list of all habitat covariates included in this analysis. To improve maximum likelihood convergence with covariates and ensure that all covariates were on the same scale, I Z-scored all continuous variables.

I calculated the trapping rates of jaguars, potential prey species, and humans. The trapping rate per 100 trap nights was calculated as the number of independent capture events for each species at each camera location divided by the number of trap nights that the cameras at that location were operational, multiplied by 100. Any photographs less than 30 minutes apart were considered to come from the same animals (i.e., same event) unless they could be determined to be different individuals.

While the protocols for this survey are likely appropriate for large carnivores, which preferentially travel down trails (Harmsen et al. 2010, Tobler and Powell 2013), this may not be true for prey species, which in many cases avoid trails (Harmsen et al. 2010). On average, trap success rates of prey species are likely biased low, however, this bias is similar across all cameras, therefore, this is likely still a useful index of prey species activity.

Trapping rates were calculated for two categories of humans: all humans and non-research. This second trapping rate was calculated by removing all photos of our field crew. This was done because the field crew was photographed many times in the course of their work maintaining cameras and, as such, were photographed at a much higher rate than non-research humans would be at a similar level of presence near a camera location. Including the field crew in the trapping rate, therefore, would likely overestimate the level of human disturbance. On the other hand, the field crew was present and was a potential disturbance, so I also included total human trap success as a covariate.

Trapping rates of jaguars were included because pumas and jaguars have a high degree of dietary overlap and, because of their larger size, we might expect jaguars to negatively affect puma occupancy and/or detection. For the calculation of trapping rates, red brocket (*Mazama americana*) and white-tailed deer were combined into one covariate because various deer species have been found to be the most important prey species in puma diet in multiple studies (Ackerman et al. 1984, Iriarte et al. 1990, Sunquist and Sunquist 2002, De Azevedo 2008). Ground birds were grouped into one covariate and included the following species: crested guan *(Penelope purparascens*), great curassow (*Crax rubra*), ocellated turkey (*Meleagris ocellata*), plain chachalaca (*Ortalis vetula*), and several species of tinamou (*Tinamus major* and *Crypurellus spp*.). Because pumas are generalist carnivores, potential mammalian prey species were grouped into two categories: medium-sized mammalian prey 1-15 kg and large mammalian prey > 15 kg. Núñez et al. (2000) and Sunquist and Sunquist (2002) found mammalian prey 1-15 kg to be most important in tropical puma diet. Medium-sized mammalian prey included Central American agouti (*Dasyprocta punctata*), common opossum (*Didelphis marsupialis*), gray four-eyed opossum (*Philander opossum*), nine-banded armadillo (*Dasypus novemcinctus*), northern raccoon (*Procyon lotor*), paca (*Cuniculus paca*), Virginia opossum (*Didelphis virginiana*), and white-nosed coati (*Nasua narica*). Large mammalian prey included collared peccary (*Pecari* *tajacu*), red brocket deer (*Mazama americana*), white-lipped peccary (*Tayassu pecari*), and white-tailed deer (*Odocoileus virginianus*). Because they weigh up to 300 kg, Baird's tapir (*Tapir bairdii*) were considered too large to be a potential prey species in this area. All of the prey species chosen for inclusion have been found in puma diet, including the smaller carnivores (Emmons 1987, Iriarte et al. 1990, Taber et al. 1997, Farrell et al. 2000, Núñez et al. 2000, Sunquist and Sunquist 2002, Novack et al. 2005, De Azevedo 2008, Foster et al. 2010). I also included the presence/absence of deer, ground birds, jaguars, medium-sized mammalian prey, and large mammalian prey as covariates.

I calculated pairwise Pearson's correlation coefficients for all continuous covariates to test for correlation. Several covariates had a moderate level of correlation (~ 0.4). These were generally between covariates we would expect to be correlated (e.g., distance to nearest water source and length of streams within 1000 m of each camera location). None of these moderately correlated covariates appear in the same model in the candidate model set.

Single-season analysis

I performed all single-season occupancy analysis in the R package *unmarked* 0.11-0 (Fiske and Chandler 2011). The eleven study site-year combinations were combined into one dataset with 277 camera locations ranging in length from 8-16 sampling occasions. Because of missing data, I dropped two sites (Chiquibul 2008 and Mountain Pine Ridge 2007) from my initial analysis. Chiquibul 2008 was missing road width data and Mountain Pine Ridge 2007 was missing road width and canopy cover data, and I expected that mean canopy cover would be a potentially important occupancy covariate and that road width was likely to be an important detection covariate. This resulted in a dataset with 223 camera locations and 14,838 trap nights. I ran a goodness of fit test (bootstrapped MacKenzie and Bailey fit statistic: MacKenzie and Bailey (2004)) on the following global model:

$$M_{global}\ (\sim time\ trend*study\ site\ \sim Canopy\ cover + Basal\ area + Dist\ to\ village + Dist\ to\ water + Dist\ to\ road + Dist\ to\ ag + Length\ of\ streams + Length\ of\ roads + Understory\ density + Understory\ CV + Total\ human\ TS + Ground\ bird\ TS + Deer\ TS + Med\ mammal\ TS + Large\ mammal\ TS)$$

The first two covariates (linear time trend*study site) were the covariates on detection. The rest of the model was the occupancy portion. I ran 5000 bootstrap analyses, resulting in a $\hat{c}$ correction factor of 3.18 to correct for overdispersion in the data relative to the global model.

I first tested several detection models. These models were the null model and detection by study site, camera type, road width, study site*road width, and study site* linear time trend. I expected that study site could potentially be an important detection covariate because the habitat seems to vary more between study sites than within study sites. I included camera type as a covariate because in 2011-2012, we switched from film to digital cameras. Film cameras were limited in the number of exposures on a roll of film (usually 36) and as a result, often missed many captures because the roll of film was fully exposed. This likely resulted in a difference in detection probability. I also tested for the effect of road width because large felids preferentially travel down roads and prefer larger roads. I also ran a detection model combining study site and road width. I did not run a detection model combining study site and camera type because most study sites had only one type of camera. I ran a detection model combining study site with a time trend because this allowed some flexibility in detection, while adding only six parameters. I did not include a model with only a time trend because such a model would not make sense. The study sites were surveyed at different times, so survey occasion 1 at one study site is not related to survey occasion 1 at a second study site. Although allowing detection to vary by occasion and by study site would be a meaningful model, this would require 105 parameters and this dataset is insufficient for that number of parameters.

The high level of overdispersion indicates that the global model does not fit the data well and the resulting inflation of variance is likely to mask any potential significance in covariates. Because of this and because road width did not appear to be an important predictor variable in the occupancy model for pumas, I performed the analysis again with ten study site-years, omitting only Mountain Pine Ridge 2007. This resulted in a dataset with 252 camera locations and 15,481 trap nights. Omitting this one study site allowed for the inclusion of all other covariates. I ran a goodness of fit test on the global model for the 10 study site-year dataset for 10,000 iterations. This resulted in a $\hat{c}$ correction factor of 2.44. I also ran a goodness of fit test on a dataset containing all 11 study site-years (with the mean canopy cover covariate removed from the global model) for 5000 iterations. This produced a $\hat{c}$ estimate of 3.15. Because the 11 study site-year dataset had more overdispersion and was missing mean canopy cover data, all further single-season occupancy analysis was performed on the dataset containing 10 study site-years.

I chose 49 *a priori* models that tested habitat and trap success covariates based on my best thinking about the biology of the study species (Table 2.4). I expected that the presence of jaguars, the wetness of the area, and mean understory density around each camera location would be the best predictors of puma occupancy. I expected that puma occupancy would be higher where understory was denser, but would be lower in wetter areas and where there was higher jaguar activity (as measured by jaguar trap success). I suspected that human disturbance could also potentially affect puma occupancy, so I included human trap success; human trap success excluding our field crew; distance to the nearest village; distance to the nearest road; and the length of roads within 1000 m of each camera location as covariates. The availability of prey species also seemed likely to affect puma occupancy, so I included the trap success rates of four groups of prey species, ground birds, deer, mammalian prey 1-15 kg, and mammalian prey > 15 kg. I did not include individual prey species as covariates because pumas are generalist predators and I did not have reason to expect that the presence of any particular prey species would dramatically affect puma occupancy. Also, including multiple prey species would quickly increase the number of covariates. The effects of individual prey species on puma occupancy will be more directly addressed by two-species occupancy models (see Chapter 3).

Models were ranked based on the Akaike Information Criterion, adjusted for overdispersion (QAIC). I ran an analysis of variance (ANOVA) to test for a difference in means of the occupancy estimates for the 10 study site-years. This test showed that a significant difference did exist (F ratio = 8.584, d.f. = 9, $p < 0.0001$), so I ran a Tukey-Kramer HSD (honestly significant difference) test (Tukey 1953, Kramer 1956) to test for differences in occupancy between each pair of study sites. This test is an exact alpha-level test if the sample sizes are the same and is conservative if the sample sizes are different (Hayter 1984), as is the case here.

It should be noted that this occupancy analysis is equivalent to a site-use analysis, rather than a true occupancy analysis, because pumas likely had home ranges that included > 1 camera location. This likely exacerbated the problem of spatial autocorrelation. When ordinary logistic regression is used to model spatial patterns of species presence/absence, locations closer together in space are likely to exhibit more similar attributes than those that are farther apart (Moore and Swihart 2005). This results in a violation of independence assumptions, resulting in artificially narrow confidence intervals for parameter estimates and potentially erroneous conclusions about the importance of predictor variables (Legendre 1993). To test for spatial autocorrelation in response variables not accounted for by predictor variables, I used Moran's *I* (R version 3.3.1), based on the methods described in Gittleman and Kot (1990). Residuals were calculated as the observed value at site *i* (detection = 1, nondetection = 0) minus the predicted probability of detecting the species at least once during the survey:

$$\widehat{D}_i = \Psi_i p_i^*,$$

where

$$p_i^* = 1 - \prod_{k=1}^{K} (1 - p_{ik}),$$

and K = the number of occasions, as described in Moore and Swihart (2005). The weight matrix was composed of the inverse of the distance between each pair of camera locations. Each study site was tested independently. Only one study site (Cockscomb) showed evidence of spatial autocorrelation (p = 0.0001), therefore, I did not attempt to model the effects of this autocorrelation.

Multi-season analysis

I ran multi-season occupancy models, also called dynamic occupancy models, in the R package *unmarked* 0.11-0 (Fiske et al. 2015). Dynamic occupancy models allow inference about the occurrence of a species at a collection of sites and how changes in occurrence are driven by colonization and local extinction while accounting for imperfect detection (MacKenzie et al. 2002, Kéry and Chandler 2012). These models have four parameters: occupancy in the initial year, site colonization rate, site extinction rate, and detection rate. It should be noted that as a site-use, rather than a true occupancy analysis, colonization and extinction actually refer to a site being newly used or abandoned, rather than true colonization or extirpation. Occupancy in subsequent years is a derived parameter calculated from occupancy in the initial year adjusted annually by the extinction and colonization rates. This requires that sites be in the same location from year to year. Kéry and Chandler (2012) found no studies formally evaluating the performance of various fit statistics for dynamic occupancy models, so I did not perform a goodness of fit test. There were multiple years of data for five study sites, Chiquibul (3 years), Mountain Pine Ridge (13 years), La Milpa (7 years), Hill Bank (7 years), and Gallon Jug (3 years).

Camera locations were generally consistent year to year, but this was not always true, especially in the early years of this study. Therefore, I removed from analysis any sites that were moved more than 250 meters from where the habitat survey was conducted. I removed Chiquibul from analysis because too few stations remained (< 10). I also removed the first 3 years of Mountain Pine Ridge data for the same reason. These models do not allow for a site to be missing in any particular year. This resulted in a further reduction in useable data. The analysis was performed on four study sites (Table 2.2): Gallon Jug (29 camera locations for 3 years), Hill Bank (26 camera locations for 3 years), La Milpa (19 camera locations for 5 years), and Mountain Pine Ridge (33 camera locations for 6 years). Because microhabitat surveys were not conducted every year, I used the survey that was the closest in time.

Because of the large number of potential models, I tested successively larger portions of the models to arrive at full models with all four parameters. I first tested eight models with different covariates on detection and with no covariates on the other three parameters. I selected the best detection model(s), then tested 19 models with different covariates on occupancy. After selecting the best of these models, I ran 16 models with different covariates on colonization and extinction. In each model, the same covariate was used for colonization rate and extinction rate because I expected that the same factors would drive both processes.

Two different approaches were used to assemble the full models. In the first method, I selected one group of best covariates for the four datasets collectively, based on AIC rankings. This involved some subjectivity because the top-ranked covariates were often different among the site-year datasets. The models run to test for the best detection covariates are shown in Table 2.5. I selected three detection covariates for further testing based on the AIC rankings of the candidate models. Eighteen covariates on initial occupancy were combined with each of these three detection covariates. This resulted in 55 models (including the null model; Table 2.6). I dropped one of the detection covariates because it was poorly supported, chose the two best occupancy covariates, and then tested 15 covariates on colonization/extinction. This resulted in 61 models (Table 2.7).

In the second approach, I assembled model components in the same order (i.e., detection, then initial occupancy, and then colonization/extinction covariates), however, instead of choosing the best covariates across datasets, I chose covariates on each component for each dataset separately. I included any covariates from models with ΔAIC < 2 in the previous step. This resulted in different candidate model sets for each of the four datasets. The Hill Bank dataset had three detection covariates with ΔAIC < 2; the other three datasets had one detection covariate. This resulted in 19 candidate models for initial occupancy for three study sites and 55 candidate models for Hill Bank. Gallon Jug and Hill Bank both had a single model with ΔAIC < 2; La Milpa and Mountain Pine Ridge both had three competing top models. This produced 16 candidate models for colonization/extinction for Gallon Jug and Hill Bank and 46 candidate models for La Milpa and Mountain Pine Ridge.

Results

Single season

From the 9 study site-year dataset (excluding Chiquibul and Mountain Pine Ridge 2007), which included all covariates, study site was the top-ranked detection covariate. Camera type was the second most highly-ranked detection covariate, with ΔQAIC = 1.6815. The null model was third, with ΔQAIC = 2.4. Road width, study site*road width, and time trend*study site all had ΔQAIC > 4 and so were not well supported by the data. Study site was used as the detection covariate for all further single-season analysis. As discussed previously, the 10 study site-year dataset (excluding Mountain Pine Ridge 2007) was used for all further single-season analysis because it had a lower level of overdispersion and it included all covariates for all sites, except road width, which did not appear to be an important predictor in puma occupancy models. Detection rates in the top-ranked model ranged from 0.094 (S.E. 0.0373) in Chiquibul to 0.3108 (S.E. 0.0276) in La Milpa (Fig. 2.3).

For occupancy, the model combining jaguar trap success, mean understory density within 100 m of each camera location, and mean canopy cover within 100 m of each camera location was the top-ranked model based on QAIC (Table 2.8). However, five models had ΔQAIC < 2, indicating that these models all drew considerable support from the data, relative to the top-ranked model. Stream density and human trap success were the only additional covariates in the top-ranked models. None of the occupancy covariates of the top-ranked models had beta estimates that included 0 (Table 2.9). Jaguar trap success, mean canopy cover within 100 m of each camera location, mean understory density within 100 m of each camera location, and human trap success all had a positive effect on puma occupancy while stream density had a negative effect on puma occupancy. From the unconditional confidence intervals, jaguar trap success and understory density (to a lesser extent) appear to be important predictors of puma occupancy, but their confidence intervals are larger because of the uncertainty associated with model selection. The other covariates drew less support. Figure 2.4 shows jaguar trap success, mean understory density, mean canopy cover, and human trap success plotted against the predicted occupancy. In each instance, the estimates were drawn from the highest-ranked model in which that covariate appeared.

Naïve occupancy (the proportion of camera locations at which pumas were detected) across all study sites was 0.6389. The estimated occupancy across all camera locations when all three covariates from the top model were at their average value was 0.8500 (S.E. 0.0414). Mean occupancy rate across all study sites was 0.740 (S.E. 0.013). Mean estimates of occupancy at the 10 study site-years ranged from a low of 0.587 (S.E. 0.042) in Chiquibul to a high of 0.924 (S.E. 0.030) in Yalbac, however, Yalbac had only 9 camera locations (Fig 2.5). Excluding Yalbac, Gallon Jug had the next highest occupancy rate at 0.879 (S.E. 0.017). Puma occupancy in Chiquibul was significantly lower than in Cockscomb, La Milpa 2013, Gallon Jug, Hill Bank 2015, and Yalbac. Hill Bank 2010 had significantly lower puma occupancy than La Milpa 2013, Gallon Jug, Hill Bank 2015, and Yalbac. La Milpa 2008 and Mountain Pine Ridge had significantly lower puma occupancy than Gallon Jug, Hill Bank 2015, and Yalbac. Puma occupancy increased significantly in Hill Bank, from 0.666 in 2010 to 0.867 in 2015; puma occupancy also increased in La Milpa, from 0.664 in 2008 to 0.814 in 2013, but the increase was not statistically significant.

Multi-season

The results of the two different approaches (one candidate model set across all four study sites and different candidate model sets for each study site) were similar, so only the results of the first approach will be shown here. In this single candidate model set approach, Gallon Jug had three models with ΔAIC < 2; Hill Bank had five models with ΔAIC < 2; La Milpa had six models with ΔAIC < 2; and Mountain Pine Ridge had seven models with ΔAIC < 2 (Table 2.10).

From the top-ranked model from each study site, only three of the covariates were well supported by the data (i.e., their 95% confidence interval did not include 0) (Table 2.11). Basal area had a positive effect on detection in Hill Bank, mean understory density had a negative effect on extinction rate in La Milpa, and canopy cover had a positive effect on detection in Mountain Pine Ridge. None of the other covariates were important predictors.

The parameter estimates from the two approaches were similar, except for the initial occupancy estimates in Hill Bank and Mountain Pine Ridge (Table 2.12). Initial occupancy was generally high, with the exception of one approach in Mountain Pine Ridge which had an initial occupancy estimate of 0. Site colonization in Gallon Jug and Hill Bank was high or 1.00, indicating that any sites that were initially unused quickly because used. Site colonization in La Milpa was 0. Site extinction at all study sites was close to 0. Detection rates were > 0.30, except for Mountain Pine Ridge, which was ~ 0.20. Table 2.13 shows the annual occupancy estimate, by study site, for both approaches. The two approaches produced very similar estimates, with the only noticeable differences being in Mountain Pine Ridge. In both approaches, the annual occupancy rate was stable over three years in Gallon Jug, ranging between 0.9345 and 0.9556. The annual occupancy rate in Hill Bank was ~ 0.75 in the initial year, but increased to > 0.90 for the next two years. Annual occupancy in La Milpa was initially ~ 0.90, then increased to > 0.96 in year three, then returned to previous levels two years later. Mountain Pine Ridge had the lowest occupancy rates overall, with an occupancy rate of ~ 0.55 in the first year. Occupancy jumped in the second year and then increased steadily (Fig. 2.6).

Discussion

Single-season

There was strong support for a positive effect of both understory density and jaguar trap success on puma occupancy. A denser understory likely provides the stalking cover that other researchers have found to be the preferred habitat of pumas (Sunquist and Sunquist 2002), but the positive association between pumas and jaguars came as a surprise. The high degree of dietary overlap between these two sympatric carnivores suggests that they would be competitors, so finding that pumas are more likely to occur where jaguar activity (i.e., trap success) is high is surprising. Of course, trap success is only an index and it has not been calibrated to abundance here, but it does suggest that jaguars are more active where their trapping rates are higher, if detection rates are similar across study sites. Puma detection rates were relatively uniform throughout the study area and there is no reason to suspect that jaguar detection would not be, as well. Of course, a simple correlation does not give us any information about the causal explanation of this association. It would seem unlikely that pumas are directly choosing to associate with a larger competitor. It would seem more reasonable to suggest that perhaps both species are independently making similar habitat choices. Perhaps both species are choosing areas with thicker understory where potential prey are more abundant or more vulnerable to predation.

Pumas were also more likely to occur in areas with a denser canopy, although there was lower support for this than for jaguar trap success or understory density. Again, it may be that pumas are showing a preference for areas where prey are more abundant. But we did not find any support for relationships between pumas and prey activity. Puma occupancy was lower in areas with higher stream density, but the evidence was not strong. I expected this because other researchers have found that jaguars prefer wetter areas, therefore we would expect pumas to avoid these areas, if they are attempting to avoid jaguars. Of course, I did not find any evidence that pumas were avoiding jaguars. This may indicate that pumas simply have an aversion to wetter areas or it could indicate that there is an interaction between pumas and jaguars that is mediated by habitat. Jaguars have been observed taking prey in water (caiman, for example), behavior that has not been reported for pumas. Therefore, pumas may find these areas less prey-dense than jaguars, so the benefits of hunting in wetter areas may not be sufficiently high to risk encountering the larger competitor. However, in drier areas, where pumas may be more comfortable hunting, the reward may justify the risk of encountering jaguars. This is just conjecture and would require further study to confirm. There was also some weak evidence that pumas were more likely to occur where human trap success was higher, but the evidence was not strong. This may simply reflect that both humans and pumas prefer to travel on roads and trails.

Although this single-season analysis did not explicitly examine puma occupancy over time, the 10 surveys in this dataset occurred over an 8-year period. Examining the mean occupancy rates by study site, there is a very clear pattern of increasing occupancy over time, with study sites after 2012 having significantly higher occupancy estimates than those before 2012. One caveat, however, is that these later surveys were all conducted in the same part of Belize. However, for the two study sites with two years of data, both showed increases in puma occupancy. Puma occupancy increased in both La Milpa and Hill Bank, with a statistically significant increase in Hill Bank.

The positive association between jaguars and pumas is noteworthy because it suggests that jaguars are not negatively impacting puma occupancy. Thus conservation efforts directed at jaguars, a charismatic species that is a high conservation priority for many countries, are likely to benefit pumas, as well. Jaguars appear to act as an umbrella species (Lambeck 1997b), rather than as a superpredator, at least in regards to pumas. The three smaller felid species in Belize, the ocelot, margay (*Leopardus wiedii*), and jaguarundi will require separate study. Two-species occupancy models, which examine the effects of one species on another more directly (see Chapter3), may give better insight into the effects that jaguars have on puma occupancy.

Multi-season occupancy

Puma occupancy was high (> 0.90) across three of the four study sites. With such high occupancy rates, there were few unoccupied sites, but site colonization rates were also high, so any patches that were unoccupied were quickly colonized. The one exception was La Milpa, which had a site colonization rate of 0. This may reflect that all sites were occupied throughout the survey, so there was never an opportunity for colonization. Site extinction rate was consistently low, indicating that sites were rarely abandoned. In a site-use analysis such as this one, extinction refers to a site no longer being used and not to extirpation.

One concern is that these models may have trouble producing estimates when occupancy is particularly high. As occupancy approaches 1, there are few sites available for colonization. And if sites are rarely abandoned, these models may have trouble estimating these two parameters. Another concern is that these models are not adjusted for overdispersion. The single-season dataset was overdispersed, so it seems likely that the multi-season dataset was as well. Unfortunately, no methods have yet been developed to address this overdispersion.

La Milpa and Mountain Pine Ridge, with five and six years of useable data, respectively, are probably more reasonable for detecting trends in yearly occupancy rates than are Hill Bank or Gallon Jug, which each had only three years of useable data. Puma occupancy in Gallon Jug, Hill Bank, and La Milpa was high and relatively constant. Hill Bank showed a marked increase between the first and second year, but this may only be an artifact of having only three years of data. Mountain Pine Ridge had considerably lower occupancy estimates than the other three study sites, but increased steadily.

Taken together, the single-season and multi-season analyses suggest that puma occupancy is steady or increasing throughout Belize, at least in the areas examined. Somewhat surprisingly, occupancy was highest in the areas that were the most disturbed (Yalbac Ranch and Cattle Corporation, Gallon Jug Estate, and Hill Bank). The timber industry in Belize practices selective harvest focusing on a few, high-value species, as mandated by the Forest Department. Our findings suggest that the current level of natural resource extraction is not harmful to puma occupancy in those areas. However, none of our study sites were in urban or agricultural areas, so we cannot speculate how land use changes in these areas are impacting pumas in Belize. Furthermore, this analysis suggests that pumas may benefit from conservation efforts directed at jaguars because of a lack of negative interaction between the two species.

Future work could involve producing population density estimates for pumas in Belize. This is more challenging for pumas than other felids because of the lack of distinctive markings. Puma density estimates have been produced using non-invasive genetic sampling of scat (Wultsch et al. 2014), but this method would be difficult to use to monitor puma populations over time. Mark-resight methods have been used to estimate puma population densities from camera trapping data (Sollmann et al. 2013, Rich et al. 2014, Zanon-Martinez et al. 2016) and the full dataset from which this study was drawn would seem to offer an ideal opportunity to use these methods. However, our agreement rates of puma identifications from photographs among three independent observers were judged to be too low (~ 40%) to continue with this method of analysis. Puma populations in Belize continue to offer numerous opportunities for further research.

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Table 2.1. Study sites and years where microhabitat data were collected. This subset of a larger Belize dataset was used in the single-season occupancy analysis for pumas. Chiquibul had an unusually low number of trap nights because of camera vandalism and theft.

Study site	Year	Camera locations	Trap nights
Chiquibul	2008	29	643
Cockscomb	2008	38	2419
Fireburn	2009	19	1504
Gallon Jug	2013	28	2017
Hill Bank	2010	19	1022
Hill Bank	2015	31	2105
La Milpa	2008	22	1347
La Milpa	2013	22	1666
Mountain Pine Ridge	2007	24	1530
Mountain Pine Ridge	2011	35	2043
Yalbac	2014	9	715
Total		276	17,011

Table 2.2. Study sites used in multi-season occupancy analysis for pumas in Belize. Any cameras that were moved > 250 m from where the microhabitat survey was conducted were dropped from analysis. Any camera locations that were missing in any year were also dropped from analysis. Microhabitat surveys were conducted the year that a study site was established and every five years subsequently. The microhabitat survey closest in time to each survey was used in analysis.

Study Site	Annual Surveys	Microhabitat Surveys	Camera locations	Trap nights
Gallon Jug	2013-2015	2013	29	6,433
Hill Bank	2013-2015	2015	26	6,271
La Milpa	2011-2015	2013	19	7,579
Mountain Pine Ridge	2010-2015	2011	33	14,498

Table 2.3. Covariates used in single-season puma occupancy analysis in Belize. All continuous covariates were Z-scored to improve maximum likelihood convergence and to ensure that all covariates were on the same scale. Those that were log-transformed are indicated as (log).

Abbreviation	Covariate
Basal area	Tree basal area (m^2/ha) in 100 m buffer (log)
Camera type	Type of camera – film or digital
Canopy cover	Average canopy cover in 100 m buffer
Dist to ag	Distance (m) to nearest agricultural field (log)
Dist to road	Distance (m) to nearest road (log)
Dist to village	Distance (m) to nearest village (log)
Dist to water	Distance (m) to nearest water source (log)
Length of roads	Length (m) of roads in 1000 m buffer
Length of streams	Length (m) of streams in 1000 m buffer
Roads P/A	Presence/absence of roads in 1000 m buffer
Road width	Width (m) of road or trail at the camera location
Study site	Study site
Understory CV	Coefficient of variation of understory density in 100 m buffer
Understory density	Mean understory density in 100 m buffer
Deer TS	Deer trap success
Ground bird TS	Ground bird trap success
Human TS	Human trap success, excluding field crew
Jaguar TS	Jaguar trap success
Large mammal TS	Large-sized mammalian prey trap success (> 15 kg)
Med mammal TS	Medium-sized mammalian prey trap success (1-15 kg)
Total human TS	Human trap success (log)
Deer P/A	Presence/absence of deer
Ground bird P/A	Presence/absence of ground birds
Jaguar P/A	Presence/absence of jaguars
Large mammal P/A	Presence/absence of large mammalian prey
Med mammal P/A	Presence/absence of medium-sized mammalian prey

Table 2.4. Candidate model set for single-season occupancy of a 10 study site-year dataset in Belize (excluding Mountain Pine Ridge 2007). Covariates that were log-transformed are indicated by (log). T.S. = Trap success.

	Detection Covariates	Occupancy Covariates
M1	Null	Null
M2	Study site	Basal area in 100 m buffer (log)
M3	Study site	Presence/absence of roads in 1000 m buffer
M4	Study site	Null
M6	Study site	Distance to nearest village (log)
M7	Study site	Distance to nearest agricultural field (log)
M8	Study site	Human T.S. (log)
M9	Study site	Human T.S., excluding field crew
M10	Study site	Distance to nearest road (log)
M11	Study site	Length of roads in 1000 m buffer
M12	Study site	Length of streams in 1000 m buffer
M13	Study site	Distance to nearest water source (log)
M14	Study site	Mean understory density in 100 m buffer
M15	Study site	Understory density C.V. in 100 m buffer
M16	Study site	Ground bird T.S.
M17	Study site	Deer T.S.
M18	Study site	Medium-sized mammalian prey T.S.
M19	Study site	Jaguar T.S.
M20	Study site	Large-sized mammalian prey T.S.
M21	Study site	Ground bird T.S. + large-sized mammalian prey T.S.
M22	Study site	Deer T.S. + ground bird T.S.
M23	Study site	Medium-sized mammalian prey T.S. + large-sized mammalian prey T.S.
M24	Study site	Jaguar T.S. + large-sized mammalian prey T.S.
M25	Study site	Jaguar T.S. + large-sized mammalian prey T.S. + ground bird T.S.
M28	Study site	Jaguar T.S. + Human T.S. (log)

Table 2.4 continued

	Detection covariates	Occupancy covariates
M29	Study site	Jaguar T.S. + length of streams in 1000 m buffer
M30	Study site	Jaguar T.S. + length of roads in 1000 m buffer
M31	Study site	Jaguar T.S. + distance to nearest village (log)
M32	Study site	Jaguar T.S. + basal area in 100 m buffer (log)
M33	Study site	Jaguar T.S. + distance to nearest water source (log)
M34	Study site	Jaguar T.S. + average understory density in 100 m buffer
M35	Study site	Jaguar T.S. + understory density C.V. in 100 m buffer
M36	Study site	Jaguar T.S. + distance to nearest agricultural field (log)
M37	Study site	Jaguar T.S. + presence/absence of roads in 1000 m buffer
M38	Study site	Jaguar T.S. + average understory density in 100 m buffer + length of streams in 1000 m buffer
M39	Study site*time trend	Jaguar T.S. + average understory density in 100 m buffer
M40	Study site*time trend	Jaguar T.S. + average understory density in 100 m buffer + length of streams in 1000 m buffer
M41	Study site	Jaguar T.S. + human T.S., excluding field crew
M42	Study site	Average canopy cover in 100 m buffer
M43	Study site	Jaguar T.S. + average canopy cover in 100 m buffer
M44	Study site	Jaguar T.S. + average canopy cover in 100 m buffer + average understory density in 100 m buffer
M45	Study site	Presence/absence of ground birds
M46	Study site	Presence/absence of deer
M47	Study site	Presence/absence of medium-sized mammalian prey
M48	Study site	Presence/absence of jaguars
M49	Study site	Presence/absence of large-sized mammalian prey

Table 2.5. Candidate models run to test detection covariates for multi-season occupancy for pumas at four study sites in Belize. These models consist of four components: initial occupancy, colonization rate, extinction rate, and detection rate. Covariates that were log-transformed are indicated as (log). T.S. = trap success.

Model	Occupancy covariates	Colonization/Extinction covariates	Detection covariate
det0	No covariate	No covariate	No covariate
det1	No covariate	No covariate	Understory density
det2	No covariate	No covariate	Total human T.S. (log)
det3	No covariate	No covariate	Human T.S., excluding field crew
det4	No covariate	No covariate	Canopy cover
det5	No covariate	No covariate	Basal area
det6	No covariate	No covariate	Road width
det7	No covariate	No covariate	Jaguar T.S.

Table 2.6. Partial candidate model set to test initial occupancy covariates of multi-season occupancy models for pumas at four study sites in Belize. These models consist of four components: initial occupancy, colonization rate, extinction rate, and detection. The top-ranked detection covariates from a previous run of models were used in each model. Models were ranked using AIC (Akaike Information Criteria). Covariates that were log-transformed are indicated as (log). T.S. = trap success.

Model	Initial occupancy covariate	Colonization/Extinction covariates	Detection covariate
occ0	No covariate	No covariate	No covariate
occ1	No covariate	No covariate	Top covariate(s)
occ2	Distance to nearest village (log)	No covariate	Top covariate(s)
occ3	Distance to nearest water source (log)	No covariate	Top covariate(s)
occ4	Distance to nearest ag. field (log)	No covariate	Top covariate(s)
occ5	Distance to nearest road (log)	No covariate	Top covariate(s)
occ6	Length of streams in 1000 m buffer	No covariate	Top covariate(s)
occ7	Length of roads in 1000 m buffer	No covariate	Top covariate(s)
occ8	Mean canopy cover in 100 m buffer	No covariate	Top covariate(s)
occ9	Basal area in 100 m buffer	No covariate	Top covariate(s)
occ10	Mean understory density in 100 m buffer	No covariate	Top covariate(s)
occ11	Understory C.V. in 100 m buffer	No covariate	Top covariate(s)
occ12	Human T.S., excluding field crew	No covariate	Top covariate(s)
occ13	Human T.S. (log)	No covariate	Top covariate(s)
occ14	Ground bird T.S.	No covariate	Top covariate(s)
occ15	Deer T.S.	No covariate	Top covariate(s)
occ16	Medium-sized mammal T.S.	No covariate	Top covariate(s)
occ17	Jaguar T.S.	No covariate	Top covariate(s)
occ18	Large-sized mammal T.S.	No covariate	Top covariate(s)

Table 2.7. Partial candidate model set for full multi-season occupancy models for pumas at four study sites in Belize. These models consist of four components: initial occupancy, colonization rate, extinction rate, and detection. In each model, the same covariates were used for both colonization and extinction. The covariates from the top-ranked models that were previously run to test detection and initial occupancy covariates were combined with 14 covariates or combinations of covariates on colonization and extinction rates. Models were ranked using AIC (Akaike Information Criteria). Covariates that were log-transformed are indicated as (log). T.S. = trap success.

Model	Initial occupancy covariate	Colonization/Extinction covariate	Detection covariate
fm0	No covariate	No covariate	No covariate
fm1	Top covariate(s)	No covariate	Top covariate(s)
fm2	Top covariate(s)	Jaguar T.S.	Top covariate(s)
fm3	Top covariate(s)	Mean canopy cover in 100 m buffer	Top covariate(s)
fm4	Top covariate(s)	Basal area in 100 m buffer (log)	Top covariate(s)
fm5	Top covariate(s)	Mean understory density in 100 m buffer	Top covariate(s)
fm6	Top covariate(s)	Understory C.V. in 100 m buffer	Top covariate(s)
fm7	Top covariate(s)	Human T.S. (log)	Top covariate(s)
fm8	Top covariate(s)	Human T.S., excluding field crew	Top covariate(s)
fm9	Top covariate(s)	Deer T.S.	Top covariate(s)
fm10	Top covariate(s)	Medium-sized mammal T.S.	Top covariate(s)
fm11	Top covariate(s)	Large-sized mammal T.S.	Top covariate(s)
fm12	Top covariate(s)	Mean understory density in 100 m buffer*Jaguar T.S.	Top covariate(s)
fm13	Top covariate(s)	Mean understory density in 100 m buffer*Medium-sized mammal T.S.	Top covariate(s)
fm14	Top covariate(s)	Mean understory density in 100 m buffer*Large-sized mammal T.S.	Top covariate(s)
fm15	Top covariate(s)	Mean understory density in 100 m buffer*Deer T.S.	Top covariate(s)

Table 2.8. Top single-season puma occupancy models (ΔQAIC <4) for the 10 study site-year dataset ranked by QAIC ($\hat{c}$ = 2.44). Only the occupancy component of each model is shown here. Study site was the covariate on detection for all models shown. Study site*time trend were also used as detection covariates, but no model with those covariates appears in the top-ranked models. K is the number of parameters in each model. ΔQAIC is the difference between QAIC of each model and the QAIC of the top model. QAIC weight is the proportion of support each model draws from the data. Cumulative weight is the sum of QAIC weight for each model and all higher-ranked models.

	Occupancy	K	ΔQAIC	QAIC weight	Cumulative weight
M44	Jaguar TS + Canopy cover + Understory density	12	0.000	0.181	0.181
M38	Jaguar TS + Understory density + Length of streams	12	0.925	0.114	0.296
M34	Jaguar TS + Understory density	11	1.246	0.097	0.393
M28	Jaguar TS + Total human TS	11	1.894	0.070	0.463
M29	Jaguar TS + Length of streams	11	1.900	0.070	0.533
M24	Jaguar TS + Large mammal TS	11	2.319	0.057	0.590
M19	Jaguar TS	10	2.684	0.047	0.638
M43	Jaguar TS + Canopy cover	11	2.924	0.042	0.680
M35	Jaguar TS + Understory CV	11	2.947	0.042	0.721
M36	Jaguar TS + Dist to ag	11	3.240	0.036	0.757
M33	Jaguar TS + Dist to water	11	3.361	0.034	0.791
M25	Jaguar TS + Large mammal TS + Ground bird TS	12	3.414	0.033	0.824
M31	Jaguar TS + Dist to village	11	3.428	0.033	0.857

Table 2.9. Untransformed estimates of coefficients for occupancy covariates (betas) from the top-ranked (ΔQAIC < 2) single-season models for puma occupancy. Unconditional 95% confidence intervals are also shown ($\hat{c} = 2.44$). The covariates are jaguar trap success, mean canopy cover within 100 meters of each camera location, mean understory density 0-1.0 m in height, within 100 meters of each camera location, length of streams within 1000 meters of the camera location, and the log transformation of human trap success. The mean puma occupancy estimate and standard error are shown for each model. Confidence intervals that do not cross 0 are shown in bold.

Model	Covariate	Estimate	95% Confidence Interval	Unconditional C.I.	Mean Occupancy
M44	Jaguar T.S.	1.8160	**0.7292 – 2.9033**	**0.17 – 3.37**	0.799 (0.051)
	Canopy cover	0.6510	**0.2197 – 1.0827**	-0.03 – 1.29	
	Understory density	0.8590	**0.3322 – 1.3850**	**0.03 – 1.48**	
M38	Jaguar T.S.	2.1133	**0.899 – 3.328**	**0.29 – 3.84**	0.795 (0.086)
	Stream density	-0.5067	**-0.908 – -0.106**	-1.12 – 0.13	
	Understory density	0.6511	**0.121 – 1.182**	-0.17 – 1.24	
M34	Jaguar T.S.	1.7608	**0.662 – 2.86**	**0.13 – 3.33**	0.8 (0.053)
	Understory density	0.7749	**0.176 – 1.374**	-0.13 – 1.43	
M28	Jaguar T.S.	1.3965	**0.327 – 2.466**	-0.33 – 2.8	0.787 (0.05)
	Human T.S.	0.7935	**0.047 – 1.540**	-4.33 – 17.21	
M29	Jaguar T.S.	2.2108	**0.950 – 3.472**	**0.25 – 3.82**	0.754 (0.041)
	Stream density	-0.5267	**-0.910 – -0.143**	-1.13 – 0.08	

Table 2.10. Top-ranked (ΔAIC < 2) multi-season models of occupancy for pumas in Belize. There was one candidate model set for all four study sites. These models consist of four components: initial occupancy, colonization rate, extinction rate, and detection rate. Models were ranked by AIC (Akaike Information Criterion) for each of four study sites. K is the number of parameters in each model. ΔAIC is the difference between AIC of each model and the AIC of the top model. AIC weight is the proportion of support each model draws from the data. MPR = Mountain Pine Ridge. T.S. = trap success.

Study site	Initial occupancy covariate	Extinction/colonization covariate	Detection covariate	K	ΔAIC	AIC weight
Gallon Jug	Basal area	Basal area	Basal area	8	0	0.22
	Basal area	Understory density	Canopy cover	8	0.42	0.18
	Basal area	Understory CV	Basal area	8	1.38	0.11
Hill Bank	Length of roads	Total Human T.S.	Basal area	8	0	0.2
	Basal area	Canopy cover	Basal area	8	0.23	0.18
	Length of roads	Basal area	Basal area	8	0.26	0.18
	Length of roads	Canopy cover	Basal area	8	0.85	0.13
	Length of roads	Basal area	Canopy cover	8	1.56	0.092
La Milpa	Length of roads	Understory density*Med mammal T.S.	Basal area	12	0	0.15819
	Length of roads	Basal area	Basal area	8	1.22	0.08615
	Length of roads	Understory CV	Basal area	8	1.49	0.07521
	Length of roads	Understory density*Jaguar T.S.	Basal area	12	1.73	0.06661
	Length of roads	Basal area	Canopy cover	8	1.84	0.06298
	Length of roads	No covariate	Basal area	6	1.85	0.06287
MPR	Length of roads	Basal area	Canopy cover	8	0	0.16
	Length of roads	Total Human T.S.	Canopy cover	8	0.87	0.1
	Length of roads	Jaguar T.S.	Canopy cover	8	1.04	0.095
	Length of roads	Canopy cover	Canopy cover	8	1.63	0.071
	Length of roads	Human T.S.	Canopy cover	8	1.76	0.066
	Length of roads	Deer T.S.	Canopy cover	8	1.84	0.064
	Length of roads	Understory density	Canopy cover	8	1.92	0.062

Table 2.11. 95% confidence intervals for the untransformed estimates of coefficients for covariates (betas) of the top multi-season models for pumas at each of four study sites in Belize. There was one candidate model set for all four study sites. These models consist of four components: initial occupancy (psi), colonization rate (col), extinction rate (ext), and detection rate (p). T.S. = trap success. Bold indicates confidence intervals that do not overlap zero.

Study site	Covariate	95% Confidence Interval
Gallon Jug	psi(Intercept)	(-79.059, 123.085)
	psi(Basal area)	(-82.677, 120.959)
	col(Intercept)	(-398.597, 431.501)
	col(Basal area)	(-353.916, 356.528)
	ext(Intercept)	(-12.7445, 2.162)
	ext(Basal area)	(-2.417, 8.407)
	p(Intercept)	(-0.907, -0.582)
	p(Basal area)	(-0.017, 0.387)
Hill Bank	psi(Intercept)	(-1.766, 5.653)
	psi(Length roads)	(-3.233, 7.575)
	col(Intercept)	(-27.864, 74.519)
	col(Total human T.S.)	(-32.748, 88.220)
	ext(Intercept)	(-24.927, 3.148)
	ext(Total human T.S.)	(-12.666, 2.580)
	p(Intercept)	(-1.024, -0.633)
	p(Basal area)	**(0.134, 0.547)**
La Milpa	psi(Intercept)	(-82.856, 322.136)
	psi(Length roads)	(-210.651, 54.867)
	col(Intercept)	(-523.576, 283.626)
	col(Understory density)	(-435.272, 242.587)
	col(Med mammal T.S.)	(-597.754, 717.265)
	col(Understory density*Med mammal T.S.)	(-544.360, 608.383)
	ext(Intercept)	**(-17.528, -3.329)**
	ext(Understory density)	(-11.120, -1.433)
	ext(Med mammal T.S.)	(-0.937, 5.948)
	ext(Understory density*Med mammal T.S.)	(-0.678, 4.515)
	p(Intercept)	(-0.887, -0.536)
	p(Basal area)	(-0.064, 0.230)

Table 2.11 continued

Study site	Covariate	95% Confidence Interval
Mountain Pine Ridge	psi(Intercept)	(-77.888, 55.672)
	psi(Length roads)	(-118.780, 82.720)
	col(Intercept)	(-1.092, 3.793)
	col(Basal area)	(-1.232, 2.414)
	ext(Intercept)	(-7.833, 0.966)
	ext(Basal area)	(-7.778, 1.812)
	p(Intercept)	(-1.663, -0.992)
	p(canopy)	**(0.227, 0.790)**

Table 2.12. Parameter estimates for multi-season occupancy for pumas for each of four study sites in Belize. The parameters for each of two approaches are shown. In the first approach (Single candidate model dataset), there was one candidate model set across all four study sites. In the second approach (Best model dataset), there were different candidate model sets for each study site.

Study site	Parameter	Single candidate model dataset	Best model dataset
Gallon Jug	Initial occupancy	1.000 (0.000)	1.000 (0.000)
	Site colonization	1.000 (0.000)	1.000 (0.000)
	Site extinction	0.005 (0.019)	0.005 (0.019)
	Detection	0.322 (0.018)	0.322 (0.018)
Hill Bank	Initial occupancy	0.875 (0.207)	0.416 (0.345)
	Site colonization	1.000 (0.000)	0.895 (0.158)
	Site extinction	0.000 (0.000)	0.000 (0.000)
	Detection	0.304 (0.021)	0.326 (0.020)
La Milpa	Initial occupancy	1.000 (0.000)	1.000 (0.000)
	Site colonization	0.000 (0.000)	0.000 (0.000)
	Site extinction	0.000 (0.000)	0.000 (0.000)
	Detection	0.329 (0.020)	0.364 (0.018)
Mountain Pine Ridge	Initial occupancy	0.000 (0.001)	0.845 (0.242)
	Site colonization	0.794 (0.204)	0.537 (0.131)
	Site extinction	0.031 (0.068)	0.104 (0.078)
	Detection	0.209 (0.028)	0.219 (0.027)

Table 2.13. Yearly puma occupancy estimates for each of four study sites in Belize. The estimates from the first approach (one candidate model set across all four study sites) is shown first. The estimates from the second approach (different candidate model sets for each study site) are shown second. Standard errors are shown in parentheses.

Study site	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Gallon Jug	0.9653 (0.028)	0.9345 (0.045)	0.9556 (0.032)			
Hill Bank	0.7488 (0.094)	0.9721 (0.035)	0.9363 (0.044)			
La Milpa	0.8949 (0.079)	0.9164 (0.062)	0.9619 (0.062)	0.9440 (0.051)	0.9211 (0.057)	
Mountain Pine Ridge	0.5523 (0.160)	0.6535 (0.109)	0.6597 (0.104)	0.6630 (0.106)	0.7583 (0.092)	0.7556 (0.098)

Study site	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
Gallon Jug	0.9653 (0.029)	0.9345 (0.047)	0.9556 (0.028)			
Hill Bank	0.7532 (0.101)	0.9144 (0.064)	0.9157 (0.046)			
La Milpa	0.8950 (0.063)	0.8981 (0.040)	0.9714 (0.040)	0.9580 (0.049)	0.9134 (0.056)	
Mountain Pine Ridge	0.5330 (0.135)	0.7287 (0.087)	0.7989 (0.083)	0.8242 (0.088)	0.8333 (0.093)	0.8365 (0.097)

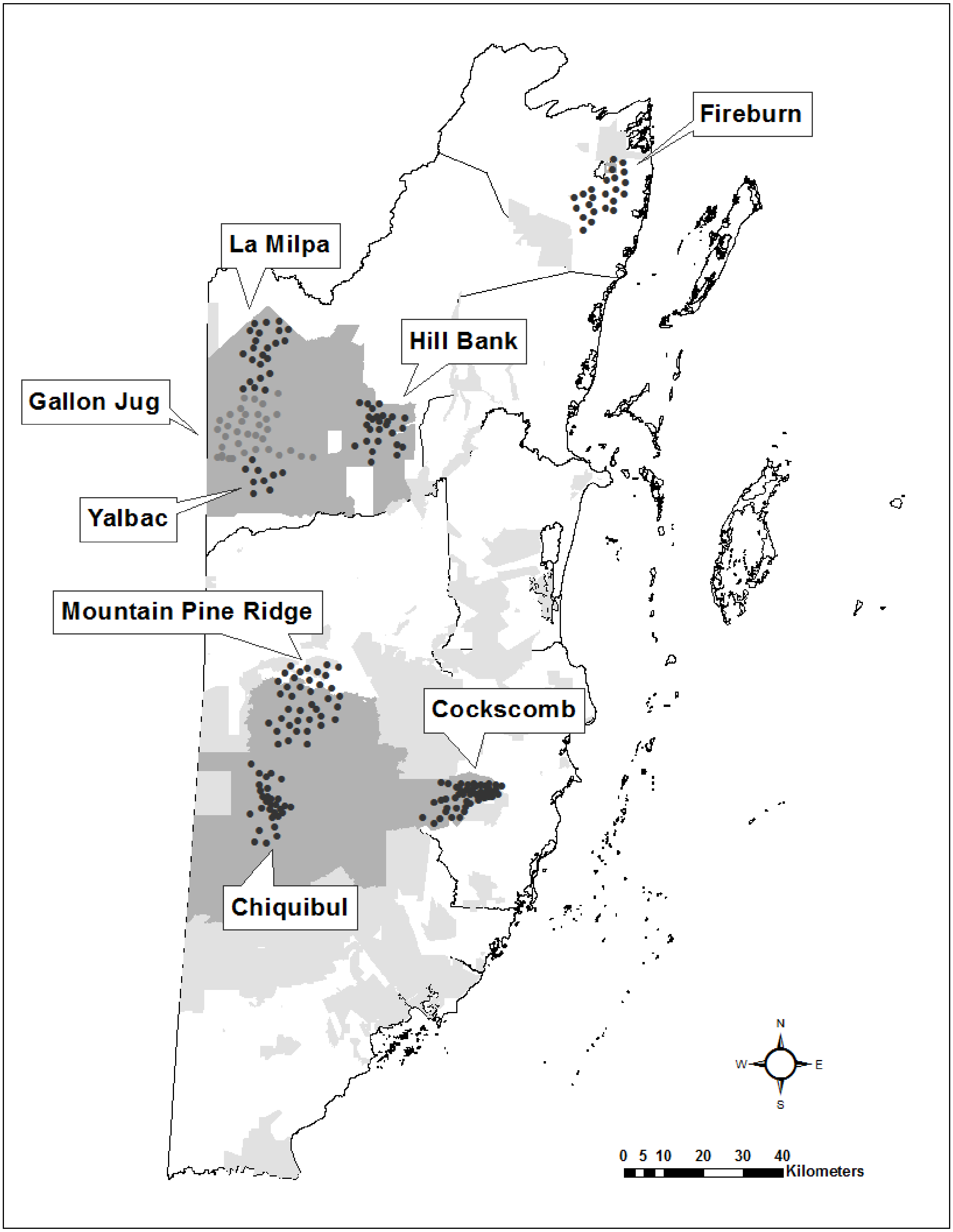

Figure 2.1. The eight study sites in Belize used in this analysis. Each dot represents one camera location as of 2015, except Chiquibul (2008), Cockscomb (2008), and Fireburn (2009). Protected areas are shown in gray. Surveyed protected areas are shown in dark gray.

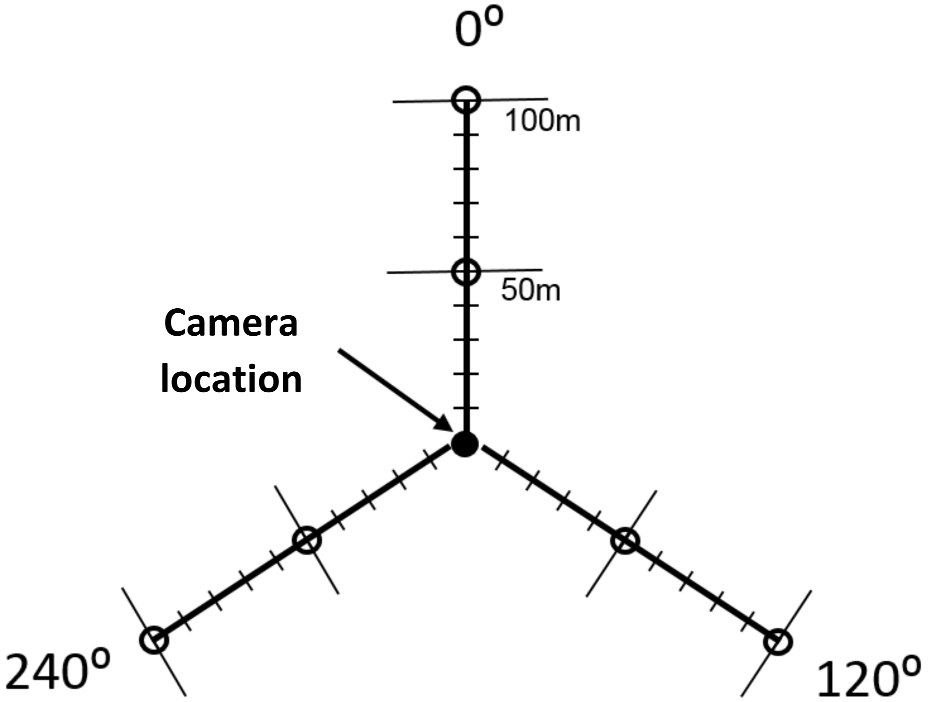

Figure 2.2. Schematic diagram of the microhabitat survey conducted at each camera location. Canopy cover data were collected between the cameras and every 10 meters along three transects radiating from the cameras (0º, 120º, 240º). Understory data were collected every 2 meters along six 40 m transects that ran perpendicular to the three main transects at 50 meters and 100 meters from the cameras. Tree data were collected at the camera location and at 50 meters and 100 meters along each of the three major transects (shown as open or closed circles).

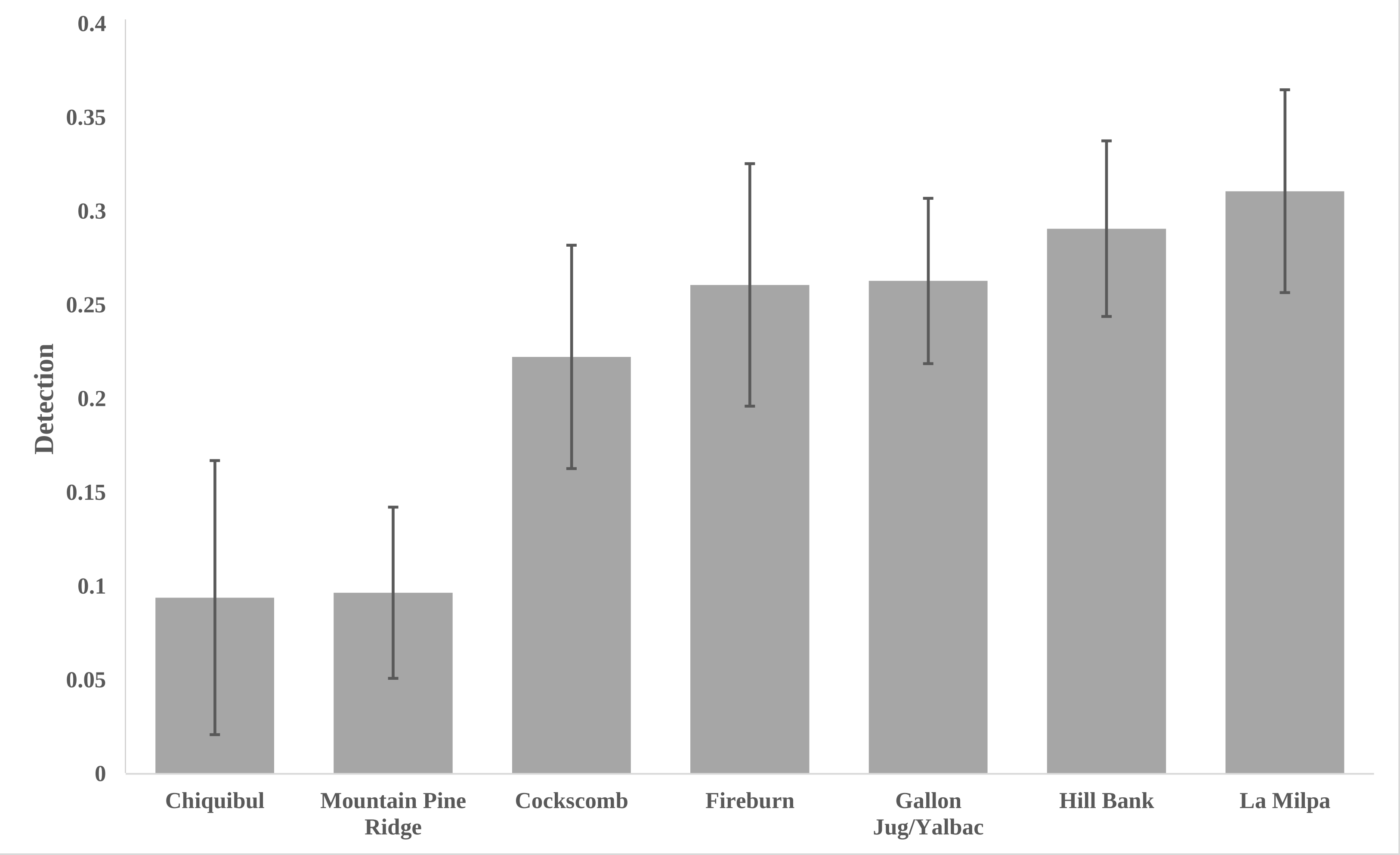

Figure 2.3. Puma detection rates at each of 7 study sites, with 95% confidence intervals. Yalbac Ranch was considered part of the contiguous Gallon Jug Estate in this analysis because it had only 9 sites. At study sites with multiple years of data (Hill Bank, La Milpa, Mountain Pine Ridge), only one detection estimate was calculated for each study site.

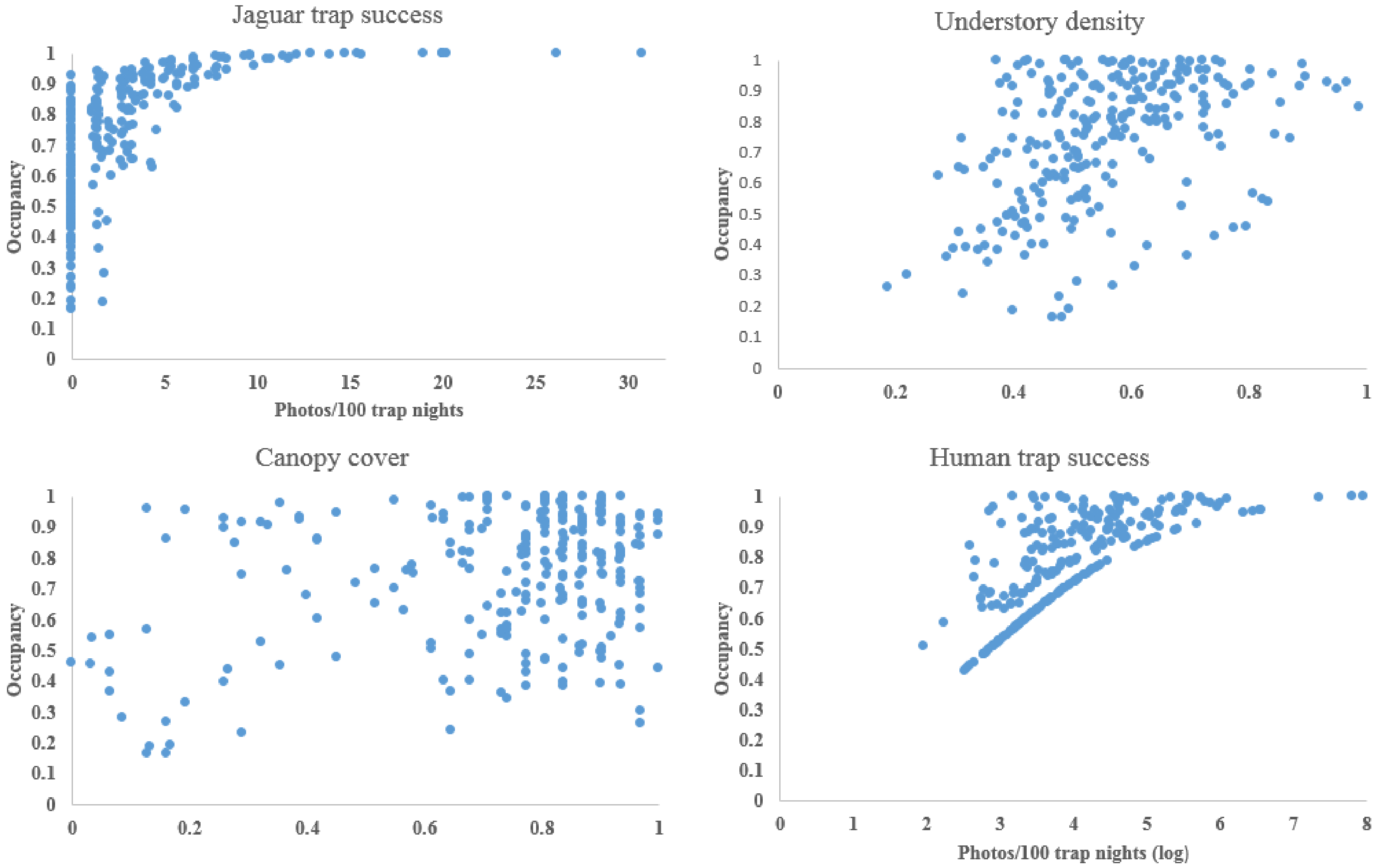

Figure 2.4. Covariates from the top-ranked single-season puma occupancy models plotted against the occupancy estimates. In each instance, the estimates come from the highest-ranked model in which that covariate appears. Jaguar trap success was the number of independent photos of jaguars at each site per 100 trap nights. Understory density and canopy cover are means of unitless scores that range between 0 and 1. Human trap success was the logarithm of the number of independent photos of humans at each site per 100 trap nights.

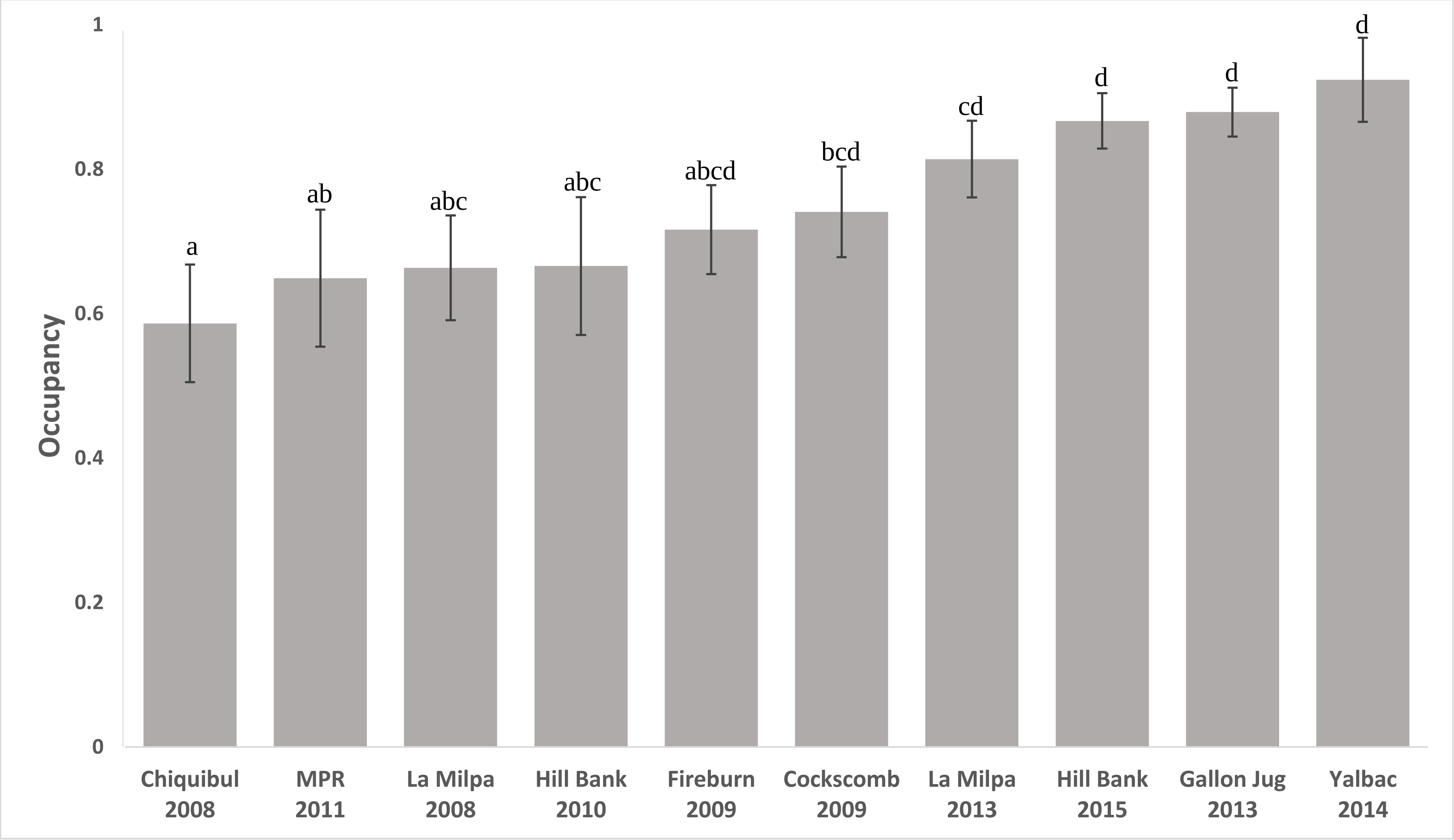

Figure 2.5. Mean puma occupancy rates at each of 10 study sites, with 95% confidence intervals. Estimates that do not share the same letter are significantly different.

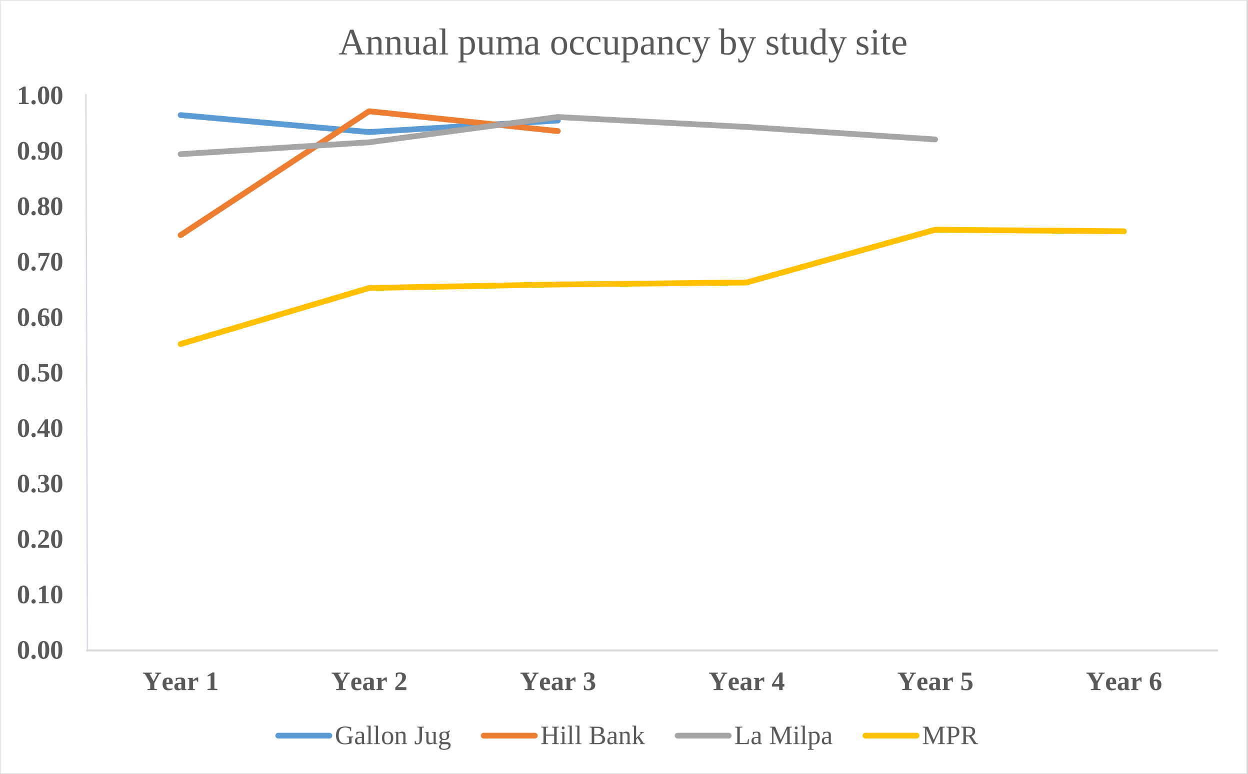

Figure 2.6. Annual puma occupancy rate for each of four study sites in Belize. There was one candidate model set across all four study sites. MPR = Mountain Pine Ridge.

III. *Co-occurrence ecology of jaguars, pumas, ocelots, gray foxes, and prey species using camera traps in Belize*

Abstract

Large carnivores play many vital biological, economic, and conservation roles, however, their biological traits (low population densities, cryptic coloration and behavior) make them difficult to monitor. Compared to temperate areas, research on large neotropical felids is particularly lacking. Mesocarnivores have received even less attention because their impacts on their communities are assumed to be relatively minor, despite becoming the de facto top predator in many ecosystems because of declines in large carnivore populations. To address this knowledge gap, I used two-species, co-occurrence analysis to examine the effects that prey species had on both jaguars and pumas, and the effects that larger carnivores had on smaller carnivores for four species: jaguar, puma, ocelot, and gray fox using camera trapping and habitat data (17,011 trap nights at 277 sites) collected at eight study sites over multiple years across Belize. Our measured covariates did not predict where jaguars were likely to occur, but puma occupancy appeared to be driven by habitat, rather than prey availability, occurring more frequently in dense forest with thick understory. There was little evidence of interactions in carnivore occupancy, however, there was some evidence that pumas avoided jaguars at low understory densities. Gray foxes had lower detection in the presence of pumas; unexpectedly, pumas and gray foxes had higher detection in the presence of a larger carnivore. The lack of negative interaction between the carnivores suggests that jaguars may be acting as an umbrella species and that conservation efforts directed at jaguars are likely to benefit the other carnivores.

Key words: Belize, Gray fox, Jaguar, Multispecies occupancy, Ocelot, Predator-prey dynamics, Puma

Introduction

Large carnivores can play critical roles in their communities, regulating entire ecosystems, and their absence can lead to “ecological meltdown” and a cascade of species losses (Terborgh et al. 1999). They also provide economic value through tourism and often serve as flagships for conservation campaigns (Walpole and Leader-Williams 2002). Despite their importance, their biological traits (e.g., naturally low population densities, large home ranges, cryptic coloration and behavior) make them difficult to monitor (Durant et al. 2011) and as a result wildlife conservationists rarely have adequate information to effectively manage these species. Interactions between carnivores further complicate management and conservation efforts. Whether top carnivores act as umbrella species (Lambeck 1997a) whose conservation indirectly protects other species or they act to suppress populations of smaller carnivores (Crooks and Soulé 1999) has important conservation implications.

Weber and Rabinowitz (1996) noted a general lack of knowledge about the predatory patterns of large felids living in the neotropics, compared to temperate areas. This knowledge gap has been reduced in the last two decades, but the ecological and behavioral factors that allow puma (*Puma concolor*) and jaguar (*Panthera onca*) coexistence still remain unclear (Scognamillo et al. 2003). This is surprising given the large number of studies focusing on jaguars (see Sunquist and Sunquist (2002) for an overview of jaguar studies) and the fact that the puma is the most well-studied felid in North America. Diet studies have shown a large degree of dietary overlap across the ranges of these two carnivores, making them potential competitors (Emmons 1987, Iriarte et al. 1991, Taber et al. 1997, Farrell et al. 2000, Núñez et al. 2000), while other studies have found evidence of diet partitioning between pumas and jaguars (Novack et al. 2005, De Azevedo 2008, Harmsen et al. 2010).

While large carnivores are understudied in Central America, the ecological role of mesocarnivores throughout the world has received relatively little attention (Roemer et al. 2009, but see Prugh et al. (2009)). This is likely due to the fact that while predation-driven direct effects and fear-driven indirect effects of large carnivores on communities and ecosystems are well documented in the literature (Ripple and Besschta 2004, Ray et al. 2005 reviewed in Roemer et al. 2009), the impacts of mesocarnivores within their communities are assumed to be relatively minor (Roemer et al. 2009) despite the fact that declines in large carnivore populations have resulted in mesocarnivores becoming the de facto apex predator in many ecosystems (Crooks and Soulé 1999). Mesocarnivores can also play ecological roles (e.g., seed disperser) that larger carnivores simply do not, but that can impact ecosystems (Roemer et al. 2009).

In this study, my aim was to provide valuable insight on the co-occurrence of both jaguars and pumas with prey species, and examine the interactions between carnivores in Belize, Central America. To achieve this goal my objectives were to 1) examine the impact of prey species on jaguar occupancy, 2) examine the impact of prey species on puma occupancy, and 3) examine the impact that larger carnivores have on the occupancy of smaller carnivores for four target species. To achieve my objectives, I conducted two-species occupancy analyses using microhabitat data, landscape habitat data from available geographic information system layers, and camera trapping data that were collected at 277 camera locations across eight study sites throughout Belize, Central America . I examined the effects of eight mammalian prey species and two size categories of prey (medium-sized mammalian prey 1-15 kg and large mammalian prey > 15 kg) on both jaguar and puma occupancy. I also examined the effects that larger carnivores had on smaller carnivores for jaguars, pumas, ocelots (*Leopardis pardalis*), and gray foxes (*Urocyon cinereoargenteus*). I predicted that jaguars would show apparent “attraction” (Φ

> 1) to medium-sized and large mammalian prey; pumas would show apparent “attraction” ($\Phi > 1$) to medium-sized mammalian prey; and that smaller carnivores would show apparent “avoidance” ($\Phi < 1$) of larger carnivores.

Materials and methods

Belize is a small country (22,963 km^2) approximately the size of Massachusetts lying on the eastern coast of the Yucatan Peninsula in Central America at 17° 15' N latitude and 88° 45' W longitude. Most of the country lies within La Selva Maya (the Mayan Forest), which also includes northern Guatemala and Mexico’s Yucatan Peninsula. At 13.3 million hectares, the Mayan Forest is the second largest tropical rainforest in the Americas, after the Amazon rainforest. Despite its small size, Belize offers a diversity of habitats including broadleaf moist subtropical forest, mountainous pine forest, lowland pine savanna, and wetlands, and elevations ranging from sea level to 1160 m, and is considered a biodiversity hotspot (Conservation International 2011).

Eight study sites located throughout Belize were used in this analysis (Fig. 3.1). The study sites included five protected areas (Chiquibul Forest Reserve and National Park, Cockscomb Basin Wildlife Sanctuary, Fireburn Reserve, La Milpa (the western portion of Rio Bravo Conservation and Management Area (RBCMA), and Mountain Pine Ridge Forest Reserve), one protected area with limited, selective logging (Hill Bank, the eastern portion of RBCMA), and two privately-owned timber companies (Gallon Jug Estates and Yalbac Ranch and Cattle Corporation).

Camera Trapping

Camera trapping techniques follow Silver et al. (2004), modified by experience in the field. At each study site, a grid was established that consisted of motion-activated cameras placed

~2-3 km apart. At each camera location, a pair of cameras was placed ~30-40 cm above the ground on either side of a road, logging road, disused logging road, or human or game trail.

Cameras were only placed on trails and roads because this study was originally designed to target jaguars, which are so wide-ranging and occur at such low densities that obtaining an adequate number of captures is of paramount importance in obtaining precise density estimates (Tobler and Powell 2013). Cameras placed off of trails in early years of this project had capture probabilities of ~ 0 for target species (Marcella Kelly, personal communication). Each survey was conducted for ~ 2 to 3 months to maximize the number of captures while attempting to meet demographic and geographic closure assumptions.

Each photographic image was stamped with the time and date that it was taken and the location was recorded. All encountered animals were recorded and mammals were identified to species, if possible. For any day that both cameras at one location were inoperative, that day was removed from analysis. I collapsed the capture histories to 7-day periods. Because this often resulted in a partial week remaining, 1-6 days were dropped as necessary from the beginning or end of the survey. Periods with inoperative cameras did not necessarily match the 7-day capture occasions, so any capture occasion that was missing > 3 days was considered a missing capture occasion.

Habitat covariates

Microhabitat data were collected at each camera location when it was established and at five-year intervals for longer running sites. Three 100 m transects were laid out at each camera location at 0^0, 120^0, and 240^0 (Fig. 3.2). Any transect that ran directly down a road was adjusted 10^0 to the right or left so that it measured vegetative features and structure. At the center of the camera location and at 50 m and 100 m along each transect, the diameter at breast height (DBH) of the nearest tree in each of four quadrants (NE, SE, SW, NW) and the distances to those trees were measured. The Point-Centered Quarter Method detailed in Pollard (1971) was then used to estimate tree density at each camera location, using the correction factor developed by Warde and Petranka (1981) for any plots that did not have a tree of sufficient size (≥ 5 cm DBH) within 50 meters of the central point. I also calculated the basal area of trees within 100 meters of each camera location. At 50 meters and 100 meters along each transect, a 40 m transect was laid perpendicular to the 100 m transect and the understory cover was measured every 2 meters. This resulted in 20 samples along each of six transects. A 2 m pole, held vertically, was placed randomly beside the transect and any vegetation (live or dead) that contacted the pole at three height intervals, 0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m was recorded. I did not differentiate between live and dead vegetation because I did not think that it would have an impact on the effectiveness of the understory to serve as stalking cover and because the difference between live and dead vegetation was not always readily apparent in areas of dense woody vines, lianas, and treefalls. To calculate the mean understory density ≤ 1 m in height, I averaged the score for 0-0.5 m and 0.5-1 m at each sample and then found the average of the 120 samples for each camera location. This height seemed the most reasonable as a measure of stalking cover. I plotted the camera locations in ArcMap 10.3 (ESRI 2011) using pre-existing geographic information system (GIS) layers available online from the Biodiversity and Environmental Resources Data System of Belize (BERDS) website, which serves as a clearinghouse for GIS data for Belize (Meerman and Clabaugh 2015). I used these GIS layers to calculate the length of streams within 1000 m of each camera location as a measure of how wet an area was. To improve maximum likelihood convergence with covariates and ensure that all covariates were on the same scale, I Z-scored all continuous variables.

Co-occurrence Modeling

Data for this analysis were drawn from larger camera trapping dataset collected in eight study sites as described above. I used only surveys where microhabitat data were collected. This resulted in an eleven study-site/year data set with 17,011 trap nights (Table 3.1). I ran two-species co-occurrence models in program PRESENCE version 11.5 (Hines 2006) for two sets of analyses: one examining the effects of potentially important prey species on jaguar and puma occupancy and a second examining the effects of larger carnivores on smaller carnivores' occupancy and detection for four carnivore species: jaguar, puma, ocelot, and gray fox. Margays (*Leopardus wiedii*), jaguarundis (*Puma yagouaroundi*), and several mesocarnivore species were also present on the landscape, but were not detected frequently enough to include in this analysis.

For the prey species, I did not run models testing for difference in detection because the carnivores were the subdominant species in these models and I did not expect that prey would affect the detection of the carnivores. Without an *a priori* expectation of an effect, these models would be simply exploratory and would invite spurious results. For the carnivore co-occurrence models, I did expect that the larger carnivores could affect the detection of the smaller carnivores, so I ran models testing the effects of the larger carnivores on both the occupancy and detection of the smaller carnivores. There are four possible combinations of these two parameters. Both parameters can be the same for the subdominant species in the presence or absence of the dominant species or either or both can differ. In what I will call type 1 models, both occupancy and detection of the subdominant species is the same in the presence or absence of the dominant species (Table 3.2). This suggests that the dominant species has no effect on the occupancy or detection of the subdominant species. In type 2 models, occupancy of the subdominant species is the same in the presence or absence of the dominant species, but detection differs. This means that the dominant species affects detection of the subdominant species, but not its occupancy. In model type 3, both occupancy and detection of the subdominant species differ in the presence or absence of the dominant species, and in model type 4, occupancy differs, but detection does not. The model type that is highest ranked based on the Akaike Information Criterion (AIC) suggests which type of interaction between the two species draws the most support from the data.

If the occupancy of the subdominant species is the same in the presence or absence of the dominant species and there are no covariates in the best-supported model, this suggests that there is no interaction between the two species and that none of the measured covariates explain the occupancy of the subdominant species. If a similar model, with covariates, is the best supported model, this suggests that there is no interaction between the two species and that the occupancy of the subdominant species is best explained by the habitat. If the occupancy of the subdominant species differs in the presence or absence of the dominant species and there are no covariates in the best supported model, this suggests that the interaction between the two species is sufficient to explain the occupancy of the subdominant species. If a similar model, with covariates, is the best supported model, this suggests that there is an interaction between the two species that changes across the landscape. The same is true for the effects of the dominant species on the detection of the subdominant species.

The second parameterization of two-species occupancy models (Richmond et al. 2010) has eight parameters, as follows (note the capitalization of the superscripts indicates occupied or detected for the particular species denoted as A or B):

ψ^{A}: probability that the area is occupied by species A
ψ^{BA}: probability that the area is occupied by species B, given that species A is present

ψ^{Ba}: probability that the area is occupied by species B, given that species A is not present

p^{A}: probability of detecting species A, given species B is not present

p^{B}: probability of detecting species B, given species A is not present

r^{A}: probability of detecting species A, given that both are present

r^{BA}: probability of detecting species B, given that both are present and species A was detected

r^{Ba}: probability of detecting species B, given that both are present and species A was not detected

In each case, species A is the dominant species and species B is the subdominant species. From these parameters we can derive the species interaction factor (Φ) from the following formula:

$$\Phi = \frac{\psi^{A}\psi^{BA}}{\psi^{A}(\psi^{A}\psi^{BA} + (1 - \psi^{A})\psi^{Ba})}$$

In the first analysis, for all species pairs, I designated jaguars or pumas as the subdominant species to test the effect that the prey species had on carnivore occupancy. For the second analysis, I designated the smaller carnivore species as the subdominant species to test the effect that the larger carnivore had on the smaller carnivore.

I chose three habitat covariates that appeared important in the single-season puma analyses (see Chapter 2) and that seemed broadly applicable to multiple species. I chose stream density (the length of streams within 1000 m of each camera location), mean understory density within 100 m of each camera locatiton, and basal area within 100 m of each camera location. I also considered canopy cover as a habitat covariate, but chose not to include it because it is likely not independent of basal area and because canopy cover data were missing from two study sites.

The prey species I included in this analysis were the Central American agouti (*Dasyprocta punctata*), collared peccary (*Pecari tajacu*), nine-banded armadillo (*Dasypus* *novemcinctus*), paca (*Cuniculus paca*), red brocket deer (*Mazama americana*), white-lipped peccary (*Tayassu pecari*), white-nosed coati (*Nasua narica*), and white-tailed deer (*Odocoileus virginianus*). I also included two groupings of prey species: medium-sized mammalian prey 1-15 kg and large mammalian prey over 15 kg. I did not include small prey because they generally do not compose a large part of jaguar or puma diet and because they were not captured by camera consistently enough to model. Medium-sized mammalian prey included Central American agouti, common opossum (*Didelphis marsupialis*), gray four-eyed opossum (*Philander opossum*), nine-banded armadillo, northern raccoon (*Procyon lotor*), paca, Virginia opossum (*Didelphis virginiana*), and white-nosed coati. Several species in this grouping were not analyzed separately because they were detected in insufficient numbers. Large mammalian prey included collared peccary, red brocket deer, white-lipped peccary, and white-tailed deer. Because they weigh up to 300 kg, Baird's Tapir (*Tapir bairdii*) were considered too large to be a potential prey species. I analyzed the following species pairs to investigate interactions between carnivores: jaguar – puma, jaguar – ocelot, jaguar – gray fox, puma – ocelot, puma – gray fox, and ocelot – gray fox. For the jaguar-puma co-occurrence analysis, I also included the occupancy estimates for nine-banded armadillo, paca, medium-sized mammalian prey, and large mammalian prey as covariates on both jaguar and puma occupancy to see if the interaction between jaguars and pumas was affected by prey availability. Armadillos were included because they were found to be the single most important prey item for jaguars in Belize (Emmons 1987, Foster et al. 2010). Similarly, Foster et al. (2010) found that paca made up nearly 60% of puma diet (by both occurrence and biomass) in Belize. The two prey groups were included because both carnivore species are opportunistic predators with wide prey niches (Sunquist and Sunquist 2002).

All models were run in Program PRESENCE (version 11.5) and were ranked by AIC, but note there are currently no methods developed for estimating overdispersion in two-species occupancy models. Because of the large number of parameters in the second parameterization of two-species occupancy models (three for occupancy and five for detection), and because these need to be repeated for up to four model types, models were built sequentially from three components (detection, dominant species occupancy, and subdominant species occupancy) to limit the number of models run. For the prey-carnivore co-occurrence analyses, I first ran null models to test for a difference in carnivore occupancy in the presence or absence of prey. In the carnivore co-occurrence analyses, I first ran four null models of the types described in Table 3.2, to test for differences in both occupancy and detection. I then tested the three habitat covariates on each of the detection parameters for the null model that was ranked highest by AIC. The top-ranked detection model was then used to test the habitat covariates, both singly and in interactive combinations, on the dominant species' occupancy. The top-ranked model was then used to test the habitat covariates for subdominant species occupancy. In most cases, the relative ranking of the model types did not change with the addition of covariates, but this was not true in every case. Therefore, the two top-ranked models were run in both (or all four, for carnivores) model types. Estimates were taken from the top-ranked model in each species pair, but I present the model results for all models with $\Delta \mathrm{AIC} \leq 2.0$. I ran Student's t-tests to determine if any differences in occupancy or detection were statistically significant.

I expected that jaguars would be more likely to occur where stream density was higher and in the presence of nine-banded armadillos and large mammalian prey and possibly medium-sized mammalian prey. I also expected that pumas would be more likely to occur where mean understory density was higher and where stream density was lower. I further expected that pumas would be more likely to occur in the presence of pacas and medium-sized mammalian prey and possibly large mammalian prey. Other species interactions were tested because these or similar species have been found in jaguar and/or puma diets. I expected that smaller carnivores would be less likely to occur in the presence of larger carnivores and that they would have lower detection rates when larger carnivores were present.

Results

Jaguar co-occurrence with prey species

Each species pair had an average of five competing models (ΔAIC ≤ 2), indicating that no single model clearly drew most of the support from the data (Table 3.3). The top-ranked model for Central American agouti-jaguar co-occurrence had several undefined beta estimates, so the estimates from the highest-ranked model without problematic estimates are given (Tables 3.4A and 3.4B). In five of the 10 species pairs, there were no covariates on jaguar occupancy, but the interaction of basal area and understory density had the largest beta estimates. Habitat covariates in the top-ranked models varied by species, but mean understory density was the most commonly included; there was strong support (i.e., the 95% confidence interval did not include 0) for this covariate in five of the eight prey species. Understory density was positively related to prey occupancy in four of these cases, with the exception being the negative relationship for collared peccaries. For the groups of prey species, the top model had no covariates on jaguar occupancy.

For both prey species groups and for six of the eight prey species-jaguar combinations, the top-ranked model had psiBA = psiBa (i.e., $\Phi = 1$). The top-ranked model showed an interaction between the two species in only two instances. The species interaction factor was < 1 for Central American agouti and was > 1 for red brocket deer, however, the estimate was not meaningfully different from 1 (i.e., the 95% confidence interval included 1) at any camera locaiton for either species (Table 3.5). Therefore, there is little evidence of an interaction between jaguars and the agouti or red brocket deer.

Puma co-occurrence with prey species

Each species pair had an average of 2-3 competing models (ΔAIC ≤ 2) (Table 3.6). The covariates on prey occupancy varied by species, but prey occupancy tended to be negatively related to stream density and positively related to basal area (Tables 3.7A and 3.7B). Understory density drew the most support as a predictor of puma occupancy, with 9 of the 10 species pairs/species groups having large beta estimates. There was also some support for the importance of basal area, with the interaction of these two covariates having the largest beta estimates. Puma detection, in the absence of prey, was negatively related to stream density for six of the eight species pairs and puma detection in the presence of prey was positively related to basal area in six species pairs. There were no clear patterns in the beta estimates for the prey species groups.

PsiBA was set equal to psiBa (i.e., $\Phi = 1$) for seven of the eight prey species (Table 3.8). The exception was nine-banded armadillo, which had $\Phi > 1$, however, the 95% confidence intervals included 1 for all camera locations, so there was no evidence for an effect of armadillos on puma occupancy. Medium-sized mammalian prey had $\Phi > 1$, but the 95% confidence intervals also included 1 for all camera locations. Large mammalian prey had Φ set to 1, indicating the presence of large mammalian prey species did not affect puma occupancy.

Carnivore co-occurrence

For carnivore co-occurrence, I included models that tested differences in both occupancy and detection, therefore there were four types of models (Table 3.2), rather than just the two types shown in the prey species-carnivore co-occurrence models. There were generally three competing models (ΔAIC ≤ 2) for each species pair (Table 3.9). Unlike the previous models, the carnivore co-occurrence models tended to be of different model types, but to include the same covariate structure on the parameters.

For the jaguar-puma co-occurrence models, the inclusion of prey occupancy rates as covariates did not improve the models as the best of these models was ranked third and was the only one to be a competing model. There were no habitat covariates on jaguar occupancy in two of the three jaguar species pairs. Puma occupancy was positively associated with basal area and mean understory density in all three puma-carnivore species pairs (Table 3.10). Ocelots also had the same covariates on occupancy for all three ocelot-carnivore species pairs. Their occupancy was positively associated with basal area and generally negatively associated with stream density. Gray foxes were generally negatively associated with basal area and with stream density, but the evidence for this interaction was not strong. Jaguars tended to have higher detection rates where stream density was higher, while pumas showed the opposite trend. Counterintuitively, ocelots and gray foxes tended to have higher detection rates in thicker understory.

PsiBA was set equal to psiBa (i.e., $\Phi = 1$) in the top-ranked models for all six species pairs. In several of the competing models, there was an estimated Φ, but in all but one instance (jaguar-puma), the 95% confidence interval included 1, so there was little evidence for interactions between carnivore species pairs. In the jaguar-puma co-occurrence analysis, there was a competing model (ΔAIC = 0.35) in which jaguar presence did affect puma occupancy, though the effect differed by habitat. The species interaction factor included 1 for 82 camera locations, but was negative for the remaining 195. Jaguar and puma interaction showed a non-linear relationship with mean understory density, which was scored between 0 and 1. There was no interaction between the species at moderate understory densities (0.6-0.7), but there were increasingly negative interactions as understory density moved outside of that range, especially as understory became less dense (Fig. 3.3).

For three of the carnivore co-occurrence pairs, the detection of the subdominant species was the same in the presence or absence of the dominant species, but for the other three these estimates differed (Fig. 3.4). Gray fox detection rates were lower in the presence of pumas. However, puma detection rates were higher in the presence of jaguars and gray fox detection was higher in the presence of ocelots. All of these differences were statistically significant at an α-level of 0.05.

Discussion

Jaguar co-occurrence with prey species

Our measured habitat covariates were not particularly insightful for explaining where jaguars occurred. There was little to no evidence that any of the eight prey species examined, or the two groupings of prey species by size, had an effect on jaguar occupancy. There was also little evidence to support the importance of any of the habitat covariates in predicting jaguar occupancy as nearly half of the competing models had no habitat covariates on jaguar occupancy and the remaining models favored no particular covariate or interaction of covariates. Most of the jaguar-prey species pairs had five or more competing models with differing habitat covariates, further suggesting that the data did not support any particular relationship between jaguar occupancy and the measured habitat covariates. This two-species occupancy analysis failed to indicate that habitat or prey availability factors explain jaguar occupancy in Belize.

Puma co-occurrence with prey species

It appears that puma occupancy is driven by habitat rather than prey availability. None of the eight prey species, or two groupings of prey species by size, were found to affect puma occupancy. Rather it appears that pumas occur more frequently in denser forests with thicker understory. Because pumas are generalist predators that freely switch from one prey type to another, it is perhaps not surprising that individual prey species do not have a strong effect on puma occupancy, however, it is surprising that we do not see some relationship to groupings of prey species, especially medium-sized mammalian prey (1-15 kg), which have been found to be the most important food source for tropical pumas (Núñez et al. 2000, Sunquist and Sunquist 2002, De Azevedo 2008). It is also somewhat surprising that pacas were found to have no effect on puma occupancy, given that Foster et al. (2010) found that they made up nearly 60% of puma diet in Belize. White-tailed deer have also been shown to make up the largest portion of puma diet in multiple studies (Núñez et al. 2000, Sunquist and Sunquist 2002), however, it should be noted that these other studies were generally conducted in more open habitat (e.g., Jalisco, Mexico and the western United States) than is found in Belize.

Unlike more open habitat (e.g., grasslands and savannas), the dense forest and understory of this habitat may not allow pumas to detect and follow prey from a distance. Rather they may encounter prey more haphazardly and may, therefore, need to be ready to seize upon any chance encounter and as such, are less able to choose their prey. Diet studies that show a prevalence of one prey type or another in puma diet may, therefore, reflect how often puma encounter that prey or how often they are able to convert a chance encounter into a meal, rather than a preference for that prey species. This could explain why researchers have found different prey preferences in different study areas. Since smaller animals tend to be more common than larger ones, it follows that pumas in closed habitats would encounter smaller prey more often than larger prey, which may explain the importance of medium-sized prey in tropical puma diet, rather than the larger prey favored in more northern and southern parts of their range.

Carnivore co-occurrence

There was little to no evidence of interactions between larger and smaller carnivores. Rather it appears that habitat better explains where smaller carnivores occur. However, habitat covariates did not explain jaguar occupancy. Pumas tended to be found in thicker forest with denser understory. Ocelots tended to occur in thicker forest and drier areas. Gray foxes tended to occur where basal area was lower and to a lesser extent there was some evidence that they occurred where stream density was lower. Although the top-ranked model showed no interaction between jaguars and puma, there was a second model that drew nearly as much support from the data that indicated that jaguars did have a negative effect on puma occupancy that changed across the landscape. At intermediate understory densities, there was no evidence of an interaction between the two species, but at low and high understory densities, jaguars had a negative effect on puma occupancy. This effect was particularly apparent at low understory densities.

I did not test for differences in detection in the prey species-carnivore co-occurrence models because the carnivores were the subdominant species and it seems unlikely that the presence of prey would make carnivores less likely to be detected. However, I did test for differences in detection in the carnivore co-occurrence models because it seems reasonable to suspect that larger carnivores may affect the detection of smaller carnivores (see Bailey et al.

(2009) for an example of congenerics affecting the vocalizations, and hence detection, of owl species). The mechanisms that may lead to lower detection rates in camera trapping surveys are less clear than some other survey methods (e.g., surveys that rely on detecting vocalizations). Gray foxes had lower detection rates when pumas were present, which conforms to what we might expect. However, pumas were more likely to be detected when jaguars were present and gray foxes were more likely to be detected when ocelots were present. These findings are counterintuitive.

It is important to note here that all of our cameras were on trails and roads, so we were likely to be capturing the felid species largely while they were traveling and, therefore, this study may not adequately capture the full range of felid activities. I generally found little evidence of interaction between the species examined, but they could be interacting during activities that were not recorded in this study.

For those species that are likely competitors (i.e., jaguars and pumas; possibly pumas and ocelots) the general lack of evidence for negative interspecific interactions may mean that they currently exist at population densities too low to produce competition. Taber et al. (1997) suggested that the similarity in diet between pumas and jaguars suggests that this may be the case. Núñez et al. (2000) warned that we need to be cautious about making evolutionary inferences based on recent dietary data because of human-induced changes to habitat that disrupt predator-prey assemblages. Anthropogenic changes likely have reduced jaguar and puma population densities and prior to these changes, it is possible that we would have seen some evidence of competitive exclusion.

While it may be possible that one or more of these species pairs could show evidence of competition at higher population densities, there was no interaction signal when looking at occupancy at their current densities. All three of these felid species are in decline, according to the IUCN Red List of Threatened Species. As such, we are unlikely to see population increases, potentially leading to competition among these carnivores in the short term. This lack of competition is potentially beneficial to the smaller carnivores. Unlike the other two felids, jaguars are currently listed as threatened on the IUCN Red List. This makes them a higher conservation priority and because of the apparent lack of competition between these carnivores, any conservation efforts directed at jaguars are likely to benefit the smaller carnivores as well. As previously suggested, jaguars may act as an umbrella species (Lambeck 1997b), indirectly benefitting other species in their ecological communities. However, with the widespread land use changes that are occurring in Belize and throughout much of the neotropics, carnivores that are sensitive to anthropogenic changes may be forced into protected areas, resulting in higher population densities in those areas that may drive different species interactions than were found in this study.

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Table 3.1. Subset of the Belize camera trapping data set used in this analysis. The number of camera locations and trap nights are shown by study site and year. Only trapping surveys that were accompanied by a microhabitat survey were included. Three of the longer-running study sites had two microhabitat surveys conducted.

Study site	Year	Camera locations	Trap nights
Chiquibul	2008	29	643
Cockscomb	2008	38	2419
Fireburn	2009	19	1504
Gallon Jug	2013	28	2017
Hill Bank	2010	19	1022
Hill Bank	2015	31	2105
La Milpa	2008	22	1347
La Milpa	2013	22	1666
Mountain Pine Ridge	2007	24	1530
Mountain Pine Ridge	2011	35	2043
Yalbac	2014	9	715
Total		276	17,011

Table 3.2. The four model types for two-species occupancy models. In model type 1, occupancy of the subdominant species is the same in the presence or absence of the dominant species. Detection rate of the subdominant species is also the same in the presence or absence of the dominant species. In model type 2, occupancy rates are the same, but detection rates differ in the presence or absence of the dominant species. In model type 3, both occupancy and detection rates of the subdominant species differ in the presence or absence of the dominant species. In model type 4, the occupancy rate of the subdominant species differs in the presence or absence of the dominant species, but the detection rate does not.

Model type	1	2	3	4
Occupancy	=	=	≠	≠
Detection	=	≠	≠	=

Table 3.3. Two-species occupancy models for jaguar and prey species in Belize, ranked by AIC. In each case, the prey species listed was the dominant species and jaguar was the subdominant species. Only models with Δ ≤ 2 are shown. The covariates are as follows: BA = basal area within 100 m of each site, STR = the length of streams within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. The number at the end of each model refers to the model type and is explained in Table 3.2. K is the number of parameters in each model. ΔAIC is the difference between the AIC of each model and the top model. AIC weight is the proportion of evidence that each model draws from the data. Prey species appear in order of increasing size.

Prey species	Model	K	ΔAIC	AIC weight
Central American agouti	psiA(STR),psiBA,psiBa,pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)4	12	0	0.2098
	psiA(STR),psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)1	14	0.10	0.1996
	psiA(STR*US),psiBA=psiBa,pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)1	13	0.22	0.188
	psiA(BA*STR),psiBA,psiBa,pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)4	14	0.36	0.1753
	psiA(STR),psiBA(STR*US)=psiBa(STR*US),pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)1	14	1.07	0.1229
	psiA(STR),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(STR),rA(BA),rBA(US)=rBa(US)1	14	1.54	0.0972
White-nosed coati	psiA(STR*US),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR)),rA(BA),rBA(BA)=rBa(BA)1	16	0	0.4331
	psiA(STR*US),psiBA(BA*US),psiBa(BA*US),pA(BA),pB(STR)),rA(BA),rBA(BA)=rBa(BA)4	17	1.9	0.1675
Nine-banded armadillo	psiA(STR),psiBA=psiBa,pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	11	0	0.1214
	psiA(STR*US),psiBA=psiBa,pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	13	0.24	0.1077
	psiA(STR),psiBA(STR)=psiBa(STR),pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	12	0.87	0.0786
	psiA,psiBA=psiBa,pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	10	0.93	0.0763
	psiA(STR),psiBA(BA)=psiBa(BA),pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	12	1.13	0.069
	psiA(STR),psiBA(US)=psiBa(US),pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	12	1.68	0.0524
	psiA(STR),psiBA,psiBa,pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)4	12	1.76	0.0504
	psiA(STR),psiBA(BA*STR)=psiBa(BA*STR),pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	14	1.87	0.0477
	psiA(STR*US),psiBA,psiBa,pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)4	14	1.98	0.0451
	psiA(STR),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(BA),rBA(STR)=rBa(STR)1	14	2	0.0447
Paca	psiA(BA*US),psiBA=psiBa,pA(BA),pB(STR),rA(BA),rBA=rBa1	12	0	0.9543

Prey species	Model	K	ΔAIC	AIC weight
Medium-sized mammals	psiA(BA*STR),psiBA=psiBa,pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	13	0	0.2189
	psiA(BA*STR),psiBA(STR)=psiBa(STR),pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	14	1.45	0.106
	psiA(BA*STR),psiBA(STR)=psiBa(STR),pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	14	1.45	0.106
	psiA(BA*STR),psiBA,psiBa,pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)4	14	1.5	0.1034
	psiA(BA*STR),psiBA(STR*US)=psiBa(STR*US),pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	16	1.61	0.0979
	psiA(BA*STR),psiBA(BA)=psiBa(BA),pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	14	1.91	0.0843
	psiA(BA*STR),psiBA(US)=psiBa(US),pA(STR),pB(US),rA(BA),rBA(STR)=rBa(STR)1	14	2	0.0805
Collared peccary	psiA(US),psiBA(BA*US)=psiBa(BA*US),pA(US),pB(STR),rA(BA),rBA(BA)=rBa(BA)1	14	0	0.4994
	psiA(US),psiBA(BA*US),psiBa(BA*US),pA(US),pB(STR),rA(BA),rBA(BA)=rBa(BA)4	15	1.76	0.2071
Red brocket	psiA(STR*US),psiBA(US),psiBa(US),pA(US),pB(STR),rA(STR),rBA(BA)=rBa(BA)4	15	0	0.1416
	psiA(STR*US),psiBA=psiBa,pA(US),pB(STR),rA(STR),rBA(BA)=rBa(BA)1	13	0.08	0.1361
	psiA(STR*US),psiBA(US)=psiBa(US),pA(US),pB(STR),rA(STR),rBA(BA)=rBa(BA)1	14	0.29	0.1225
	psiA(STR*US),psiBA,psiBa,pA(US),pB(STR),rA(STR),rBA(BA)=rBa(BA)4	14	0.67	0.1013
	psiA(STR*US),psiBA(BA*US),psiBa(BA*US),pA(US),pB(STR),rA(STR),rBA(BA)=rBa(BA)4	17	1.26	0.0754
White-lipped peccary	psiA(BA*US),psiBA(BA*STR)=psiBa(BA*STR),pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)1	15	0	0.1347
	psiA(BA*US),psiBA=psiBa,pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)1	12	0.12	0.1269
	psiA(BA*US),psiBA(STR)=psiBa(STR),pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)1	13	0.62	0.0988
	psiA(BA*US),psiBA,psiBa,pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)4	13	0.83	0.0889
	psiA(BA*US),psiBA(BA*STR),psiBa(BA*STR),pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)4	16	1.34	0.0689
	psiA(BA*US),psiBA(STR*US)=psiBa(STR*US),pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)1	15	1.97	0.0503
	psiA(BA*US),psiBA(BA)=psiBa(BA),pA(BA),pB,rA(STR),rBA(STR)=rBa(STR)1	13	1.99	0.0498
White-tailed deer	psiA(STR*US),psiBA=psiBa,pA(STR),pB(STR),rA(STR),rBA(STR)=rBa(STR)1	13	0	0.2683
	psiA(STR*US),psiBA,psiBa,pA(STR),pB(STR),rA(STR),rBA(STR)=rBa(STR)4	14	0.77	0.1826
	psiA(STR*US),psiBA(US)=psiBa(US),pA(STR),pB(STR),rA(STR),rBA(STR)=rBa(STR)1	14	1.66	0.117
	psiA(STR*US),psiBA(STR)=psiBa(STR),pA(STR),pB(STR),rA(STR),rBA(STR)=rBa(STR)1	14	1.77	0.1107
	psiA(STR*US),psiBA(BA)=psiBa(BA),pA(STR),pB(STR),rA(STR),rBA(STR)=rBa(STR)1	14	1.84	0.1069

Prey species	Model	K	ΔAIC	AIC weight
Large mammals	psiA(BA*STR),psiBA=psiBa,pA(BA),pB(STR),rA(STR),rBA=rBa1	12	0	0.1591
	psiA(STR*US),psiBA=psiBa,pA(BA),pB(STR),rA(STR),rBA=rBa1	12	0.19	0.1446
	psiA(BA*STR),psiBA(US)=psiBa(US),pA(BA),pB(STR),rA(STR),rBA=rBa1	13	1.37	0.0802
	psiA(BA*STR),psiBA(BA)=psiBa(BA),pA(BA),pB(STR),rA(STR),rBA=rBa1	13	1.58	0.0722
	psiA(BA*STR),psiBA,psiBa,pA(BA),pB(STR),rA(STR),rBA=rBa4	13	1.71	0.0676
	psiA(BA*STR),psiBA(STR)=psiBa(STR),pA(BA),pB(STR),rA(STR),rBA=rBa1	13	1.97	0.0594

Table 3.4A. Untransformed estimates of coefficients for the covariates (betas) of two-species occupancy models for eight prey species using a combined data set (8 study sites with 277 camera trap locations) in Belize, Central America. In each instance, the species listed was the dominant species (labeled A) and jaguar was the subdominant species (labeled B). Standard errors are given in parentheses. The covariates are as follows: BASAL = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. Estimates with 95% confidence intervals that do not include 0 are shown in bold. The top-ranked white-lipped peccary model had problematic beta estimates, so the highest-ranked model with no problematic betas is also shown. Prey species appear in order of increasing size.

	Central American agouti	White-nosed coati	Nine-banded armadillo	Paca	Collared peccary	Red brocket	White-lipped peccary	White-tailed deer
psiA	-0.80 (0.26)	0.49 (0.36)	-0.17 (0.23)	0.45 (0.32)	0.81 (0.38)	1.15 (0.31)	7.92 (7.48)	0.65 (0.20)
psiBA	1.08 (0.50)	1.54 (0.28)	2.04 (0.35)	1.25 (0.22)	1.6 (0.31)	1.71 (0.38)	1.39 (0.27)	1.17 (0.18)
psiBa	1.09 (0.31)					0.31 (0.54)		
psiA.BASAL				**1.37 (0.38)**			15.49 (14.00)	
psiA.STR	**-0.69 (0.19)**	**-0.76 (0.31)**	0.32 (0.2)			0.21 (0.26)		**0.64 (0.20)**
psiA.US		**0.90 (0.45)**		**1.02 (0.36)**	**-0.62 (0.35)**	**0.63 (0.31)**	-6.94 (5.94)	**0.94 (0.26)**
psiA.BASAL*STR								
psiA.BASAL*US				**1.76 (0.53)**			-10.31 (9.88)	
psiA.STR*US		**-1.32 (0.47)**				**-0.52 (0.27)**		**-0.42 (0.24)**
psiBA.BASAL		0.55 (0.33)			**0.78 (0.39)**		**0.38 (0.29)**	
psiBA.STR								
psiBA.US		**0.97 (0.31)**			**1.22 (0.33)**	**-0.35 (0.22)**	**1.07 (0.31)**	
psiBA.BASAL*STR								
psiBA.BASAL*US		**1.32 (0.46)**			**1.68 (0.51)**		**1.35 (0.47)**	
pA	-3.03 (1.25)	-2.94 (0.33)	-0.88 (0.22)	-2.85 (0.43)	-4.76 (0.84)	-2.2 (0.37)	-4.20 (0.42)	-3.96 (0.76)

	Central American agouti	White-nosed coati	Nine-banded armadillo	Paca	Collared peccary	Red brocket	White-lipped peccary	White-tailed deer
pB	-1.10 (0.07)	-2.00 (0.24)	-2.24 (0.22)	-1.72 (0.28)	-1.65 (0.23)	-0.73 (0.23)	-1.95 (0.20)	-0.64 (0.13)
rA	-1.01 (0.10)	-3.09 (0.17)	-3.39 (0.22)	-1.82 (0.14)	-3.34 (0.19)	-2.57 (0.12)	-3.83 (0.22)	-1.73 (0.1)
rBA	-1.45 (0.11)	-0.97 (0.08)	-0.71 (0.09)	-0.93 (0.12)	-1.27 (0.09)	-1.27 (0.08)	-0.89 (0.08)	-1.29 (0.08)
pA.BASAL		**0.72 (0.33)**	**-0.53 (0.27)**	0.19 (0.37)				
pA.STR	-0.71 (0.90)							**-1.35 (0.78)**
pA.US					**-1 (0.66)**	**-1.48 (0.53)**		
pB.STR	**0.15 (0.07)**	**-0.73 (0.2)**	0.07 (0.15)	**0.46 (0.11)**	**-1.22 (0.24)**	**1.31 (0.3)**	**-0.46 (0.17)**	**1.12 (0.16)**
pB.US								
rA.BASAL	**0.26 (0.08)**	0.17 (0.13)	**0.87 (0.13)**	0.04 (0.07)	**0.38 (0.15)**			
rA.STR						**-0.53 (0.12)**		**-0.88 (0.1)**
rA.US		**0.29 (0.07)**			**0.25 (0.09)**	0.09 (0.08)	0.40 (0.30)	
rBA.STR			0.11 (0.1)					**-0.16 (0.08)**
rBA.BASAL							0.40 (0.30)	
rBA.US	**0.48 (0.15)**							

Table 3.4B. Untransformed estimates of coefficients for the covariates of two-species occupancy models for two groups of prey species using a combined data set (8 study sites with 277 camera trap locations) in Belize, Central America. In each instance, the species listed was the dominant species (labeled A) and jaguar was the subdominant species (labeled B). Standard errors are given in parentheses. The covariates are as follows: BASAL = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. Estimates with 95% confidence intervals that do not include 0 are shown in bold. The top-ranked white-lipped peccary model had problematic beta estimates, so the highest-ranked model with no problematic betas is also shown.

	Medium-sized mammalian prey	Large-sized mammalian prey
psiA	2.22 (0.32)	1.61 (0.41)
psiBA	1.03 (0.17)	1.05 (0.17)
psiA.BASAL	**1.24 (0.44)**	1.09 (0.58)
psiA.STR	0.15 (0.32)	0.11 (0.43)
psiA.BASAL*STR	**0.91 (0.41)**	**1.19 (0.49)**
pA	-0.93 (0.13)	-2.29 (0.22)
pB	-0.92 (0.18)	-1.56 (0.22)
rA	-0.67 (0.06)	-1.20 (0.07)
rBA	-1.15 (0.06)	-1.12 (0.07)
pA.BASAL		**0.61 (0.21)**
pA.STR	**-0.25 (0.13)**	
pB.STR		**0.62 (0.15)**
pB.US	**-0.38 (0.15)**	
rA.BASAL	**0.16 (0.05)**	
rA.STR		**-0.44 (0.08)**
rBA.STR	**0.16 (0.07)**	

Table 3.5. Species interaction factor (Φ) for jaguar and prey species co-occurrence models across eleven study-site/years in Belize. Co-occurrence models calculate Φ for every site; this table displays the mean estimate of Φ at each of the 11 study-site/years. Eight species and both species groups had Φ set to 1. Only those species or species groups with Φ ≠ 1 are shown. Φ < 1 indicates that the two species occur together less often than would be expected by chance; Φ > 1 indicates that the two species occur together more often than would be expected by chance; and Φ = 1 indicates no relationship between the two species. All of the 95% confidence intervals included 1.

Study site	Central American agouti	95% CI	Red brocket	95% CI
Mountain Pine Ridge 2007	0.998	0.710 - 1.286	1.071	0.959 - 1.183
Chiquibul 2008	0.999	0.801 - 1.197	1.142	0.954 - 1.330
Cockscomb 2008	0.998	0.708 - 1.288	1.067	0.971 - 1.163
La Milpa 2008	0.998	0.792 - 1.204	1.121	0.970 - 1.272
Fireburn 2009	0.999	0.823 - 1.175	1.119	0.970 - 1.268
Hill Bank 2010	0.999	0.823 - 1.175	1.114	0.971 - 1.257
Mountain Pine Ridge 2011	0.998	0.710 - 1.286	1.076	0.937 - 1.215
Gallon Jug	0.998	0.778 - 1.218	1.085	0.971 - 1.199
La Milpa 2013	0.998	0.777 - 1.219	1.069	0.969 - 1.169
Yalbac 2014	0.999	0.797 - 1.201	1.063	0.971 - 1.155
Hill Bank 2015	0.999	0.815 - 1.183	1.064	0.970 - 1.158

Table 3.6. Two-species occupancy models for puma and prey in Belize, ranked by AIC. In each instance, the prey species listed was the dominant species and puma was the subdominant species. Only models with Δ ≤ 2 are shown. The covariates are as follows: BA = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. The number at the end of each model refers to the model type and is explained in Table 3.2. K is the number of parameters in each model. ΔAIC is the difference between the AIC of each model and the top model. AIC weight is the proportion of evidence that each model draws from the data. Prey species appear in order of increasing size.

Species	Model	K	ΔAIC	AIC weight
C.A. agouti	psiA(STR),psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(STR),rA(BA),rBA(BA)=rBa(BA)1	14	0	0.633
	psiA(STR),psiBA(BA*US),psiBa(BA*US),pA(STR),pB(STR),rA(BA),rBA(BA)=rBa(BA)4	15	1.26	0.3371
White-nosed coati	psiA(STR*US),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(BA),rBA(BA)=rBa(BA)1	16	0	0.4331
	psiA(STR*US),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(BA),rBA(BA)=rBa(BA)4	17	1.9	0.1675
Nine-banded armadillo	psiA(BA*STR),psiBA(BA*US),psiBa(BA*US),pA(STR),pB(BA),rA(BA),rBA(STR)=rBa(STR)4	17	0	0.2407
	psiA(BA*STR),psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(BA),rA(BA),rBA(STR)=rBa(STR)1	16	0.15	0.2233
	psiA(BA*STR),psiBA(STR*US)=psiBa(STR*US),pA(STR),pB(BA),rA(BA),rBA(STR)=rBa(STR)1	16	1.24	0.1295
	psiA(BA*STR),psiBA(STR*US),psiBa(STR*US),pA(STR),pB(BA),rA(BA),rBA(STR)=rBa(STR)4	17	1.47	0.1154
Paca	psiA(BA*STR),psiBA(STR*US)=psiBa(STR*US),pA(BA),pB(BA),rA(STR),rBA(BA)=rBa(BA)1	16	0	0.274
	psiA(BA*STR),psiBA(STR*US)=psiBa(STR*US),pA(BA),pB(BA),rA(STR),rBA(BA)=rBa(BA)4	17	1.69	0.1177
	psiA(BA*STR),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(BA),rA(STR),rBA(BA)=rBa(BA)4	17	1.74	0.1148
Medium-sized mammals	psiA(BA*US),psiBA=psiBa,pA(BA),pB(BA),rA(US),rBA(STR)=rBa(STR)4	14	0	0.2446
	psiA(BA*STR),psiBA=psiBa,pA(BA),pB(BA),rA(US),rBA(STR)=rBa(STR)4	14	1.3	0.1277
	psiA(BA*STR),psiBA=psiBa,pA(BA),pB(BA),rA(US),rBA(STR)=rBa(STR)1	13	1.64	0.1077
Collared peccary	psiA(US),psiBA(BA*US)=psiBa(BA*US),pA(US),pB(STR),rA(BA),rBA(BA)=rBa(BA)1	14	0	0.5132
	psiA(US),psiBA(BA*US)=psiBa(BA*US),pA(US),pB(STR),rA(BA),rBA(BA)=rBa(BA)4	15	1.76	0.2129
Red brocket	psiA(BA*STR),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(STR),rBA(BA)=rBa(BA)1	16	0	0.3904
	psiA(BA*STR),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(STR),rBA(BA)=rBa(BA)4	17	0.77	0.2656
White-lipped peccary	psiA(BA*US),psiBA(BA*US)=psiBa(BA*US),pA,pB(STR),rA(US),rBA(BA)=rBa(BA)1	15	0	0.3702
	psiA(BA*US),psiBA(BA*US)=psiBa(BA*US),pA,pB(STR),rA(US),rBA(BA)=rBa(BA)4	16	0.41	0.3016
White-tailed deer	psiA(STR*US),psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(STR),rA(STR),rBA(BA)=rBa(BA)1	16	0	0.6717
	psiA(STR*US),psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(STR),rA(STR),rBA(BA),rBa(BA)4	17	1.54	0.311
Large mammals	psiA(BA*STR),psiBA(BA*US)=psiBa(BA*US),pA(BA),pB(STR),rA(US),rBA(BA)=rBa(BA)1	16	0	0.5689

Table 3.7A. Untransformed estimates of coefficients for the covariates of 10 two-species occupancy models for combined data set (8 study sites with 277 camera trap locations) in Belize. In each instance, the species listed was the dominant species (labeled A) and puma was the subdominant species (labeled B). Standard errors are given in parentheses. The covariates are as follows: BASAL = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. Estimates with 95% confidence intervals that do not include 0 are shown in bold. The top-ranked white-lipped peccary model had problematic beta estimates, so the highest-ranked model with no problematic betas is also shown. Prey species appear in order of increasing size.

	Central American Agouti	White-nosed Coati	Nine-banded Armadillo	Paca	Collared Peccary	Red Brocket	White-lipped Peccary	White-tailed Deer
psiA	-0.94 (0.18)	0.49 (0.36)	-1.29 (0.22)	0.06 (0.26)	0.81 (0.38)	0.37 (0.24)	0.88 (0.63)	-0.61 (0.18)
psiBA	1.59 (0.32)	1.54 (0.28)	2.09 (0.73)	1.08 (0.23)	1.60 (0.31)	1.54 (0.28)	1.38 (0.29)	1.35 (0.28)
psiBa			1.06 (0.27)					
psiA.BASAL			**0.78 (0.21)**	**0.41 (0.21)**		**0.71 (0.26)**	**3.49 (1.19)**	
psiA.STR	**-0.71 (0.19)**	**-0.76 (0.31)**	0.36 (0.20)	**-0.79 (0.26)**		-0.25 (0.22)		**-0.65 (0.20)**
psiA.US		**0.90 (0.45)**			-0.62 (0.35)		0.95 (0.71)	**0.79 (0.20)**
psiA.BASAL*STR			0.18 (0.21)	0.35 (0.19)		**0.77 (0.23)**		
psiA.BASAL*US							3.55 (1.42)	
psiA.STR*US		**-1.32 (0.47)**						-0.29 (0.20)
psiBA.BASAL	**1.10 (0.40)**	0.55 (0.33)	0.56 (0.34)		**0.78 (0.39)**	0.67 (0.34)		**0.95 (0.37)**
psiBA.STR				**-0.70 (0.20)**			**-0.71 (0.23)**	
psiBA.US	**1.26 (0.35)**	**0.97 (0.31)**	**0.98 (0.30)**	**0.78 (0.24)**	**1.22 (0.33)**	**1.16 (0.31)**	**0.94 (0.30)**	**1.07 (0.32)**
psiBA.BASAL*US	**1.95 (0.50)**	**1.32 (0.46)**	**1.55 (0.45)**		**1.68 (0.51)**	**1.65 (0.47)**		**1.72 (0.46)**
psiBA.STR*US				**-0.62 (0.20)**			**-0.59 (0.22)**	
pA	-1.66 (0.43)	-2.94 (0.33)	-2.46 (0.66)	-2.40 (0.29)	-4.76 (0.84)	-2.64 (0.30)	-3.79 (0.46)	-2.71 (0.35)
pB	-1.46 (0.09)	-2.00 (0.24)	-1.11 (0.08)	-1.56 (0.19)	-1.65 (0.23)	-1.78 (0.17)	-2.03 (0.17)	-1.33 (0.09)
rA	-1.07 (0.11)	-3.09 (0.17)	-1.85 (0.19)	-1.63 (0.13)	-3.34 (0.19)	-2.20 (0.14)	-3.75 (0.23)	-1.07 (0.12)
rBA	-0.88 (0.11)	-0.97 (0.08)	-1.34 (0.14)	-0.99 (0.10)	-1.28 (0.09)	-1.02 (0.08)	-0.78 (0.10)	-1.03 (0.09)
rBa								
pA.BASAL		**0.72 (0.33)**		0.27 (0.32)		**0.66 (0.26)**		

	Central American Agouti	White-nosed Coati	Nine-banded Armadillo	Paca	Collared Peccary	Red Brocket	White-lipped Peccary	White-tailed Deer
pA.STR	-0.17 (0.44)		1.08 (0.64)					-0.12 (0.35)
pA.US					-1.00 (0.66)			
pB.BASAL			**0.46 (0.09)**	0.09 (0.07)				
pB.STR	**-0.24 (0.08)**	**-0.73 (0.20)**			**-1.22 (0.24)**	**-0.74 (0.17)**	-0.16 (0.17)	**-0.26 (0.09)**
rA.BASAL	**0.28 (0.08)**	0.17 (0.13)	0.02 (0.08)		**0.38 (0.15)**			
rA.STR				**0.63 (0.13)**		**-0.36 (0.14)**		-0.10 (0.14)
rA.US							0.37 (0.33)	
rBA.BASAL	**0.24 (0.08)**	**0.29 (0.07)**		**0.30 (0.08)**	**0.25 (0.09)**	**0.24 (0.07)**	0.03 (0.06)	**0.33 (0.09)**
rBA.STR			**-0.44 (0.15)**					

Table 3.7B. Untransformed estimates of coefficients for the covariates of two-species occupancy models for combined data set (8 study sites with 277 camera trap locations) in Belize. In each instance, the species listed was the dominant species (labeled A) and puma was the subdominant species (labeled B). Standard errors are given in parentheses. The covariates are as follows: BASAL = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. Estimates with 95% confidence intervals that do not include 0 are shown in bold. The top-ranked white-lipped peccary model had problematic beta estimates, so the highest-ranked model with no problematic betas is also shown.

	Medium-sized Mammalian Prey	Large-sized Mammalian Prey
psiA	2.56 (0.41)	1.33 (0.25)
psiBA	1.02 (0.19)	1.29 (0.26)
psiBa	-0.11 (0.43)	
psiA.BASAL	**1.91 (0.55)**	0.66 (0.30)
psiA.STR		**-0.52 (0.26)**
psiA.US	**0.99 (0.39)**	
psiA.BASAL*STR		**0.81 (0.26)**
psiA.BASAL*US	**1.33 (0.53)**	
psiBA.BASAL		**0.67 (0.34)**
psiBA.US		**0.99 (0.30)**
psiBA.BASAL*US		**1.55 (0.46)**
pA	-1.22 (0.15)	-2.15 (0.19)
pB	-0.56 (0.27)	-1.75 (0.18)
rA	-0.50 (0.05)	-1.10 (0.07)
rBA	-1.25 (0.07)	-1.05 (0.07)
pA.BASAL	0.03 (0.14)	**0.33 (0.20)**
pB.BASAL	**1.25 (0.46)**	
pB.STR		**-0.44 (0.16)**
rA.US	**-0.46 (0.08)**	**0.39 (0.09)**
rBA.BASAL		**0.23 (0.07)**
rBA.STR	**-0.30 (0.07)**	

Table 3.8. Species interaction factor (Φ) for puma and prey species co-occurrence models across eleven study-site/years in Belize. Co-occurrence models calculate Φ for every site; this table displays the mean estimate of Φ at each of the 11 study-site/years. Seven species and one species group had Φ set to 1. Only those species or species groups with Φ ≠ 1 are shown. Φ < 1 indicates that the two species occur together less often than would be expected by chance; Φ > 1 indicates that the two species occur together more often than would be expected by chance; and Φ = 1 indicates no relationship between the two species. All of the 95% confidence intervals included 1.

Study site	Nine-banded armadillo	95% CI	Medium-sized mammals	95% CI
Mountain Pine Ridge 2007	1.216	0.969 - 1.463	1.095	0.969 - 1.463
Chiquibul 2008	1.27	0.917 - 1.623	1.081	0.917 - 1.623
Cockscomb 2008	1.171	0.973 - 1.369	1.029	0.973 - 1.369
La Milpa 2008	1.245	0.947 - 1.543	1.066	0.947 - 1.543
Fireburn 2009	1.215	0.952 - 1.478	1.051	0.952 - 1.478
Hill Bank 2010	1.231	0.955 - 1.507	1.073	0.955 - 1.507
Mountain Pine Ridge 2011	1.243	0.941 - 1.545	1.102	0.941 - 1.545
Gallon Jug	1.123	0.978 - 1.268	1.027	0.978 - 1.268
La Milpa 2013	1.102	0.967 - 1.237	1.007	0.967 - 1.237
Yalbac 2014	1.133	0.974 - 1.292	1.054	0.974 - 1.292
Hill Bank 2015	1.128	0.975 - 1.281	1.016	0.975 - 1.281

Table 3.9. Two-species occupancy models for carnivores in Belize, ranked by AIC. In each species pair, the first species listed was the dominant species and second species was the subdominant species. Only models with Δ ≤ 2 are shown. The covariates are as follows: BA = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. The number at the end of each model refers to the model type and is explained in Table 3.2. K is the number of parameters in each model. ΔAIC is the difference between the AIC of each model and the top model. AIC weight is the proportion of evidence that each model draws from the data.

Species	Model	K	ΔAIC	AIC weight
Jaguar-puma	psiA,psiBA(BA*US)=psiBa(BA*US),pA(STR),pB(STR),rA(STR),rBA(STR),rBa(STR)2	14	0	0.386
	psiA,psiBA(BA*US),psiBa(BA*US),pA(STR),pB(STR),rA(STR),rBA(STR),rBa(STR)3	15	0.35	0.3241
	psiA,psiBA(US*PACA)=psiBa(US*PACA),pA(STR),pB(STR),rA(STR),rBA(STR),rBa(STR)2	14	1.91	0.1486
Jaguar-ocelot	psiA,psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR)=rBa(STR)1	13	0	0.4095
	psiA,psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR)=rBa(STR)4	14	0.56	0.3095
	psiA,psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR)=rBa(STR)2	14	1.97	0.1529
Jaguar-gray fox	psiA(STR*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR),rBa(STR)1	16	0	0.3972
	psiA(STR*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR),rBa(STR)2	17	1.66	0.1732
	psiA(STR*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(STR),rBA(STR),rBa(STR)4	17	1.93	0.1513
Puma-ocelot	psiA(BA*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(BA),rBA(US)=rBa(US)1	16	0	0.3152
	psiA(BA*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(BA),rBA(US)=rBa(US)4	16	0.13	0.2954
	psiA(BA*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(BA),rBA(US)=rBa(US)2	17	0.99	0.1922
	psiA(BA*US),psiBA(BA*STR)=psiBa(BA*STR),pA(STR),pB(US),rA(BA),rBA(US)=rBa(US)3	17	1.11	0.181
Puma-gray fox	psiA(BA*US),psiBA(STR*US),psiBa(STR*US),pA(STR),pB(BA),rA(STR),rBA(US),rBa(US)2	17	0	0.3844
	psiA(BA*US),psiBA(BA*US),psiBa(BA*US),pA(STR),pB(BA),rA(STR),rBA(US),rBa(US)2	17	0.8	0.2576
	psiA(BA*US),psiBA(STR*US),psiBa(STR*US),pA(STR),pB(BA),rA(STR),rBA(US),rBa(US)3	18	2	0.1414
Ocelot-gray fox	psiA(BA*STR),psiBA(BA*STR),psiBa(BA*STR),pA,pB(BA),rA(STR),rBA(US)=rBa(US)2	16	0	0.3547
	psiA(BA*STR),psiBA(BA*STR),psiBa(BA*STR),pA,pB(BA),rA(STR),rBA(US)=rBa(US)1	15	0.74	0.245
	psiA(BA*STR),psiBA(BA*STR),psiBa(BA*STR),pA,pB(BA),rA(STR),rBA(US)=rBa(US)3	17	1.61	0.1586

Table 3.10. Untransformed estimates of coefficients for the covariates of 10 two-species occupancy models. In each instance, the first species listed in each pair was the dominant species. Standard errors are given in parentheses. The covariates are as follows: BASAL = basal area within 100 m of each site, STR = the length of STRs within 1000 m of each site, US = mean understory density to 1.0 m in height, within 100 m of each site. Estimates with 95% confidence intervals that do not include 0 are shown in bold.

	Jaguar-Puma	Jaguar-Ocelot	Jaguar-Gray Fox	Puma-Ocelot	Puma-Gray Fox	Ocelot-Gray Fox
psiA	1.47 (0.24)	1.15 (0.19)	1.33 (0.2)	1.46 (0.26)	1.22 (0.20)	1.44 (0.41)
psiBA	1.52 (0.30)	2.11 (1.28)	0.46 (0.15)	0.89 (0.21)	0.68 (0.16)	0.45 (0.15)
psiA.BASAL				**0.74 (0.32)**	**0.65 (0.27)**	**1.68 (0.59)**
psiA.STR			-0.06 (0.2)			**-0.40 (0.38)**
psiA.US			0.28 (0.21)	**1.08 (0.29)**	**0.83 (0.23)**	
psiA.BASAL*STR						**1.21 (0.56)**
psiA.BASAL*US				**1.80 (0.42)**	**1.21 (0.34)**	
psiA.STR*US			**-0.48 (0.20)**			
psiBA.BASAL	**0.87 (0.37)**	2.69 (1.89)	**-0.86 (0.18)**	**0.90 (0.30)**		**-0.88 (0.18)**
psiBA.STR		0.56 (1.20)	-0.10 (0.15)	**-0.51 (0.22)**	0.16 (0.16)	-0.05 (0.16)
psiBA.US	**1.12 (0.33)**				**0.56 (0.19)**	
psiBA.BASAL*STR		2.21 (1.63)	**-0.61 (0.17)**	**0.68 (0.29)**		**-0.64 (0.18)**
psiBA.BASAL*US	**1.77 (0.47)**					
psiBA.STR*US					**0.61 (0.21)**	
pA	-2.46 (0.25)	-1.72 (0.22)	-1.24 (0.11)	-1.69 (0.16)	-0.94 (0.10)	-1.80 (0.17)
pB	-1.96 (0.29)	-2.45 (0.28)	-1.06 (0.28)	-2.19 (0.23)	-2.44 (0.50)	-0.32 (0.24)
rA	-0.99 (0.06)	-1.04 (0.07)	-1.19 (0.07)	-1.03 (0.07)	-1.45 (0.08)	-0.82 (0.09)
rBA	-0.68 (0.11)	-1.01 (0.08)	-0.06 (0.06)	-0.88 (0.07)	-0.62 (0.13)	-0.40 (0.13)
rBa	-1.40 (0.09)				-0.25 (0.07)	-0.63 (0.09)
pA.STR	0.28 (0.20)	**0.38 (0.17)**	**0.26 (0.09)**	**-0.48 (0.16)**	**-0.21 (0.10)**	
pB.BASAL					**-3.94 (0.65)**	**-1.17 (0.31)**
pB.STR	-0.26 (0.24)					
pB.US		**-0.49 (0.31)**	**1.92 (0.31)**	**-0.45 (0.22)**		
rA.BASAL				**0.12 (0.05)**		
rA.STR	**0.27 (0.06)**	**0.22 (0.07)**	**0.15 (0.07)**		**-0.39 (0.09)**	-0.06 (0.10)
rBA.STR	**-0.39 (0.07)**	**-0.22 (0.08)**	**0.27 (0.06)**			
rBA.US				**0.26 (0.09)**	**0.37 (0.08)**	**0.64 (0.10)**

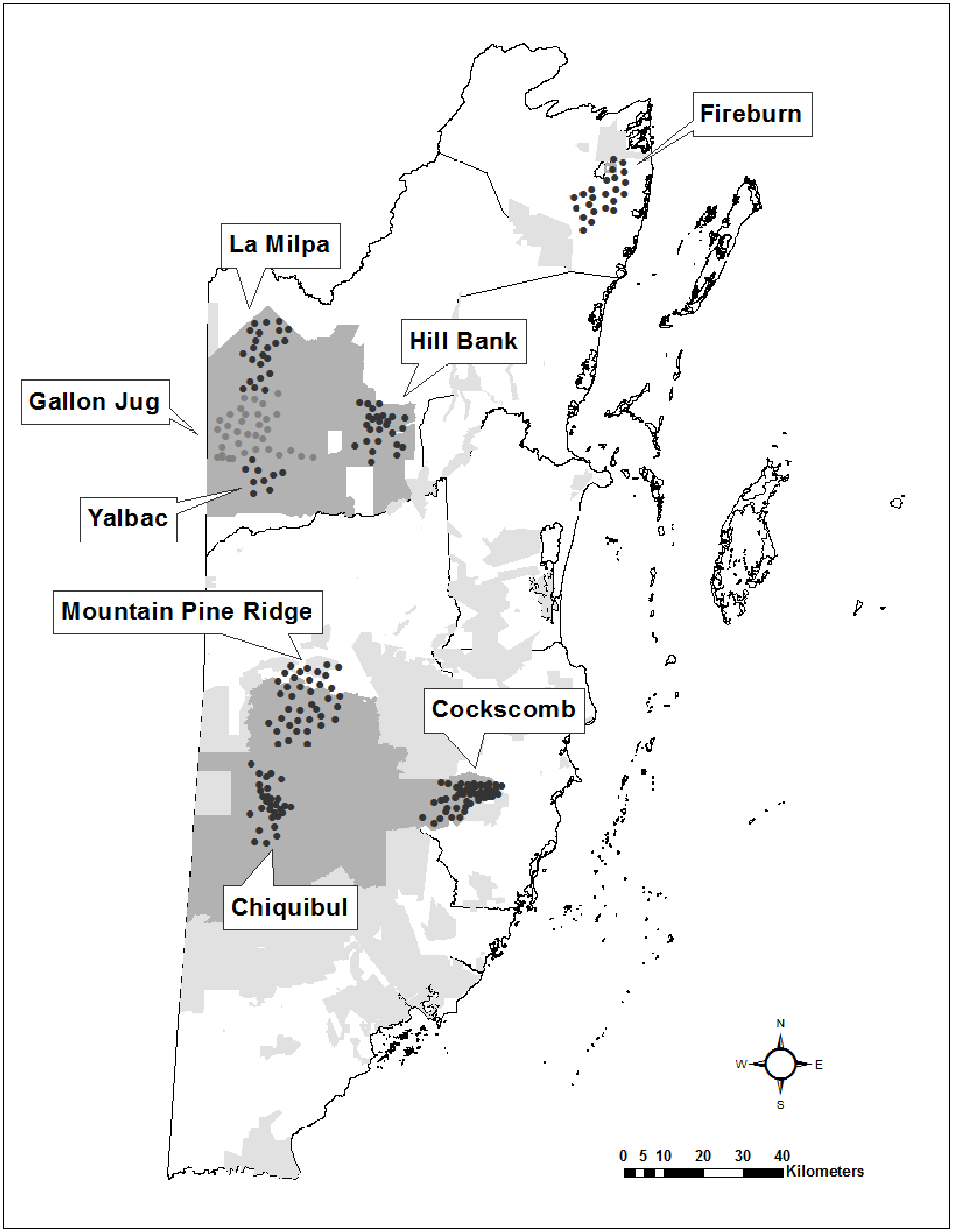

Figure 3.1. The eight study sites in Belize used in this analysis. Each dot represents one camera location in 2015, except Chiquibul (2008), Cockscomb (2008), and Fireburn (2009). Protected areas are shown in gray. Surveyed protected areas are shown in dark gray.

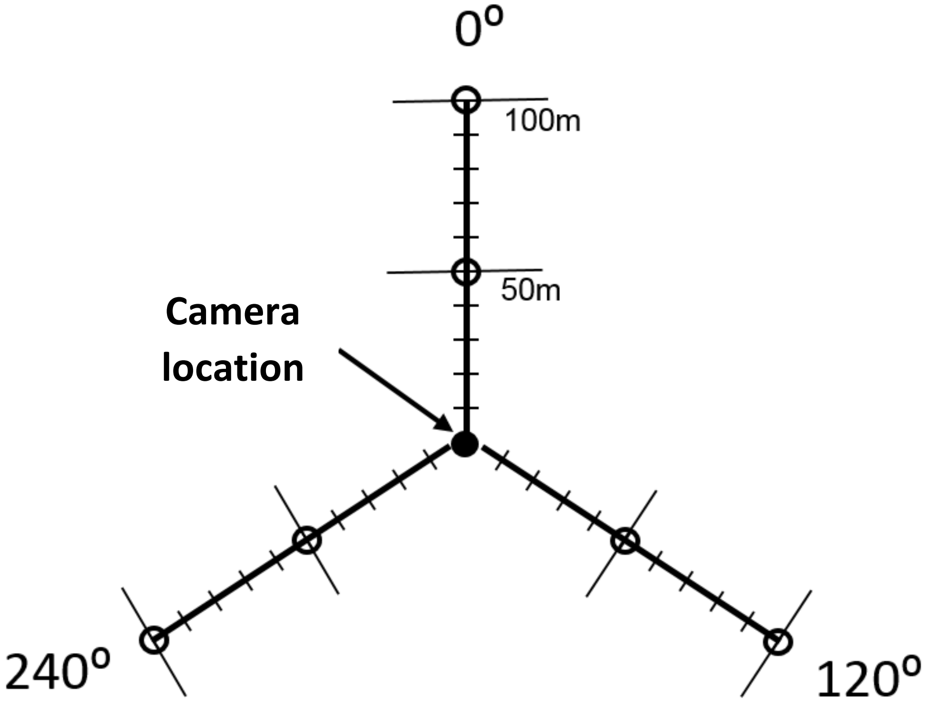

Figure 3.2. Schematic diagram of the microhabitat survey conducted at each camera station. Tree data were collected at the camera station and at 50 meters and 100 meters along each of the three major transects (shown as open or closed circles). Understory data were collected every 2 meters along six 40 m transects that ran perpendicular to the three main transects at 50 meters and 100 meters from the cameras.

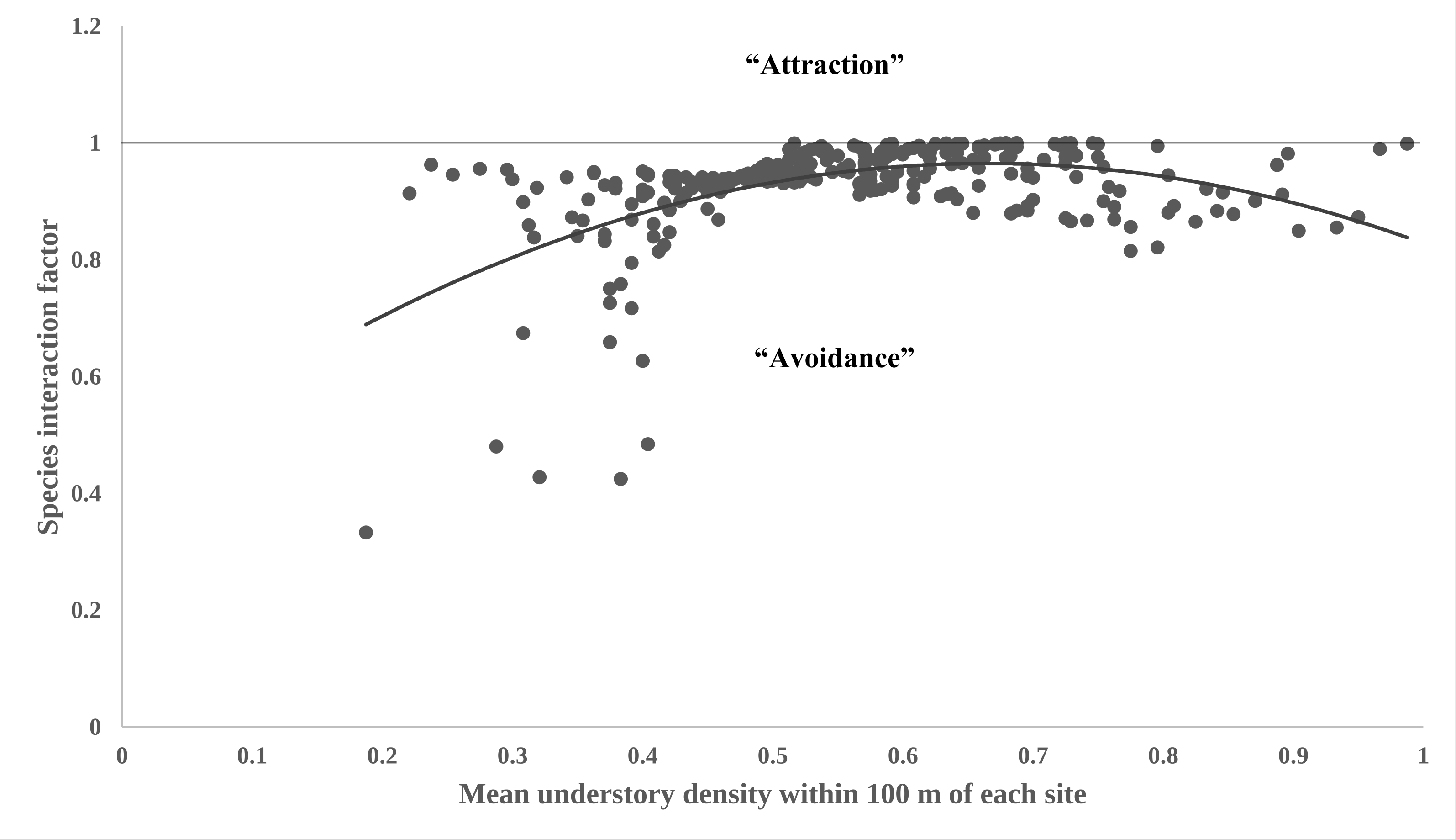

Figure 3.3. The species interaction factor (Φ) for jaguars and pumas from the second-ranked two-species co-occurrence model plotted against the mean understory density to 1 m in height, within 100 m of each site. Jaguar was designated as the dominant species in this model; pumas were the subdominant species. If Φ < 1, that indicates that the two species occur together less often than should happen by chance alone (apparent "avoidance"), if Φ > 1, the two species occur together more often than should happen by chance (apparent "attraction"), and if Φ = 1, there is no evidence for an interaction between the two species. A thin black line on the graph marks Φ = 1. The second-order polynomial trend line is a thicker gray line.

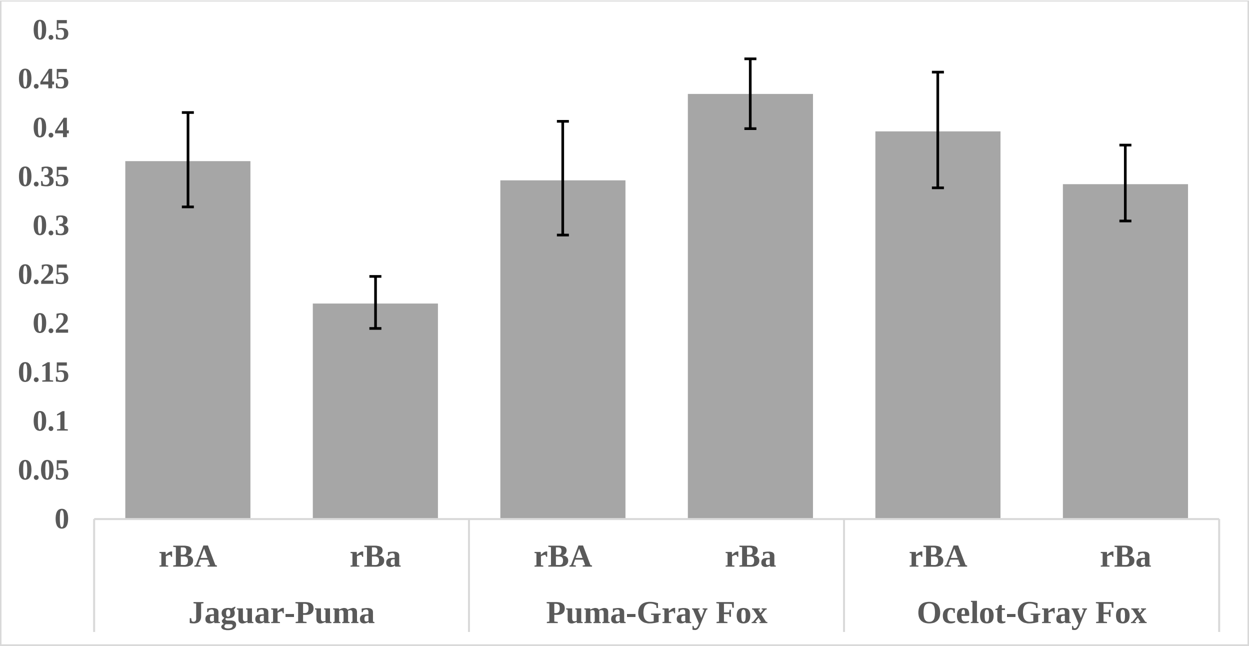

Figure 3.4. Detection probabilities for two-species occupancy models for carnivores in Belize. In each species pair, the first species listed is the dominant species. rBA is the detection probability of the subdominant species in the presence of the dominant species. rBa is the detection probability of the subdominant species in the absence of the dominant species. The jaguar-ocelot, jaguar-gray fox, and puma-ocelot pairs are not shown because the best model indicated rBA = rBa. The error bars show the 95% confidence intervals. Student's t-tests demonstrated that rBA and rBa were significantly different in all three pairs of estimates.

Conclusion

While pumas are well studied elsewhere in their range, less is known about the species in Central America. Tropical pumas are roughly half the size of their temperate counterparts and favor smaller prey. These differences suggest that tropical pumas may play a different role in their communities than temperate pumas and that the numerous studies from North America, Chile, and Argentina may not be directly applicable to pumas in Central America. As such, Central American pumas warrant further study.

I used both single-species occupancy models and two-species co-occurrence models to analyze multiple years of camera trapping data from 277 locations across eight study sites in Belize to examine the effects that habitat, prey availability, and interspecies competition had on puma occupancy. Habitat was the main driver of where pumas occurred. Pumas showed a strong preference for sites with dense understory, as we would expect from an opportunistic predator that typically attacks prey from short distances. Several researchers have found that pumas avoid wetter areas around rivers and attribute this to avoidance of competition with larger, sympatric jaguars, which favor these areas (Schaller and Crawshaw 1980, Emmons 1987). I found some support for this avoidance of wetter areas, but the evidence was weak, perhaps because wet areas are abundant in this region and thus harder to avoid.

The presence of prey was not found to affect where pumas occurred. In general, this is not surprising for a generalist predator that freely switches among prey species. However, it is somewhat surprising to find no association with pacas, given that Foster et al. (2013) found that they made up nearly 60% of puma diet in Belize. It is also surprising that puma occupancy was not affected by the presence of medium-sized mammalian prey species (1-15 kg), as a group, as this has been found to be the most important prey type for tropical pumas (Núñez et al. 2000, Sunquist and Sunquist 2002).

There was no evidence that jaguars had a negative effect on puma occupancy in Belize. In fact, jaguar activity (trap success) was the strongest predictor of where pumas occurred across Belize. This is somewhat surprising given the large degree of dietary overlap between the two species and suggests that they may currently exist at population densities too low to produce interspecies competition (Taber et al. 1997). We should be cautious about making evolutionary inferences based on recent dietary data because of anthropogenic changes to habitat that disrupt predator-prey assemblages (Núñez et al. 2000), but it does appear that, at current population densities, jaguars may be acting as an umbrella species (Lambeck 1997b) for the other carnivore species in this study (puma, ocelot, and gray fox). This is likely to benefit these smaller carnivores because jaguars are listed as threatened on the IUCN Red List of Threatened Species and so are a higher conservation priority than the other sympatric carnivores. Conservation efforts directed at jaguars, therefore, are likely to benefit the other carnivores, as well. Jaguarundis, margays, and other mesocarnivores were not included in this study, as sample sizes were too small, and thus those species would benefit from separate, targeted investigations.

Multi-season occupancy analysis showed that puma occupancy was stable or increasing in the areas surveyed. However, whether this truly represents a stable population requires further investigation. While occupancy has been used as a surrogate for abundance or to monitor trends in populations (MacKenzie and Nichols 2004, Tempel and Gutiérrez 2013), population density estimates would provide more certainty in population trends. Also, these estimates apply only to protected areas surveyed in this study. If pumas were being driven from other areas into protected areas, that could explain why occupancy was increasing at some sites, but would also require further investigation.

Somewhat surprisingly, puma occupancy was found to be highest in the most disturbed areas surveyed (Gallon Jug Estate, Hill Bank, and Yalbac Ranch and Cattle Corporation). All of these areas are subject to some degree of logging. As part of an NGO-owned protected area, Hill Bank has only limited logging, but the other two study sites are owned by for-profit timber companies. These companies practice selective logging of a few high-value species, as mandated by the Belize Forest Department. All three areas follow similar logging practices (40 year rotation, leaving 20 seed trees per hectare). The high puma occupancy rates in these areas suggest that this current level of natural resource extraction is not detrimental to puma distribution.

One caveat for this study is that the multi-season, single-species occupancy models and the two-species co-occurrence models were not adjusted for overdispersion because I am unaware of any currently developed techniques that can address this issue. This overdispersion can lead to underestimated standard errors and the selection of overly complex models. This may lead to incorrectly finding significance in individual covariates. In other words, we may find support for covariates that the data do not actually support. We should, therefore, be cautious about interpreting covariates that are not strongly supported by the data in these two analyses. However, the fact that results were similar between the single-species and two-species analyses suggests that this may not be a problem in this data set.

Also, surveys were only conducted in relatively protected areas. Although, some of these were privately-owned timber companies, they still controlled access to their properties, often to a greater degree than is possible on public protected land in Belize. We did not conduct surveys in agricultural areas or in populated areas, therefore, we are unable to address how puma occupancy may change in these areas. With widespread land use changes occurring in Belize and throughout Central America, the effects of these changes on pumas and other carnivores warrant further investigation.

Occupancy is a somewhat coarse tool for assessing population status, so I attempted to estimate puma population density from our camera trapping data. Mark–resight models (Arnason et al. 1991, McClintock et al. 2009), provide an alternative to capture–recapture techniques when only a subset of the animals is uniquely identifiable, in this case by subtle, natural marks (e.g., scars, tail kinks, subtle coat patterns). Although camera trapping data have been used to estimate puma population density using mark-resight models (Sollmann et al. 2013, Rich et al. 2014, Zanon-Martinez et al. 2016), agreement rates of the identity of pumas from photographs between three independent observers in our lab were ~ 40% and this was judged to be too low to proceed with this technique. Addressing this problem would be a logical next step for future research.

This study represents a successful application of single-species and two-species occupancy analyses using camera trapping data to address the knowledge gap of the habitat, prey availability, and interspecies competition factors that affect puma occupancy in Belize. This study also demonstrates the utility of using camera trapping surveys to assess populations of non-target species. In addition to the academic value of this study, this large scale, country-wide assessment should also be of practical use to the Forest Department and other government agencies of Belize, as well as conservation NGOs (e.g., Programme for Belize).

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