

Determining habitat and biotic factors driving puma (*Puma concolor*) space use and underlying dynamic processes (colonization and extinction) over 20 years in protected and private areas throughout Belize, Central America.

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ACADEMIC ABSTRACT

Despite being a top carnivore, there is relatively scant information on pumas (*Puma concolor*) in the neotropics especially compared to the more well-studied jaguar (*Panthera onca*). Understanding long-term puma distribution can affect land management decisions such as appropriate size of buffer zones around protected areas since pumas influence, and are influenced by, sympatric carnivore populations, lower trophic levels, and habitat. We used single-species, single-season and multi-season occupancy modeling to explore factors influencing distribution and persistence of pumas across the country of Belize. We used camera trapping data from 7 protected areas over 20 years with 2,198 camera stations covering ~5,000 km². For both approaches, detection was mostly affected by distance to roads, enhanced vegetation index (EVI), and elevation, with variable directionality depending on site. In single season modeling, Occupancy increased at lower elevations and intermediate EVI in one site, and closer to water sources at another, while in multi-season modeling, intermediate EVI and canopy cover influenced occupancy. Biotic covariates were highly variable across sites and methods, but detection and occupancy were generally positively associated with prey, jaguar and ocelot trap rates, canopy cover, and elevation, while human trap rates negatively affected occupancy at one site. Colonization was positively affected by deer (*Odocoileus virginianus* and *Mazama americana*) trap rates while extinction had no supported covariates. Puma occupancy ranged from 0.41-0.96 in single season models and 0.55-0.90 in multi-season models across all site/years. Compared to other single-season studies, Belize generally had higher occupancy, even in areas of selective logging, however there are no other multi-season studies to compare. While sites with heavy human impacts had lowest occupancy, these areas are still used and likely serve as steppingstones between protected areas of higher occupancy. Such areas could be targets for protection to preserve landscape connectivity. Additionally, due to high occupancy and colonization across varying habitat and biotic factors the jaguar is likely an effective umbrella species for puma space use, however more analysis on other species is needed to ensure efficiency for more than just pumas.

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GENERAL AUDIENCE ABSTRACT

The neotropics is an important global zone known for high biodiversity and carbon sequestration. Felids (wild cats) play an important role in maintaining biodiversity and structure in ecosystems, however, they are facing threats to their survival due to habitat loss and fragmentation, and negative human-wildlife conflict. To protect ecosystem health, managers often employ the umbrella species concept, meaning if they protect the jaguar with its large spatial requirements, other wildlife species that fall within that area will also be protected. However, there have been few studies on the effectiveness of this strategy, especially for species like the puma, that might be competitive with jaguars. Occupancy modeling is a powerful tool in wildlife management that uses presence absence analysis to determine where species occur on a landscape. We used camera trapping data across multiple protected areas over 20 years to determine what influences pumas across the landscape. We found pumas were affected by differing variables depending on habitat. Important variables were: thickness of vegetation, elevation, distance to roads and water, prey and there were positively associated with jaguars and ocelots. Additionally, pumas were more likely to move into a new site if the activity of their favored prey, deer, was high. Pumas occurred at 41-96% of camera stations depending on site, across all years, indicating they are widespread across Belize. Compared to 11 other occupancy studies from Latin America, Belize generally had higher occupancy, even in areas of selective logging, compared to the other available studies in the neotropics. While sites with heavy human impacts had lowest occupancy, these areas are still being used by pumas and likely serve as steppingstones between protected areas of higher occupancy. Such areas could be targets for protection to preserve landscape connectivity across Belize, which is rapidly developing in infrastructure. Overall, jaguars appear to be a suitable umbrella species for the puma, however, further analysis is needed for more specialized species such as threatened Baird's tapir, crested guan, black howler monkey, and smaller cat species, the margay and jaguarundi, to ensure that the jaguar is a suitable umbrella species that supports a wide variety of species within the community.

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I. Introduction

Due to exponential human population growth and rising per capita demand for land cover the last century, the world is facing increasing resource pressures resulting in a 0.57% decrease in forests per year from resource extraction, agricultural expansion, and increasing incidences of large-scale fire (Otto 2018). This has led to three-quarters of Earth's ice-free surface to be altered, consequently degrading, and altering habitat for forest-dependent wildlife (Ellis and Ramankutty 2008). Direct human impacts, along with climate change, are causing the sixth mass extinction on the planet and population declines and extirpations of many wildlife species, including large mammals such as big cats (felids), have occurred (Ceballos 2017). Habitat loss and fragmentation are prevalent in tropical ecosystems where large felid species that exert top-down control on ecosystems (Terborgh 2001) tend to disappear first due to their large home ranges, naturally low densities, and conflicts with humans. This loss is exacerbated by climate change in tropical areas through a combination of increasing frequency and intensity in weather patterns like hurricanes and shifts in seasonality (longer dry seasons and shorter rainy seasons) (Pascale et al. 2015, Knutson et al. 2019), thus negatively affecting wildlife populations.

Tropical ecosystems in Latin America are known as biodiversity hotspots such that they are highly biologically rich yet threatened regions (Biodiversity Hotspots Defined 2021). Studies have supported that through top-down control, large wild felids play important roles in maintaining biodiversity and structuring ecological communities in tropical forest ecosystems (Soule et al. 1999). For example, on islands that lose apex felids, herbivores at lower trophic levels increase and overexploit vegetation, causing system collapse (Terborgh 2001, Estes et al. 2011). Losing biodiversity, especially in these tropical biodiversity hotspots, can be detrimental to ecosystem function and stability needed to provide sustainable future resources for both people and animals.

Understanding interactions between co-occurring predators, and the mechanisms that allow coexistence, is important to biodiversity conservation. Top predators may influence subordinate ones within their own guild through competition. Competition theory suggests that dominant competitors exploit preferred habitat resources to the detriment of subordinate carnivores, which either are reduced in number through competition or are forced to avoid desirable locations (Schoener 1974, Caro & Stoner 2003, Gehrt & Clark 2003). Alternatively, the umbrella species concept suggests protection of a large charismatic species, that have large spatial requirements, often the jaguar in the Neotropics, can indirectly protect smaller species living within the umbrella's area (Sanderson et al. 2002, Burnham et al. 2012, Maslo et al. 2016). While some studies support protection of top predators to protect biodiversity, others suggest they are poor umbrellas (Schoener 1974). Thus, the umbrella concept is complex due to interspecific competition that can result in negative distribution and abundance relationships between top- and meso-predators (Crooks & Soule 1999, Ritchie & Johnson 2009).

As sympatric species, the potential for interspecies conflict among jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*) is high due to overlap in diet, similar hunting strategies, and taxonomy (Donadio & Buskirk 2006). For example, Moreno et al. (2006) found that when jaguars were absent from island ecosystem, ocelot diet changed to include larger prey items than when in the presence of the top felid. However, niche partitioning (separation in resources) among felids has been difficult to determine due to their elusive and wide-ranging nature resulting in mixed research results, particularly in mainland ecosystems (Crawshaw and Quigley 1991, Noss et al. 2006, Harmsen et al. 2011). Testing support for these concepts is difficult due to lack of long-term monitoring data collected on multiple predators simultaneously, especially in forested areas with wide-ranging species. Preliminary results from Belize have not

found negative relationships between jaguars and ocelots over 6 years (Satter and Kelly 2017), but the potential mediating influence of pumas (as the intermediate-sized species between the two) has not been addressed. While competition is more likely to happen within a carnivore guild, body size is one of the most important factors contributing to competition, thus jaguar-puma, and likewise puma-ocelot, pairs may be more likely to interact negatively due to similarities in size (Donadio & Buskirk 2006). Thus, it may not be surprising that preliminary results did not find negative relationships in population size between jaguars and ocelots in Belize since their size differences are substantial. This could mean that jaguars suppress pumas, thereby releasing ocelots from competition with pumas, a phenomenon coined the mesopredator release hypothesis (Ritchie and Johnson 2009). However, a study conducted in the Mountain Pine Ridge Forest Reserve in Belize showed that carnivores did not spatially partition habitat and the jaguar could potentially function as an umbrella species (Davis et al. 2011). Without information on puma numbers though, we do not know if this theory holds weight or if all predator numbers rise and fall in synchrony. I plan to address this missing link between jaguar and ocelots by estimating puma distribution over time and at landscape scale (including multiple sites) for comparison to jaguar and ocelot landscape distribution to determine if spatial partitioning is occurring and assess drivers of occupancy on a large scale.

Puma Taxonomy, Distribution, Habitat, and Morphology

Because pumas are the least well studied of the 3 large felids in Belize, I conducted a review of pumas focusing on tropical areas. The puma, currently listed as Least Concern under the International Union for Conservation of Nature (IUCN), is the largest member of the subfamily Felinae, second largest felid in the Americas after the jaguar, and fourth largest felid in the world. After much debate over taxonomic designations concerning variation in puma

morphology and distribution, an extensive genetic study was conducted throughout the entirety of the puma range, which determined there to be seven subspecies of *Puma concolor* compared to the 32 past subspecies classified. The subspecies, *Puma concolor cougar*, resides in North America, Mexico, Belize, and Guatemala, while the five other subspecies reside in the remainder of Central and in South America (Culver et al. 2000). Finally, there is a much-debated seventh subspecies, the Florida panther (*Puma concolor coryii*) that occupies fragmented habitat in Florida and is currently listed as endangered by the IUCN (Network et al. 2014).

Historically, pumas were found throughout most of southern Canada and the contiguous United States, spanning from coast to coast and from sea-level to 5,800 m in elevation (Young and Goldman 1946). However, the pumas' range has been reduced by two-thirds of its original size due to widespread extirpation, especially from the eastern United States, excluding the small population in Florida (Sunquist and Sunquist 2002). Populations have declined and are susceptible to fragmentation, which could cause genetic isolation and consequently loss of genetic diversity (Saremi et al. 2019). Despite these anthropogenically-imposed challenges, pumas are still the most widely distributed terrestrial mammal with the largest geographic range in the Western Hemisphere and they occupy increasingly urbanized and human-altered landscapes (Figure 1).

One of the reasons pumas are the most widely distributed felid in the Americas is due to their generalist life-history strategy, allowing them to occupy a myriad of habitats from arid deserts and humid rainforests to cold high elevation mountain ranges. There have been multiple studies on preferred habitat selection of pumas in the Nearctic and from southernmost South America, but little to none in the Neotropics. The studies from the Nearctic suggest that pumas commonly prefer complex mountainous and/or canyon terrain with dense vegetative cover (Beier

et al. 1995, Sweanor et al. 2000). Studies that did quantify habitat characteristics found vegetation and topography to be the most significant criterion. For example, Beier et al. (1995) found that pumas prefer dense vegetation, higher elevation, and rugged terrain, which most likely correlates with the pumas' stalk and pounce (ambush) type hunting strategy. Much like Beier et al. (1995), Franklin et al. (1999) found in Patagonia, Southern Chile that pumas also utilized areas with high canopy cover and tree density and when they were most active, they used areas with bushes, grasses, rocks, and cliffs for cover. Sweanor et al. (2000) found that because of puma population dynamics and dispersal behavior, pumas exhibited a metapopulation structure, where they inhabited suitable areas and dispersed across less suitable habitat, which ultimately enhanced gene flow.

With large variation in geographical distribution and preferences for specific habitat and prey, a pumas' morphological characteristics such as coat length and overall body size can vary. However, all pumas have the same tan coat, long black tipped tail, and light undersides. There is minimal sexual dimorphism in pumas except for mass where males tend to be on average 40-60% larger than females in all study areas (Gay and Best 1995). In general, animals are smaller near the equator possibly due to Bergmann's Rule (Blackburn et al. 1999), which correlates higher environmental temperatures with smaller body mass to maintain better balance of energy in warm-blooded animals (Gohli and Voje 2016). Therefore, both male and female pumas are smaller in size and stature closer to the equator. However, based on an extensive study of Bergmann's rule among 22 mammalian families, there are potentially other major drivers of body mass, such as resource availability, stress, and humidity, rather than just temperature and latitude (Gohli and Voje 2016). Nevertheless, pumas found in the more extreme northern and southern ranges are roughly twice the weight with males averaging ~100 kg (220 lbs) and

females averaging ~64 kg (140 lbs) compared to ~55 kg (120 lbs) for males and ~30 kg (64 lbs) for females in the tropics (Sunquist and Sunquist 2002). Pumas in the northern and southern extremes also have larger home ranges than pumas in the tropics (Sunquist and Sunquist 2002).

Diet/Feeding Strategy

While pumas in North America are thought to be white-tailed deer, *Odocoileus virginianus*, specialists (Trani et al. 2007), pumas also are known to be flexible, generalist predators, which suggests they can survive in a wide variety of habitats and consume a wide array of prey species. Pumas have been noted eating prey ranging in size from moose to mice, which illustrates their adaptability to what is available in their environment (Iriarte et al. 1990). However, they will choose the most energetically profitable prey according to optimal foraging theory, so in their more northern and southern ranges where they are larger, pumas will choose larger prey, particularly white-tailed deer (Cooley et al. 2008). When closer to the equator, like in Belize, they will prey more on medium- and small-sized prey about 1-15 kg (Monroy-Vilchis et al. 2009). Pumas in the tropics could be exploiting smaller prey species in habitat types that reduce encounter rates with larger prey species like white-tailed deer, and where smaller prey may be more abundant, especially towards the equator where body mass of most mammals tends to be smaller in general (Iriarte et al. 1990, Harmsen et al. 2011). Alternatively, pumas may be choosing smaller prey to avoid competition and interactions with much larger jaguars, with which they have a large degree of dietary overlap of species such as the armadillo, white-tailed and red brocket deer, and paca (Iriarte et al. 1990, Harmsen et al. 2011). However, prey selection studies on pumas are limited because they require comparisons of available prey and most studies have limited information on prey availability and they also have not addressed potential biases in prey detection in scats (Pierce and Bleich 2003).

Pumas, as well as jaguars and ocelots, are known as ambush predators that hunt opportunistically using stalking behavior, which correlates with their preference for habitat with concealment cover (Emmons 1987, Sunquist and Sunquist 2002). A study conducted in southern California found that when hunting, pumas stalk or sit to ambush on average for ~42 minutes at a time, and then move an average distance of 1.4 km for up to six times in a night (Beier et al. 1995). Pumas will prey on vulnerable species that present debilitating diseases or environmental stresses due to low foraging success or lean seasons (Krumm et al. 2010). Elbroch and Quigley (2019) found that puma prey selection is age dependent. For instance, mature adults tend to hunt large prey such as rocky mountain elk 99% of time while subadult pumas hunt medium sized prey like mule deer until reaching a mature age (Elbroch and Quigley 2019). Pumas kill their prey by using quick bursts of speed to knock unsuspecting individuals off balance and then deliver a bite to the throat or neck area to sever arteries/vertebrae or to suffocate (Sunquist and Sunquist 2002). When hunting smaller prey like rodents, pumas are known to deliver a crushing bite to the preys' body while grasped in its claws. Once prey is caught, the puma will lessen its movement until the carcass is consumed. For instance, if pumas catch small prey their movement will only be lessened for 4-6 hours, however, if they catch larger mammals their movement will be lessened for up to two to five days due to the preys' size and spoilage rates (Beier et al. 1995, Nunez et al 2000). Pumas cache (bury or cover) large prey that require multiple days to consume to reduce consumption by scavengers (Beier et al. 1995).

Behavior/Reproduction

Pumas like all other felids besides the African lion (*Panthera leo*) are generally thought to be primarily solitary and spend most of their lives apart from each other due to their extreme territorial nature. Traditional exceptions of cat sociality include when females raise their young,

when young disperse with siblings, during mating, or while feeding (see below) (Pierce and Bleich 2003, Elbroch and Quigley 2016). Recent studies have shown that cats exhibit a degree of sociality with one another, for example, there is evidence to support the resource dispersion hypothesis, which states that solitary animals like pumas can exhibit temporary social behaviors otherwise known as adaptive social strategies due to resource fluxes and cost-benefit tradeoffs (Elbroch and Quigley 2017, Elbroch et al 2017). For instance, there was a documented case where nine pumas were gathered around a single elk kill (Elbroch and Quigley 2017). Studies that collared pumas found that males had larger home ranges than females that did not overlap other males, and that they also travelled longer net daily distances than females, which had home ranges about half the size of males such that several females occur within each male's home range (Seidensticker et al. 1973, Beier et al. 1995). This allows males to mate with multiple females (Robinette et al 1961). However, there is only one home range study from pumas in the Neotropics (Nunez and Miller 2019) and no published study conducted in Belize. Pumas locate each other during mating season via olfactory and auditory signals and will typically spend 2-5 days together during the mating process, copulating up to 70 times a day (Eaton 1976, Currier 1983, Beier et al 1995). After an 82-96 day gestation, females will typically produce two to four kittens and provide maternal care for 1-2 years.

Umbrella species concept

The umbrella species concept suggests that the protection of large charismatic species, with large spatial requirements, often protects many smaller, naturally co-occurring species living in the same area under their 'umbrella' (Caro and O'Doherty 1999; Fleishman et al. 2000; Seddon and Leech 2008). Due to economic and public constraints tied to landscape and wildlife conservation management, it is not possible to protect all areas and all wildlife species, therefore

this concept gained much popularity in efforts to preserve landscapes for the largest number of wildlife species (Fleishman et al. 2000). The umbrella species concept continues to be used as justification for management decisions such as the minimum size for conservation areas and corridors in vital ecosystems, based on the spatial and habitat requirements of the umbrella species present (Roberge and Angelstam 2004).

Despite its wide application, there are relatively few empirical tests of the utility and success of the umbrella species concept (Caro 2003, Roberge and Angelstam 2004, Seddon et Leech 2008, Branton and Richardson 2011). Branton and Richardson (2011) performed a meta-analysis that showed this concept's implementation and success was highly variable and context-dependent in saving more than just the umbrella species.

There is some evidence that supports the effectiveness of using the jaguar as an umbrella species for the larger ecological community in the Neotropics. Thornton et al. (2016) assessed the use of jaguars as an umbrella species through a wide range of conservation networks from Mexico to Argentina using indices of ~1,500 co-occurring mammals for species richness, habitat quality, and fragmentation. They found that protecting areas of high jaguar use was a better method than protecting random areas of high-quality, interior habitat. However, due to Branton and Richardson's (2011) findings, there is much need to research implications and success in specific areas before widespread implementation of this strategy.

Niche Partitioning and Competition Theory

A species' niche is typically defined by the resources, habitat, and interactions needed to survive, or its ecological role in the ecosystem (Polechova and Storch 2019). When two species niches overlap, resource partitioning and/or competition can occur often causing the subordinate species to utilize lower quality habitat or preferred prey species. This ties into competition theory

that states that dominant carnivores exploit preferred resources to the detriment of subordinate carnivores, which either are reduced in number or forced to avoid desirable locations, which can result in an inverse density relationship between carnivore species. While most carnivores have traits that decrease the effects of interspecific competition on fitness and allow for coexistence, increased anthropogenic effects that fragment landscapes can elevate rates of conflict, potentially shifting normal intraguild interactions (Schuette et al. 2013).

Jaguars and pumas are sympatric across the jaguars' range, implying some form of coexistence, however the influence of increasing anthropogenic impacts (e.g. deforestation, increasing infrastructure, hunting and logging - Figure 1) on coexistence of these species is little studied (Harmsen et al. 2010). Further studies may indicate that coexistence is becoming more difficult as co-occurring species are crowded onto smaller and smaller protected areas, potentially causing increased competition and pushing subordinate carnivores (i.e. puma), to the fringes of high-quality habitat or causing declines in their numbers.

The ocelot, the smallest predator in this guild, also overlaps ranges with pumas and jaguars. In Panama, there was evidence of considerable dietary overlap between pumas and ocelots (Moreno et al 2006). However, ocelots typically rely on small prey (<1 kg) while pumas and jaguars focus on medium to larger prey (>9.7 kg), which is in line with the energetic model of carnivores (Carbone et al. 1999). Satter and Kelly (2017) found no evidence that ocelots numbers are inversely related to jaguar numbers in Belize. However, the relationships between distribution of pumas and ocelots, and pumas and jaguars, have not been studied in this study system.

Study Sites and History of Land Use Change and Ownership

My research was conducted in seven field sites in Belize, Central America: 1. combined Greater Belize Maya Forest consisting of: Rio Bravo Conservation and Management Area (La Milpa and Hill Bank), Belize Maya Forest (Yalbac and Laguna Seca), Gallon Jug Estates (Gallon Jug), 2. Mountain Pine Ridge Forest Reserve, 3. Chiquibul Forest Reserve, 4. Cockscomb Basin Wildlife Sanctuary, the 5. Belize Central Corridor, 6. Manatee Forest Reserve, and 7. Fireburn in Belize (Figures 3, 4). I outline details of these study areas below.

Greater Belize Maya Forest: Rio Bravo Conservation and Management Area

Rio Bravo Conservation and Management Area includes two field sites La Milpa and Hill Bank and is owned by a Belizean NGO, the Programme for Belize (PfB) since 1988, whose goal is “to promote the conservation of the natural heritage of Belize and to promote wise use of its natural resources”. It is the largest private reserve and second largest protected area in the country, at approximately 1,053 km². This area forms part of the Yucatan Platform and includes broadleaf forest areas, pine savannah, and wetlands (PfB 2016). It also contains 75% of the watersheds in Northern Belize. It has amazing biodiversity with over 745 flora species, 70 mammal species, 350 bird species recorded, and 12 endangered animal species (PfB 2016). This area is also part of La Selva Maya, which is the second largest tropical forest (behind the Amazon) in the Americas located within Belize, Guatemala, and Mexico. It possesses high biodiversity of endemic and endangered species and is a conservation area critical for jaguars and other wildlife in this region (<https://www.iucn.org/regions/mexico-central-america-and-caribbean/selva-maya-natural-resources-protection-project>).

La Milpa study area is strictly reserved for conservation and tourism due to the rise of ecotourism in Belize and the cultural heritage found within the area. Ancient Mayan sites can be

found throughout including the third largest archaeological (La Milpa) site in Belize. There is no logging in the interior of this site, which is primarily broadleaf forest and wetlands. This site is considered a control for our other GBMF sites that are all similarly sustainably logged (PfB 2016) until 2021, when logging was discontinued in all other sites except for Hill Bank.

Hill Bank like all forests in Belize had been logged for over 300 years mostly for mahogany until the logging camps were abandoned in the 1980s. Hill Bank was later purchased by PfB in 1989. It contains pine savannah, broadleaf forest, and wetland habitat. PfB began practicing sustainable timber harvesting in 1997 with the mission of “To Conserve the biodiversity and promote the sustainable development of Belize through the proper management of the Rio Bravo Conservation and Management Area and other lands entrusted to it”. They follow the Belize Forest Department guidelines of sustainable harvest and are certified under the Forest Stewardship Council by Wood Mark and Smart Wood (PfB 2016). However, the effect of sustainable logging on the species such as the jaguar and other felids on PfB lands had not been studied until Dr. Marcella Kelly began camera trapping in 2008.

Greater Belize Maya Forest: Gallon Jug Estates/Laguna Seca/Yalbac

Gallon Jug Estate is owned by the Bowen family, a well-known established Belizean family and Belizean business enterprise (a.k.a. Bowen and Bowen). Bowen and Bowen own many companies in Belize such as Crystal water, Coca-Cola, Belikin Beer, and the Gallon Jug Estate, which produces coffee, hot sauces, and owns and manages an ecolodge that supports ecotourism of wildlife and supports research on a local Mayan archeological site. The family sold 423 km² of the 530 km² of their land (the Laguna Seca portion) effective in 2015 to Yalbac Ranch and Cattle Corporation, which was owned by a Virginia-based company (Forest Lands Group). This land is mostly broadleaf forests with wetland areas and many bodies of water.

Yalbac Ranch and Cattle Corporation Limited, a corporation in Texas that originally bought land in the Yalbac Hills in Belize in 1994. The corporation logged the area with several management objectives in mind and following the Principles and Criteria of the Forest Stewardship Council (as in Rio Bravo) to harvest in sustainable ways with minimal effects on the forest and to preserve archeological resources and bodies of water (Yalbac 2020). In 2010, however, a major hurricane passed through the area, followed by subsequent forest fires, which disturbed approximately 60% of the forest (Yalbac 2020). The corporation sold a portion of this ‘unprofitable’ land to the local Mennonites who practiced slash and burn, clear-cutting of forest in 2013 to present, thus dramatically altering and clearing land. In 2019, the company sold the remaining land to the Belize Maya Forest Trust (see below). Camera-trap surveys began in this area in 2014 and have continued since then (Table 1).

Greater Belize Maya Forest: Belize Maya Forest

The Belize Maya Forest Trust (BMFT) comprises of over a dozen non-governmental organizations (NGOs) that came together in 2020 and in 2021, purchased all of Yalbac and Laguna Seca 960 km² of land and they discontinued all logging in the area. Even though these areas, Rio Bravo, Gallon Jug, and BMFT have differing histories and ownership, this is one continuous patch of forest totaling over 2,000 km². Despite differences in management like allowing extraction or not, all areas have manned gates 24/7 on roads where entry would be the highest. Then each area has a team of rangers to patrol the forest and minor roads that can be accessed less easily. Patrols are meant to lessen the threat of wildlife poachers that mostly poach for subsistence hunting and to lessen illegal logging. Rangers are also responsible to mitigate natural disasters ie fire and collaborate with researchers in the area.

Mountain Pine Ridge Forest Reserve

The Mountain Pine Ridge Forest Reserve (MPR) is 430 km² of tropical pine forest constituting one of only six tropical pine forest ecosystems in the world. This ecosystem is dominated by Caribbean pine trees, which have harder wood than other pines due to the ability to grow year-round. This area contains dramatic ecotones from pine forest to broadleaf forest at the edges due to a granite massif that pushed up through the surrounding limestone during the shifting of tectonic plates that made the soil too acidic for broadleaf forest (Kesler et al. 1974). Altitude ranges from 120-1016 meters causing mean annual nighttime temperatures to be lower than the Greater Belize Maya Forest. Annual rainfall averages from 1,550-2,100 mm. Many local people thought that this area was not suitable for jaguars in Belize, but Dr. Kelly's surveys since 2004 have shown jaguars to be living and breeding there.

Chiquibul Forest Reserve (CFR)

The Chiquibul Forest Reserve, established in 1959, is approximately 598 km² and located within the Maya Mountains. It is bordered by Chiquibul National Park, Caracol Archaeological Reserve, the Mountain Pine Ridge Forest Reserve, and in close proximity to the Belize/Guatemala border. The area contains 17 distinct ecosystems however they are all variants of lowland and submontane tropical broadleaf forest that receives an average of 2,000mm of annual rainfall (Penn et al. 2004). The reserve supports high biodiversity including the endangered scarlet macaw (Boris 2016).

CFR is the largest managed reserve in Belize, which is needed as there are high levels of poaching due to its proximity to the Guatemalan border where there are historical border disputes and plentiful resources. Xateros (poachers) from Guatemala get their name because of their heavy poaching of the Xate palm but also poach scarlet macaws (Groff and Axelrod 2013, Boris

2016). The area is managed by the Belize Forest Department, Friends for Conservation and Development, and Bulridge Limited, a sustainable logging company for timber and non-timber forest products.

Cockscomb Basin Wildlife Sanctuary

Cockscomb, a flat area hemmed in by steep mountain ridges surrounding the basin, is a 488 km² forest reserve established in 1984 and became the first jaguar reserve in the world in 1986. Before then, this area was logged and home to Mayan communities. It is known for its expansive mountain ranges with elevation reaching 1120 m and network of water sources. It is comprised of moist tropical jungle with 2,540-4,570 mm of rainfall annually and is home to hundreds of species of flora and fauna. It is currently administered by the Belize Audubon Society and surveyed with remote cameras by our collaborators within the international NGO, Panthera.

Central Belize Corridor

The Central Belize Corridor extends over 750 km², is 1 of 3 movement corridors in the country, and is said to be “the most critical” of the corridors (<https://www.uberibz.org>). This corridor connects the Maya Forest area, a part of La Selva Maya, to Manatee Forest Reserve and other protected areas in the south. Most notably this corridor is a part of the Mesoamerican Biological Corridor to connect La Selva Maya to Mexico and Guatemala. It consists of both private and protected lands containing broadleaf forest and low-lying savanna land holding many flora and fauna species. Rainfall ranges from 1,680-3,850 mm (<https://belize.com/belize-annual-rainfall/>). This area is currently not protected.

Manatee Forest Reserve

Manatee Forest Reserve is one of 17 forest reserves in Belize and is surveyed by Panthera. This is the eastern most study site within the central corridor and is a coastal moist tropical forest that is approximately 469 km². It is comprised of a variety of broadleaf and pine trees, shrubs, grasses, and wildlife. This area receives approximately 2,000-2,700 mm of rainfall annually with the majority happening in the rainy season (June-December) causing seasonal marsh land (Guy and Eitnien 2012).

Fireburn Reserve

Fireburn Reserve (FR) is approximately 8 km², a part of the Northeast corridor, and holds similar biodiversity of flora and fauna to the field sites listed above. It contains tropical evergreen, seasonal broadleaf, lowland swamp forests, and agricultural lands. It receives less than 2,000 mm of rainfall annually. Fireburn Reserve is privately managed by Wildtracks (Wildtracks accessed 2024).

Camera Trapping

Remote camera trapping has become a standard technique for studying elusive, medium to large carnivores that are difficult to study by physically capturing and handling due to extensive time, money, and physical exertion (Kelly et al. 2012). It is often more feasible to utilize camera traps rather than live trapping to collect data over large areas and longer time periods to photo-capture more individuals, increasing sample size, which leads to more precise density estimates when modeling low-density populations (Kelly et al. 2012). Camera traps ‘capture’ animals in photos by using heat and motion sensors that trigger when animals pass by. The technique is particularly effective on species that have individual markings allowing for

individual identification and the application of mark-recapture statistics to estimate abundance (Silver et al. 2004).

Each survey site in this study had a camera trap grid that operated for 1-3 months, 24 hours a day. This short time frame relative to the lifespan of the target species (i.e.-large predators) enables us to assume demographic and geographic closure (no deaths, births, immigration, or emigration) during that survey season. We check cameras at each station every 10-14 days to ensure correct functioning and to download data at regular intervals. Once the survey is complete, the date and time-stamped photos of all animals, vehicles, and people are organized, entered, and analyzed. Capture histories of felids are constructed for further analyses.

My study

I studied a widespread Neotropical guild consisting of the jaguar and puma in Belize, Central America, using a long-term, camera-trapping dataset (Table 1), to elucidate whether jaguars limit or not, the space use of the puma. Understanding the role of competition is vital for supporting or rejecting the jaguar as an umbrella species, which can affect management decisions for subordinate species.

In contrast to jaguars and ocelots, there have been few studies on pumas in the Neotropics. So far, the only studies indicating negative relationships among species in this Neotropical guild come from small islands (Terborgh 2001), which may not be generalizable to mainland systems where most populations of these felids occur. Thus, my study in Belize can function as a case study for this guild in mainland Central America to guide management and spur other research to examine how widespread such findings are. My thesis work consists of 2 primary objectives: 1) Determine landscape factors driving species distribution (i.e. site use) through single season occupancy modeling for pumas and jaguars across the landscape using data from our sites and those of collaborators, covering the northern half of Belize, and 2) Determine changes in habitat

and landscape factors over 10-20 years driving species distribution within our sites through multi-season occupancy modeling for pumas and including spatial overlap with jaguars in our broadleaf and pine forest sites of Belize.

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Figures/Tables

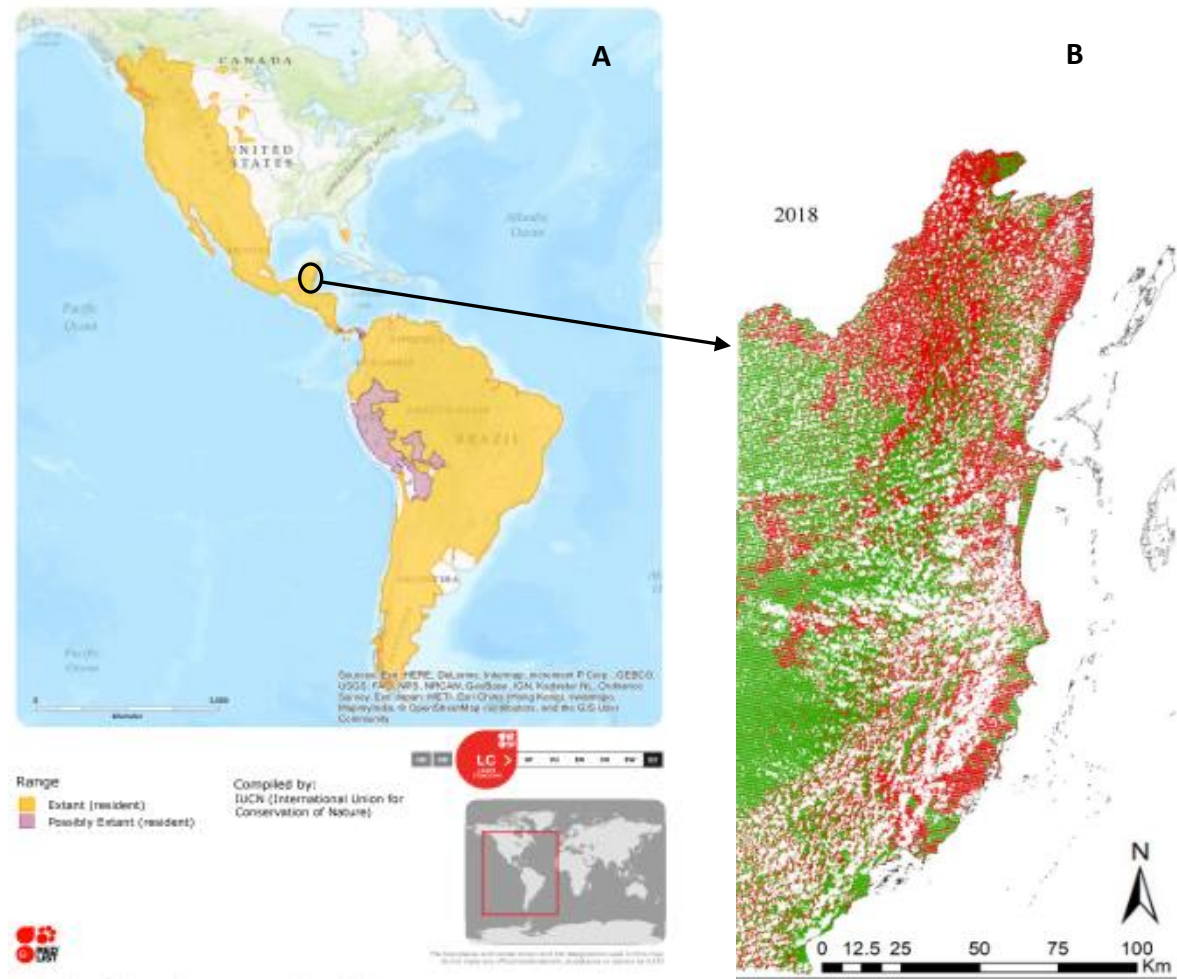


Figure 1. Current distribution of pumas (yellow-extant and purple-possibly extant) from the IUCN Red List report accessed February 23, 2021 (A). Black circle indicates the location of Belize, Central America. Shown is the amount of forested (green) to non-forested (red) land throughout Belize, in 2018 (B). Non-forested lands include areas deforested primarily for agriculture, livestock, and urbanization (Folkard-Tapp 2020).

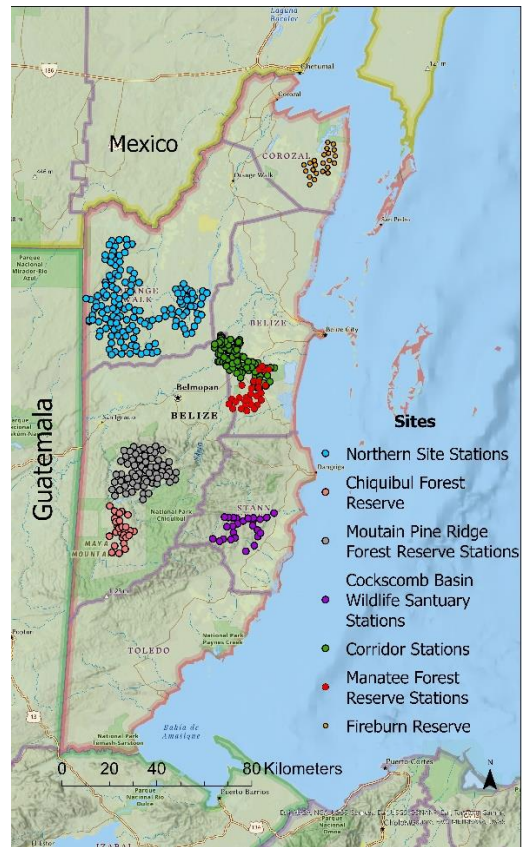


Figure 2. Camera trapping survey sites (different colors) and stations (dots) throughout Belize, Central America: Central Belize Corridor (green), Cockscomb Basin Wildlife Sanctuary (purple), Fireburn Reserve (yellow), Greater Belize Maya Forest (blue), Mountain Pine Ridge Forest Reserve (grey), Manatee Forest Reserve (red), and Chiquibul Forest Reserve (pink).

Table 1. All study sites with total years running from the beginning to the present with total trap nights functioning and current number of stations in each site in Belize, Central America used in the analysis.

Site	Years Running	Total Trap Nights	Stations
Greater Belize Maya Forest	2009-2019, 2021	72,585	20-147
<i>Yalbac</i>	2014-2019, 2021	10,036	9-35
<i>Gallon Jug</i>	2013-2019, 2021	21,226	29-42
<i>La Milpa</i>	2010-2019, 2021	17,497	20-27
<i>Hillbank</i>	2009-2019, 2021	23,826	20-43
Chiquibul Forest Reserve	2002-2008	3,540	10-30
Mountain Pine Forest Reserve	2004-2008, 2009-2021	50,654	19-65
Cockscomb Basin Wildlife Sanctuary	2012-2017, 2019, 2021	14,400	20-22
Belize Central Corridor	2009, 2011-2013	28,254	32-100
<i>Big Falls</i>	2009, 2012-2013	8,370	29-32
<i>Bonzana</i>	2009, 2011	4,080	20
<i>Cox Lagoon</i>	2009, 2011	2,852	31
<i>Cox Logging Road</i>	2012	1,012	11
<i>Runaway Creek</i>	2009, 2011	2,100	20-21
<i>LCJCWS</i>	2012	1,380	15
Manatee Forest Reserve	2019-2021	8,460	20-37
Fireburn Reserve	2009	1704	23
Total	2002-2021	181,025	2,221

II. Assessing anthropogenic, environmental, and biotic factors driving wide-scale species distribution through single-species, single-season occupancy modeling for pumas in Belize, Central America

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Abstract

While pumas are well-studied in North America, there is relatively scant information on their habitat use in Latin America, particularly in the Neotropics. Understanding puma occupancy can impact land management decisions since pumas influence, and are influenced by, sympatric carnivore populations and lower trophic levels. We used micro-habitat, macro-habitat, and biotic covariates in a single-species, single-season occupancy modeling approach, to explore factors influencing puma distribution across the country of Belize. We used camera trapping data across 7 protected areas of varying habitats (interior to coastal habitat, pine to tropical broadleaf forest, low to high elevation) and management regimes for modeling puma occupancy and detection. We used data for up to 20 years (2002-2021) and 2,198 camera stations covering ~5,000 km² of protected areas and private lands. Top models indicated that mostly macrohabitat followed by biotic factors strongly influenced occupancy or detection, while microhabitat covariates rarely were included in top models, with the exception of positive influence of canopy cover. Detection was mostly affected by macrohabitat covariates with distance to roads being prevalent. In areas with lower human activity, pumas were detected closer to roads, while in more human dominated landscapes, pumas were detected farther from roads, and occasionally puma detections were lowest at intermediate distances from roads. EVI either positively influenced detection or detection was highest at intermediate levels of EVI. Other supported variables included elevation, and distances to settlements and water, with study site specific directions of influence. Occupancy was affected by macrohabitat such that detection increased at lower elevations in one site, was highest at intermediate EVI, and was higher in closer proximity to water sources. Biotic covariates were highly variable, but detection and occupancy were generally positive associated with prey, jaguar, and ocelot trap rates, while human trap rates negatively affected occupancy at one site. Occupancy was usually higher in interior protected tropical broadleaf forests compared to other habitats and was lower in atypical habitats and those with smaller areas and higher human impacts. Overall, puma occupancy ranged from 0.41-0.96 across all landscapes over all years. Some study sites exhibited extremely high occupancy from 0.80 to 0.95 and no sites appeared to be declining or increasing over time. Compared to other studies in the neotropics, Belize had higher occupancy in general, even across multiple land use types including areas of selective logging. While sites with heavy human impacts had lowest occupancy, these areas are still being used and likely currently serve as steppingstones between protected areas of higher occupancy. Thus, such areas could be targets for protection to preserve landscape connectivity. Our positive associations between competing felids, the jaguar, puma, and ocelot, indicate the jaguar could be used as an umbrella species in driving management decisions for protecting habitat, assuming their populations are stable.

Keywords: single-season occupancy, detection, covariates, maximum likelihood estimation, competition, niche partitioning, *Puma concolor*, Neotropics

Potential Journals: Canadian Journal of Ecology species symposium on pumas/cougars

Introduction

Not only are tropical forest ecosystems in Latin America biodiversity hotspots holding thousands of wildlife species, but also they are an integral part of carbon sequestration, ecotourism, acquisition of resources, and culture (CEPF accessed 2021). Many of the countries that hold these ecosystems are developing nations and to meet increased demands, forests are converted to agricultural, livestock, and urban lands leading to habitat loss, fragmentation, and degradation, which increases potential for negative human-wildlife interactions (e.g. Ripple et al. 2014). Large wild cat (felid) species that exert top-down control through maintaining biodiversity and structuring ecological communities in tropical forest ecosystems (Soule et al. 1999, Terborgh 2001) tend to disappear first due to their large area requirements, naturally low densities, and conflicts with humans (Ripple et al. 2014). For instance, historically, pumas were found throughout most of southern Canada, the contiguous United States, to southern Argentina and Chile (Young and Goldman 1946). As the human population has grown, landscapes have been altered, prey availability has declined, and hunting of pumas has led to widescale decline reducing puma range by two-thirds of its original size (Sunkist and Sunkist 2002).

Despite these anthropogenically imposed challenges, pumas are still the most widely distributed terrestrial mammal with the largest geographic range of all felids, occurring only in the Western Hemisphere and occupying increasingly urbanized and altered environments (Sunkist and Sunkist 2002). However, puma decline is further exacerbated by climate change in tropical areas through a combination of increasing frequency and intensity in weather patterns like hurricanes, and a shift in seasonality generally resulting in longer dry seasons and shorter rainy seasons (Pascale et al. 2015, Knutson et al. 2019), thus negatively affecting predator and prey populations. Losing biodiversity, especially in these tropical biodiversity hotspots, can be

detrimental to ecosystem function and stability needed to provide sustainable future resources for both people and animals.

Due to high biodiversity, tropical forest ecosystems are critical targets for wildlife, environmental, and cultural conservation. Since it is not plausible to protect all areas and species, conservationists tend to focus efforts on top predators that require large areas and that exert top-down control in ecosystems (Seddon and Leech 2008) but also rely on healthy prey populations to survey (Harmsen et al. 2011). A common management strategy to combat extinction rates, biodiversity loss, and climate change accelerated by the threats listed above, is to apply the umbrella species concept for landscape management (Seddon and Leech 2008). The umbrella species concept is the notion that by protecting the habitat requirements of a large, charismatic species that has large area requirements such as the jaguar, that will in turn protect other wildlife species that live within that area (Maslo et al. 2016). However, there are mixed results in the literature on whether this is an efficient strategy (Schoener 1974, Seddon and Leech 2008). Competition theory suggests that dominant competitors exploit preferred habitat resources to the detriment of subordinate carnivores and can reduce abundance of subordinates or shift their distribution to less desirable areas (Schoener 1974; Caro & Stoner 2003; Gehrt & Clark 2003). Thus, the umbrella concept is complex due to interspecific competition that can result in negative distribution and abundance relationships between top- and meso-predators (Crooks & Soule 1999, Ritchie & Johnson 2009), especially as such predators get increasingly crowded into few remaining protected areas (Wolf & Ripple 2016).

As sympatric species, the potential for interspecies conflict among jaguars (*Panthera onca*), pumas (*Puma concolor*), and ocelots (*Leopardus pardalis*) is high due to overlap in diet, similar hunting strategies, and phylogenetic ancestry (Donadio & Buskirk 2006). The puma is the

largest member of the subfamily Felinae, second largest felid in the Americas after the jaguar. Body size is important in competition, resulting in higher potential for negative interactions between jaguars and pumas than with ocelots, which are much smaller than the other two species (Donadio & Buskirk 2006). Furthermore, niche partitioning (separation in resources) among felids has been difficult to determine due to their elusive, often nocturnal, and wide-ranging nature (Crawshaw and Quigley 1991, Noss et al. 2006, Harmsen et al. 2011).

Understanding factors such as habitat and diet influence on distribution of sympatric large predators is necessary to better understand potential competition or coexistence. We might expect spatial coexistence in the tropics despite the puma being the subordinate carnivore due to their generalist life-history strategy, resulting in plasticity in habitat and diet. While pumas in North America are thought to be white-tailed deer specialists (Trani et al. 2007), pumas also are known to be flexible, generalist predators (Hornocker & Negri, 2010), which suggests they can survive in a wide variety of habitats and consume a wide array of prey species. A potential way pumas avoid competition with larger predators is by changing their diet from larger vertebrates to medium to small prey sources (Karandikar et al. 2022). Pumas will choose the most energetically profitable prey according to optimal foraging theory, such that in their more northern and southern ranges where they are larger (and there are no jaguars), pumas will choose larger prey, particularly white-tailed deer and guanacos (Cooley et al. 2008). When closer to the equator where they are smaller, like in Belize, pumas will prey more likely on medium- and small-sized prey about 1-15 kg (Monroy-Vilchis et al. 2009). Pumas in the tropics could be exploiting smaller prey species due to habitat types that reduce encounter rates with larger prey species like white-tailed deer, and where smaller prey may be more abundant, especially towards

the equator where body mass of most mammals tends to be smaller in general (Iriarte et al. 1990, Harmsen et al. 2009).

Alternatively, pumas may choose smaller prey to avoid competition and interactions with larger jaguars, however studies have shown a large degree of dietary overlap (Iriarte et al. 1990, Harmsen et al. 2009). Therefore, it is unclear whether predator avoidance, small prey abundance, or even human impacts, is the stronger driver of puma distribution near the equator. As for habitat, there have been multiple studies on preferred habitat selection of pumas in the Nearctic and from southernmost South America, but little to none in the Neotropics. The studies from the Nearctic suggest that pumas commonly prefer complex mountainous and/or canyon terrain with dense vegetative cover (Beier et al. 1995, Sweanor et al. 2000). Beier et al. (1995) found that pumas prefer dense vegetation, higher elevation, and rugged terrain, which most likely correlates with pumas' stalk and pounce (ambush) style hunting strategy. Much like Beier et al. (1995), Franklin et al. (1999) found in Patagonia, southern Chile that pumas also utilized areas with high canopy cover and tree density and when they were the most active, they used areas with bushes, grasses, rocks, and cliffs for cover. Therefore, despite preferences, due to their adaptability, pumas may spatially avoid higher quality habitat preferred by jaguars (Harmsen et al. 2009, Romero-Munoz et al. 2010). For instance, Sollmann et al. (2012) found that jaguars primarily stayed within the protected area, Emas National Park in Brazil, while pumas would travel outside the boundaries to search for resources. Additionally, Foster et al. (2010) found that puma scats were found outside of reserve boundaries more than jaguar scats indicating spatial separation where pumas may be pushed to less desirable habitat in more human dominated areas.

Testing support for the umbrella species concept is difficult due to lack of long-term data on multiple predators simultaneously. Also, there is relatively scant information on pumas or

their habitat use in Central America, especially compared to the more well studied jaguars (e.g. Sanderson et al. 2002, Kelly et al. 2008, Gonzalez-Borrajo et al. 2016). One of the reasons pumas are less studied compared to jaguar for example, is due to their uniform coat making it difficult to identify individuals. Therefore, occupancy modeling has been used instead of density estimation to address the challenge of obtaining information useful for conservation of pumas across a landscape (Zanon Martinez 2023).

The use of detection, non-detection data from camera traps, while adjusting for imperfect detection, to estimate occupancy is a powerful tool used in many studies to determine factors influencing species distribution or space-use across a landscape. This provides vital information for landscape management. For instance, a study conducted in California, USA used occupancy modeling to determine how prey availability, habitat, and human factors affected puma space use to better manage land in San Francisco (Coon et al. 2020). Another study in south-eastern Mexico used occupancy modeling to study co-existence of jaguars and pumas in an ecological reserve to ensure management was supporting both felids, which resulted in conflicting species-specific results (Ávila-Nájera et al. 2020). Additionally, a study conducted across a multitude of landscapes in Argentina using camera traps to gather information for management to halt the extirpation of pumas where potential for negative human-puma interactions is high, especially outside of protected areas (Zanon Martinez et al. 2023).

Understanding interactions between co-occurring predators, and the mechanisms that allow spatial coexistence over time, is critical to biodiversity conservation (Vellend 2016). Therefore, we used a single season occupancy modeling approach to assess microhabitat, macrohabitat, and biotic factors (including other species) influencing puma distribution and space use. Other occupancy studies on pumas have occurred in the United States, Central, and South America,

mostly within national parks and protected areas spanning a few years per study and using small to large scale camera trapping (Sollman et al. 2012, Meyer et al. 2020, Coon et al. 2020). In this study, we also used camera trapping data from long-term surveys and from collaborative efforts among several international and Belizean non-governmental organizations (NGOs), the Belize Forest Department, private landowners, and community members beginning in 2004, making this, globally, of the longest running (over 20 years) and largest scale (over 4,848 km²) camera trapping projects.

To contribute to broader knowledge of pumas in the tropics, our goal was to tease apart the relative importance of bottom up (e.g., habitat, prey) versus top down (e.g., jaguars, humans) by: 1) assessing drivers of distribution across Belize using one of these largest camera trapping data sets in conjunction with surrounding microhabitat, macrohabitat, and biotic factors as covariates, 2) estimating occupancy over large spatial and temporal scales and multiuse landscapes to examine evidence for constriction in range indicating a potential decline and 3) comparing our results to occupancy results from the literature to assess how pumas are faring in Belize relative to other areas. These findings will contribute to both academic insight and practical landscape management in Belize and beyond. Wolf and Ripple (2016) found that most large carnivores maintain strongholds in public protected areas and private protected landscapes, however there is often not enough space to allow large carnivores to meet all their resource demands. Therefore, our study can serve as a case study for the larger Latin American community providing insight on how pumas fare across multi-use landscapes managed by multiple stakeholder groups.

Methods

Study area

Our research was conducted in, and based on our findings from, 7 field sites across the country of Belize, Central America: the Greater Belize Maya Forest (Rio Bravo La Milpa, Rio Bravo Hill Bank, Gallon Jug Estate, and Belize Maya Forest), Mountain Pine Ridge Forest Reserve (MPR), Chiquibul Forest Reserve (CFR), Cockscomb Basin Wildlife Sanctuary (CBWS), the Belize Maya Corridor (BMC: Big Falls, Runaway Creek, Bonzana, Cox Lagoon, Cox Logging, LCJCWS), Manatee Forest Reserve, and Fireburn (Figure 1; Table 1). Belize has an area of 22,966 km² with 8,221.8 km² being protected (World Bank 2020). The area within boundary lines of our study sites ranges from 430 km² to 1,053 km², totaling 4,855 km² (17% of the country and 50% of protected areas) and consists of varying amounts of broadleaf moist and rain forest, savannah, wetlands, and pine forest. While all these sites are on private or protected lands, they vary in management style and level of protection. We outline details below.

Rio Bravo Conservation and Management area encompasses our two field sites La Milpa (RBLM) and Hill Bank (RBHB) and has been owned by Programme for Belize (PfB) since 1988. It is the largest private reserve and second largest protected area in Belize, at approximately 1,053 km². This area forms part of the Yucatan Platform and includes broadleaf forest areas, pine savannah, and wetlands. It also contains 75% of the watersheds in Northern Belize (Rio Bravo 2016). This area is also part of La Selva Maya, which is the second largest tropical forest of the Americas located across portions of Belize, Guatemala, and southeast Mexico. It possesses high biodiversity and numerous endemic and endangered species.

La Milpa area is strictly reserved for conservation and tourism. There is no logging in the interior of this site, which is primarily broadleaf forest and wetlands. In 1997, PfB began sustainable logging in Hill Bank, however the area had been previously logged up until the

1980s. This area contains pine savannah, broadleaf forest, and wetland habitat. PfB follows the Belize Forest Department guidelines for sustainable harvest and timber is certified under the Forest Stewardship Council by Wood Mark and Smart Wood (Rio Bravo 2016).

Gallon Jug Estate (GJLS) is owned by the Bowen family, a well-known established Belizean family and Belizean business enterprise. They previously conducted sustainable logging, however, the company sold 423 km² of the 530 km² of their land effective in 2015 to Yalbac Ranch and Cattle Corporation, which was subsequently sold to the Belize Maya Forest Trust (see below). This land is mostly broadleaf forests with wetland areas and many bodies of water and is within a forest block of about 16,187 km² that spans into Mexico and Guatemala (Global Conservation 2024). There currently is a small cattle ranch, a coffee production area, and an ecolodge within Gallon Jug.

Yalbac Ranch and Cattle Corporation Limited, a corporation in Texas that originally bought land in the Yalbac Hills in Belize in 1994. The corporation logged the area with several management objectives in mind such as to follow the Principles and Criteria of the Forest Stewardship Council (as in Rio Bravo) to harvest in sustainable ways with minimal effect on the forest and to preserve archeological resources and important bodies of water called cenotes (Yalbac 2020). The corporation sold a portion of this ‘unprofitable’ land, following a severe hurricane, to the local Mennonites who clear-cut the forest from 2013 to present, thus dramatically altering land. In 2019, the company sold the remaining land the Belize Maya Forest Trust.

Starting in 2020, the Yalbac and Laguna Seca area, 960 km², changed ownership to the Belize Maya Forest Trust, an NGO whose purpose is to preserve the forest. They discontinued all logging in the area. This area is also a part of La Selva Maya, the second largest tropical

forest in Latin America and mainly consists of broadleaf forest and wetlands with a multitude of water hole sources with a wide array of fauna and flora species.

All of the areas noted as the GBMF are contiguous habitat and entry into the areas requires permission to pass through manned gates. With the purchase and creation of the lands now known as the Belize Maya Forest (BMF) in 2021, the area went from 3 sites with sustainable logging (Hill Bank, Gallon Jug/Laguna Seca, Yalbac) and one without (La Milpa), to currently only 1 site with sustainable logging (Hill Bank), while on all other lands logging has been discontinued. Annual rainfall averages from 1,550-1,600 mm.

The Mountain Pine Ridge Forest Reserve (MPR) is 430 km² of tropical pine forest constituting one of only six tropical pine forest ecosystems in the world (Buchhorn et al. 2020). This fire adapted ecosystem is dominated by Caribbean pine trees (*Pinus caribaea* and *Pinus oocarpa*), dramatic ecotones going from pine forest to broadleaf forest at the edges and in the riparian areas (Kesler et al. 1974). Elevation ranges from 120-1,016 meters causing mean annual nighttime temperatures to be lower than the GBMF. Annual rainfall averages from 1,550-2,100 mm.

The Chiquibul Forest Reserve (CFR), established in 1959, is approximately 598 km² making it the largest managed reserve in Belize and located within the Maya Mountains. It is bordered by Chiquibul National Park, Caracol Archaeological Reserve, the Mountain Pine Ridge Forest Reserve, and sits near the Belize/Guatemala border. Its proximity to the border poses security challenges as xateros (poachers primarily of the xate plant species) have been known to take other flora and fauna from the area. The area contains 17 distinct ecosystems, however they are all variants of lowland and submontane tropical broadleaf forest that receives an average of 2,000 mm of annual rainfall (Penn et al. 2004). The reserve supports high biodiversity including

the endangered scarlet macaw (Arevelo 2016). CFR is managed by the Belize Forest Department, Friends for Conservation and Development, and Bulridge Limited, a sustainable logging company for timber and non-timber forest products.

Cockscomb Basin Wildlife Sanctuary (CBWS), a flat area hemmed in by steep mountain ridges surrounding the basin, is a 488 km² forest reserve established in 1986. Before then, this area was logged and home to Mayan communities. It is known for its expansive mountain ranges with elevation reaching 1,120 m and network of water sources. It is comprised of moist tropical forest to true rainforest with substantially more rainfall (2,540-4,570 mm) annually than other sites and contains high biodiversity. This area is administered by the Belize Audubon Society and has the highest level of protection. It is remote with only 1 road leading into and out of the Sanctuary.

The Belize Maya Corridor extends over 750 km², is 1 of 3 corridors in the country, and is said to be “the most critical” of the corridors (UB-ERI, accessed 2024). This corridor connects the GBMF in our study, a part of La Selva Maya, to Manatee Forest Reserve and other protected areas in the south. Most notably this corridor is a part of the Mesoamerican Biological Corridor to connect La Selva Maya to Mexico and Guatemala. It consists of both private and protected lands containing broadleaf forest and low-lying savanna land, holding thousands of flora and fauna species. Rainfall ranges from 1,680-3,850 mm (Belize.com 2021). This area is considered the least well protected of our study areas currently.

Manatee Forest Reserve is approximately 469 km² and contains coastal moist tropical forest. It is comprised of a variety of broadleaf and pine trees, shrubs, grasses, and wildlife. This area receives approximately 2,000-2,700 mm of rainfall annually with the majority happening in

the rainy season (June-December) causing seasonal marsh-land (Guy and Eitniear 2012). This area is managed by the Forest Department and under national protected status.

Fireburn Reserve (FR) is approximately 8 km² containing tropical evergreen, seasonal broadleaf, lowland swamp forests, and agricultural lands. It receives less than 2,000 mm of rainfall annually. It is a part of the Northeast corridor holding similar biodiversity of flora and fauna to the field sites listed above. Fireburn Reserve is privately managed by Wildtracks (Wildtracks accessed 2024).

Camera Trapping

Each study site was surveyed with a grid of camera traps that ranged from a low of 9 stations to a high of 65 per study site and total camera stations used across all study sites ranged from 10 to 271 depending on the year. Some grids expanded over time to increase sample sizes (Table 1). The number of years surveyed within each site ranged from 1 to 20 years (Table 1). For Cockscomb, we limited the total years used to 8 years (2012-2017, 2019, 2021) because earlier years had not been entered into the database in a comparable way to the other sites (i.e. not all animals/humans entered as in other sites). Within study sites, we set cameras approximately 30-40 cm above the ground on trails, game trails, old logging roads, and active logging roads. Placement on roads and trails has been shown to enhance detectability for elusive cat species (Kelly et al. 2012). Each station had two cameras set on opposite sides of the road/trail to increase the chance of ‘capturing’ animals and to ‘capture’ both sides of felids to identify them by natural marks (i.e. for jaguars and ocelots). Distance between camera stations ranged from 1.5-3 kilometers apart, originally based on the smallest estimated female jaguar home range in Belize of 10 km² to ensure that no home range of a jaguar can be located entirely between cameras (Rabinowitz and Nottingham 1986). Even though the original study design

targeted jaguars, pumas are similar enough that the design is still likely appropriate for them (Harmsen et al. 2011). Across sites and surveys, cameras consisted of a variety of brands including Reconyx, Scout Guard, Moultrie, Browning, Trail Master, Camtrakker, Deercam, Cuddeback, Panthera, etc. and operated 24 hours a day for up to 3 months, and no baits or lures were used.

Single season occupancy

Because pumas are difficult to distinguish to the individual level in remote camera trap photos, we used an occupancy modeling framework to assess local (microhabitat), landscape (macrohabitat), and biotic factors (trap rates of predators and prey) influencing puma distribution and detection across the landscape. Occupancy modeling was developed to estimate the proportion of area occupied while accounting for imperfect detection (MacKenzie et al. 2006). Occupancy modeling is considered an improvement over presence-only data, since animals may be present in an area but go undetected representing a false negative (MacKenzie et al. 2006). Incorporating covariates in relation to the locations of target species across camera stations can clarify factors influencing occupancy and detection and is likely to result in more precise estimates (MacKenzie et al. 2006). Due to camera spacing being closer together than the estimated home range size within each study area, a single individual puma may be photographed at multiple cameras and thus our estimation within each site is likely equivalent to probability of use within sites rather than true occupancy (Farris et al. 2015), yet we will use both terms in the results and discussion.

We used single season occupancy to model each year and site separately because some sites were surveyed only 1 year, many sites across the country were not surveyed in the same year, and some surveys in some years had local microhabitat data collected manually while

others did not both across, and within, the same site. Therefore, we wanted to determine the relative influence of microhabitat versus landscape variables when possible, to make use of manually collected habitat data at some sites and years.

Our study design does not violate any of the assumptions of single-season occupancy modeling which are: (1) the occupancy state of the sites does not change during the period of surveying (pumas are not migratory and surveys were short); (2) the probability of occupancy is constant across sites (or it is accounted for by covariates); (3) the probability of detecting the species in a survey, given presence, is constant across sites (or it is accounted for by covariates); (4) the detection of the species in each survey of a site is independent of detections during other surveys of the site; and (5) the detection histories observed at each location are independent. Because cubs travel with their mothers and are thus not likely to be observed independently, we did not include cubs in this analysis. The remote cameras were the detectors across the landscape and each encounter occasion was a single day, constraining overall survey periods to 90 days, to ensure surveys were relatively short, yet still obtained enough photo-captures to conduct occupancy modeling. For detection histories for pumas at each camera station, we created a matrix of detections and non-detections (1s and 0s, respectively) for each site and survey for each year. We used the patterns of detection and non-detection to estimate two population parameters: detection probabilities (p) and the proportion of sites occupied (ψ), both of which are bounded by 0 and 1, with 0 being never detected or occupied and 1 being 100% detection or occupancy at a site. We used the delta method, which incorporates within and across site variance (Powell 2013), to calculate an overall ψ and confidence intervals for ψ for each site.

Occupancy modeling and model selection

We created a set of *a priori* models by considering the biology of pumas and the covariates that might influence occupancy and detection, as well as the scale at which the influence might extend by defining appropriate circular buffers surrounding camera traps and extracting habitat data from those buffers (Supplement S1). For instance, we expected that enhanced canopy cover and vegetation index (EVI) (i.e. canopy and some ground vegetation) would positively influence parameter ψ as higher vegetation index may also provide more ambush/caching cover and more resources for prey species (Terborgh et al. 2015, Gray et al. 2016), while avoiding other predators (Ironsides et al. 2017). This could also change due to spatial scale. For instance, small buffer sizes like 100 m and 250 m radii surrounding camera traps could be more pertinent to detection, which refers to the ability of a camera trap to detect an object in its general vicinity, while larger buffer sizes like 750 m and 1,000 m could be more pertinent to occupancy by being indicative of overall habitat quality of the area. Proximity to the nearest road might also increase likelihood of detection, p , while moving through the area due to easier paths to follow (Sollmann et al. 2015). We also predicted how biotic factors like prey and predator trapping rates (e.g. activity proxies) would impact puma ψ and p (Supplement S1). For example, Central American agouti trapping rates could influence both ψ and p as pumas will choose areas with higher preferred prey species (Harmsen et al 2009, Karandikar et al 2020) and follow prey signs in front of cameras thus increasing detection. Predator trapping rates could be variable as the subordinate carnivore to the jaguar, pumas could avoid areas with higher jaguar activity in the vicinity, decreasing both occupancy and detection (Harmsen et al 2009), while as the dominant carnivore to the ocelot, pumas could key in on shared preferred niche requirements thus following signs (i.e. scent, sound, visuals) of ocelots, thus increasing both occupancy and detection (Donadio & Buskirk

2006). For a complete list of all *a priori* hypotheses regarding expected directions of relationships, rationale, and supporting references, see Supplemental Table S1.

Microhabitat covariates collected manually

All manual covariates were collected at and around each camera station to use as unique, site-level covariates with one value per camera station. Microhabitat covariates for study sites included: canopy cover, basal area, tree density, understory density, and heterogeneity. We collected this data from manual habitat surveys at only some sites (GBMF and MPR) conducted every 3-5 years surrounding each camera station. These covariates assessed habitat structure that cats are known to be sensitive to (Ludlow & Sunquist 1987). For canopy cover and understory measurements, we laid out three 100 meter transects at 0, 120, and 240 degrees and adjusted 10 degrees to the right or left if the transect ran directly on the trail or road so as to ensure the survey represents the habitat structure surrounding each camera station. Every 10 meters along each transect and at the camera station itself, we recorded canopy cover as either broadleaf, pine, or none resulting in 31 canopy points for each camera station. To estimate understory cover, we used a two-meter pole with three height intervals, 0-0.5 m, 0.5-1.0 m, and 1.0-2.0 m, and at every two meters along the transect we recorded ground cover, leaf litter, dead debris, soil, rock, water, and a binary (0, 1) category for any vegetation that made contact within the pole at the three height intervals. We also used a Point-Centered Quarter method (Mitchel 2010) for calculating tree density at the 50- and 100-meter points along the three transects where distance to nearest tree, diameter breast height, tree height, alive or dead, and type of tree (broadleaf, pine, or palm) were recorded in the four quadrants: NE, SE, SW, NW (Supplement S2). We also recorded trail width, percent of canopy, elevation, and land type at each camera station.

For understory density estimates, we averaged each height intervals and calculated the coefficient of variance (CV) as a measure of habitat heterogeneity in understory structure. Both average and CV were used separately in models to determine whether pumas were responding to understory density or its variation.

For our point-centered quarter measurements, the initial center measurements at the camera stations were removed when calculating average basal area and tree density because all stations were set on roads and larger trees were often chosen in setting cameras station. We calculated measurements with the initial center measurements and without the initial center measurements and conducted a Student's t-test to compare whether tree basal area was larger at the camera stations than on the transects. The measurements were not significantly different ($p=0.21$, $t \text{ stat}=-0.82$), however, we used the measurements that did not include the camera station trees as we included canopy cover and road width at station.

For all landscape microhabitat data collected via manual habitat surveys, there were several instances with missing data at a station only for certain years. Therefore, through spatial interpolation, we averaged data from that time period from surrounding stations to fill in the missing data. While not ideal, this method has been used in other studies (Donovan and Hines 2007). We did not extrapolate missing station data when there was no microhabitat data collected in that year and we simply did not incorporate microhabitat data in those survey site/years.

Landscape macrohabitat covariates

Landscape macrohabitat data were obtained from geographic information system (GIS) layers from the Biodiversity and Environmental Resources Data System (BERDS) of Belize maintained by Jan Meerman (Meerman BERDS accessed 2021) and we derived GIS products from Moderate Resolution Imaging Spectroradiometer or MODIS (USGS-MODIS accessed

2021), for all sites and survey years. We used ArcGIS Pro to estimate the following landscape covariates: distance from each station to water sources, human settlements, roads, and logging blocks. We additionally used a quadratic formula on such variables to account for a potential preferred distance to roads, settlements, and water sources and road width, which might not be strictly linear, but instead peak at intermediate levels of covariates of interest. We also estimated enhanced vegetation index (EVI). EVI is an index that quantifies canopy greenness unbiased due to atmospheric conditions and noise, which is a more accurate vegetation index for tropical, dense forest than normalized difference vegetation index or NDVI (Huete et al. 2011). For EVI, we only included layers from the time period where cameras were functioning in each season. We estimated EVI using both linear and quadratic functions. For example, pumas might choose, or be detected more, initially as vegetation gets denser, but then might decrease in occupancy and/or detection if the vegetation gets too dense to travel through or hunt in.

We created circular buffers surrounding each camera trap with radii of 100 m, 250 m, 500 m, 750 m, and 1,000 m and used a GIS to extract EVI and fire presence from the buffers. For the 100 m buffer, we used spatial interpolation within GIS because the resolution for EVI layers was set at 231.65 m and resolution for fire layers was 463.31 m. Therefore, we used surrounding cells whose center fell within the buffer and averaged those cells to create a smaller resolution for covariates. We then determined the best buffer size by separately running models with each buffer size and determining which was most supported using model selection (see below).

Biotic Covariates

For each survey and site, we calculated trap rates an index of species activity at each station for each survey time period for sympatric felid predators (jaguar, ocelot), prey species (white-tailed deer [*Odocoileus virginianus*], red brocket deer [*Mazama temama*], white-lipped

peccary [*Tayassu pecari*], collared peccary [*Dicotyles tajacu*], Central American agouti [*Dasyprocta punctata*], paca [*Cuniculus paca*], nine-banded armadillo [*Dasypus novemcinctus*], plain chachalaca [*Ortalis vetula*], great curassow [*Crax rubra*], crested guan [*Penelope purpurascens*], ocellated turkey [*Meleagris ocellata*]), and humans (researchers, tourists, loggers, workers, poachers, unknown). Trap rates were calculated by dividing the number of capture events by the total number of functioning trap nights per camera station. We defined a capture event as the number of distinctly different individuals of a species within 30-minute interval after initial capture, and a trap night was a 24-hour period the camera was functioning (Di Bitetti et al. 2006; Kelly et al. 2012). Trap rates were used as covariates on parameters ψ and p in occupancy models to better understand whether prey availability could influence space use and detectability of pumas on the landscape. Prey species were used individually as well as grouped into size categories (small <5 kg, medium 5-10 kg and large >10kg) as that is an important factor for hunting (Karandikar et al. 2022, Davis et al. 2011). They were also grouped by similar species such as combining red brocket and white-tailed deer for one “deer” estimate and combining Central American agouti and paca for one “rodent” estimate.

Jaguar and ocelot trap rates were used on parameter ψ and p to determine if pumas shifted or contracted space use and movement in front of cameras when jaguar/ocelot activity was high, to better understand coexistence or competition on the landscape. These areas also have variable human use, so we included human trap rates to predict how human activity affects puma space use and detectability.

We used a Pearson correlation matrix for each year and study site resulting in 45 sets of pairwise comparisons of covariates from all site/years and any highly correlated variables ($|r|=0.7$) were not used in the same model. We z-scored all continuous variables throughout all

years combined together within each study site to standardize them across all sites and year to be centered on zero to improve maximum likelihood convergence for models (Ragazzini and Zadeh 1952) and to more easily compare the magnitude of beta (β) coefficients to each other across years. The exception being in the MPR where we z-scored 2004-2008 separately from 2009-2021 due the transition from film cameras to a majority of digital camera traps, which affected biotic covariate bias due to fewer animals photographed with film, which substantially lowered trap rates (Trolliet et al. 2013).

All covariates were placed individually on each parameter. We first added covariates to detection (p) while keeping occupancy (ψ) constant according to our *a priori* model expectations (Supplement S1). We ran models through the R package Rpresence, 4.0.4 (R Core Team 2021). We then ranked models using Akaike Information Criterion (AIC) to determine the best model for p (Akaike 1973; Burnham and Anderson 2002). If there were competing models (i.e. those within two delta AIC), we considered model weights and model likelihoods (Burnham and Anderson 2002) to determine the best model. After determining the best model(s) for p , we placed covariates on ψ and followed the same AIC approach to determine the best models for ψ . We then created post hoc models with covariates that emerged from top models for parameters p and ψ to ultimately determine the best overall model. For instance, if models were within 2 delta AICs we created post-hoc models with additive and interactive effects using those top covariates. We considered covariates strongly supported if the confidence intervals (CIs) on the β coefficients did not overlap zero.

We used the derived ψ estimates from the top models to create puma distribution maps in ArcGIS using Empirical Bayesian Kriging and masked them to protected and private area layers for each year showing what areas have high versus low occupancy for pumas. We did this

in 2 ways: first we plotted highest to lowest estimated occupancy within each site/year to visualize fine scale changes, and second, we standardized all sites/year to be on the same 0-1 scale to visualize true occupancy across time. Finally, we conducted a literature review using Google Scholar from years 2014 to 2024 and search words (pumas, occupancy, tropics) to find studies of puma occupancy for comparison to our results to determine whether puma occupancy in Belize is higher or lower relative to other study areas in the neotropics.

Results

Over 20 years of data collection, spanning over 4,848 km² across 7 sites in Belize, we used a total of 2,221 camera stations and accumulated 181,025 trap nights (Table 1). The puma and sympatric felids, the jaguar and ocelot, were “captured” within all study areas. However, not all target prey species were captured within all study areas. Naïve occupancy (# stations “capturing” pumas out of the total stations per site) ranged from 0.35 to 0.94 in the GBMF, 0.11 to 0.71 in Chiquibul, 0.30 to 0.65 in the MPR, 0.80 to 1.00 in Cockscomb, 0.27 to 0.38 in the Belize Maya Corridor, 0.52 to 0.86 in Manatee Reserve, and 0.64 in Fireburn Reserve (Table 2). In general, results come from top models chosen in the MLE framework, while a few models were chosen over top models due to better numerical estimation (i.e. model convergence) than the top model (Tables 3-8). There were also 5 out of the 50 site-year data sets that had too few puma detections resulting in little variation in the detection history that caused lack of fit of single-season occupancy models. For these years we present the naïve occupancy results only (or the constant model only). Only covariates that strongly affected detection (CLs that do not overlap zero) are presented.

Covariates affecting detection across sites (micro, macro and biotic)

Detection of pumas in the GBMF was not affected by any microhabitat covariates but was strongly affected by numerous landscape macrohabitat and biotic covariates (Table 3). For

the macro habitat variables extracted from GIS, we found detection was positively influenced by elevation in 2011 ($\beta = 0.70$, $SE = 0.16$) and in 2012 ($\beta = 0.56$, $SE = 0.16$), increased closer to roads in 2015 ($\beta = -0.21$, $SE = 0.06$) and in 2017 ($\beta = -0.16$, $SE = 0.05$) and increased closer to water in 2021 ($\beta = -0.30$, $SE = 0.08$) (Figures 2 and 3). Detection was affected positively by EVI within a 250 m buffer in 2009 ($\beta = -3.89$, $SE = 0.50$). EVI within a 100 m buffer displayed a negative quadratic relationship (peaking at intermediate EVI) with puma detection in 2016 ($\beta = -0.54$, $SE = 0.12$) (Figure 2). For biotic covariates, detection was affected positively by human trap rate in 2010 ($\beta = 0.67$, $SE = 0.21$), positively ocelot trap rates in 2014 ($\beta = 1.08$, $SE = 0.25$) and in 2018 ($EST = 0.24$, $SE = 0.05$), and positively by jaguar trap rates in 2019 ($\beta = 0.17$, $SE = 0.03$) (Table 3, Figures 2 and 3, S4). In the Chiquibul Forest Reserve, detection was affected by 0 microhabitat, 1 macrohabitat, and 0 biotic covariates with no strongly supported relationships (Table 4, Table S4).

In the MPR, 2 microhabitat covariates influenced detection (Table 5) including positive influences of canopy cover at station in 2015 ($\beta = 0.55$, $SE = 0.15$) and 2016 ($\beta = 0.31$, $SE = 0.09$), and overall percent canopy cover within 100 m in 2018 ($\beta = 0.52$, $SE = 0.11$). For macro covariates, detection was affected positively by EVI within a 750 m and 100 m buffer in 2011 and 2014, respectively ($\beta = 1.72$, $SE = 0.50$; $\beta = 1.63$, $SE = 0.46$), and negatively by elevation in 2017 ($\beta = -0.76$, $SE = 0.19$) (Figures 2 and 4). For biotic covariates, detection was positively affected by white-tailed deer trap rates in 2008 ($\beta = 0.40$, $SE = 0.10$), jaguar trap rates in 2010 ($\beta = 0.49$, $SE = 0.20$), crested guan trap rates in 2012 ($EST = 0.49$, $SE = 0.17$), agouti trap rates in 2019 ($\beta = 0.20$, $SE = 0.03$), and plain chachalaca trap rates in 2020 ($\beta = 0.30$, $SE = 0.08$). Detection was negatively affected by plain chachalaca trap rates in 2004 ($\beta = -28.13$, $SE = 11.88$) and small prey trap rates in 2009 ($\beta = -4.25$, $SE = 0.99$) (Table 5 and S5, Figures 2 and 4).

Detection of pumas across 8 years in CBWS was not influenced by any microhabitat features as they were not collected during these survey periods (Table 6). For macrohabitat covariates, detection increased as distance from settlements increased in 2019 ($\beta = 0.17$, $SE = 0.03$) (Figures 2 and 5). We found a positive quadratic relationship for detection in distance to roads in 2012 ($\beta = 0.33$, $SE = 0.12$). For biotic covariates, detection was positively affected by agouti trap rates in 2014 ($\beta = 3.72$, $SE = 0.81$) and negatively affected by white-lipped peccary trap rates in 2015 ($\beta = -7.84$, $SE = 2.80$) and ungulate trap rates in 2017 ($\beta = -1.55$, $SE = 0.44$), (Tables 6 and S6, Figures 2 and 5).

In the Belize Maya Corridor, we did not collect microhabitat covariates and detection was only affected by macrohabitat covariates (Table 7). Detection increased with increased distance from roads in 2009 ($\beta = 0.52$, $SE = 0.16$), and in 2011 ($\beta = 0.33$, $SE = 0.16$), and also increased with distance from settlements in 2013 ($\beta = 1.19$, $SE = 0.40$) (Tables 7, S7, Figures 2 and 5).

In the Manatee Forest Reserve, no manual covariates were collected and detection was only affected by macrohabitat covariates and no biotic covariates (Table 8). Detection increased closer to water sources in 2020 ($\beta = -3.30$, $SE = 0.83$) and increased at closer distances to settlements in 2021 ($\beta = -0.48$, $SE = 0.15$) (Table 8, Figures 2 and 5, S8).

In the GBMF, daily detection estimates ranged from 0.00 to 0.56 and while they were much lower at 0.00-0.02 in the Chiquibul Forest Reserve. Puma detection from 2009-2021 in the MPR ranged from 0.00-1.21, while in CBWS from 2012-2017, 2019, 2021 it ranged from 0.00-0.17. In the Belize Maya Corridor, puma detection from 2009-2013 ranged from 0.00-0.14 and in Manatee Forest Reserve detection from 2019-2021 ranged from 0.00-0.10. Detection in 2009 in Fireburn Reserve was 0.24 (LCI=0.18, UCI=0.30).

Covariates affecting occupancy

Puma occupancy in the GBMF (RBHB, RBLM, YB, GJLS) from 2009-2019, and in 2021 was only affected by covariates in 1 of the 11 years total, with no important microhabitat or macrohabitat covariates (Table 3). Occupancy was influenced positively by biotic covariate of ocelot trap rates ($\beta = 7.74$, $SE = 3.50$) in 2009 (Figures 6 and 7). All other top models for the GBMF indicated that occupancy was constant (Tables 3, 9, S4), as was the case for all years for the Chiquibul Forest Reserve, where puma occupancy was not affected by any covariates (Table 4, 10, S4).

Puma occupancy for the MPR was only affected by covariates in 3 of the 18 years and was not influenced by any microhabitat features (Table 5). Macro habitat variables indicated that occupancy decreased with increasing elevation ($\beta = -1.31$, $SE = 0.45$) in 2020 and with distance away from water ($\beta = -2.02$, $SE = 0.96$) in 2008 (Figures 6 and 7). Biotic effects included a negative relationship with human trap rates ($\beta = -7.43$, $SE = 3.03$) in 2019 on puma occupancy (Table 5, S5).

Puma occupancy in CBWS was only influenced by 1 macrohabitat covariate in 2019 and no microhabitat (not collected) or biotic covariates (Table 6). We found a negative quadratic relationship between occupancy and EVI within a 500 m buffer in year 2019 ($\beta = -12.16$, $SE = 5.58$) such that puma occupancy was highest at intermediate EVI (Figures 6 and 7, Table S6). In the Belize Maya Corridor and the Manatee Forest Reserve, there were no covariates that affected occupancy (Tables 7, 8, S7, S8). Across all sites and years, macrocovariates had most influence on detection and occupancy, followed by biotic covariates, while microcovariates had little influence (Table 9).

In the GBMF, puma occupancy estimates ranged from 0.78 to 0.96 with the exception of 2009 where ψ was 0.41 (Figure 8). In Chiquibul Forest Reserve, occupancy ranged from 0.75 to

0.79. Puma occupancy from 2004-2021 in the MPR ranged from 0.30-0.92 while in CBWS from 2012-2017, 2019, 2021, it ranged from 0.80-0.95. In the Belize Maya Corridor puma occupancy from 2009-2013 ranged from 0.46-0.88 and in Manatee Forest Reserve occupancy from 2019-2021 ranged from 0.72-0.88 (Figure 8). Fireburn Reserve's occupancy in 2009 was 0.78 (LCI=0.69, UCI=0.87). Cockscomb had the overall highest occupancy estimates, followed by the GBMF. Occupancy across all study areas oscillated throughout the years, however, CIs generally overlapped from year to year and displayed no discernable positive or negative trends over time (Figure 8).

We found only 15 papers on puma occupancy from the Neotropics spanning southern Mexico to northern Argentina from 2006-2024, with 2006 being the date occupancy modeling became prevalent. Number of stations ranged from 45 to 480. Trap nights ranged from 2,800 to 72,835. Occupancy ranged from 0.02 to 1.00 (Table 9). However, our estimates of puma occupancy were higher than literature in broadleaf forest in 12 out of 15 papers from 10 different countries. Only northern Argentina had overlap with our broadleaf sites in occupancy estimates. Our mixed forest sites were more similar to the literature while our pine forest site was highly variable compared to the literature.

Our unscaled heat maps show subtle differences in puma distribution with a general pattern of highest occupancy in the center of large reserves or bordering other protected areas, while pine forest areas and those with higher human impacts had lower occupancy (Figure 9). Additionally, year to year shifts did occur depending on different or changing covariate effects. However, when scaled from 0-1 for each year, occupancy was extremely high throughout most sites and years, with some exceptions where occupancy is lower in years 2009, 2011, 2012, 2013 within the corridor sites (BMC) and Hill Bank in the GBMF, both of which have higher human

impacts (Figure 10). Additionally, the pine forest (MPR) also had lower occupancy than the remaining sites in most years except 2013 and 2014 when occupancy was very high.

Discussion

Our main goals were to conduct a broad spatial and temporal scale analysis to tease apart the relative importance of microhabitat, macrohabitat, and biotic drivers of puma detection and distribution across numerous multi-use protected areas in a little-studied Neotropical region. For detection, we tallied the number and type of covariates included in top models throughout all sites, and found 3 microhabitat, 19 macrohabitat, and 14 biotic supported covariates in all top models (Table 10). However, not all sites had micro habitat data collected, but the proportion that included microhabitat variables in the top models out of the total sites that had such data collected was low at 3 out of 30 (10%), calling into question the efficacy of collecting such data. Nonetheless, of the 4 out of 7 study sites collecting microhabitat in over 20 years, only 1 site had the three microhabitat covariates in top models, whereas there were 5 sites that had macrohabitat covariates and 3 sites that had biotic covariates that affected detection.

For occupancy 0 microhabitat, 3 macrohabitat, and 2 biotic covariates were supported across top models (Table 10). Two sites had macrohabitat covariates and 2 sites had biotic covariates that affected occupancy. Thus, overall, macrohabitat had more impacts on detection than biotic variables, while macrohabitat and biotic covariates had similar numbers of influences on puma occupancy.

Based on *a priori* models and hypotheses for detection covariates, for those covariates that entered into the top models, we were correct about the direction of the relationship 3 out of 3 times for microhabitat, 11 out of 19 times for macrohabitat, and 6 out of 14 times for biotic covariates. For occupancy covariates, we were correct 2 out of 3 times for macrohabitat and 1 out of 2 times for biotic covariates.

Influence of microhabitat, macrohabitat, and biotic covariates on detection

Microhabitat

For microhabitat covariates, only the Mountain Pine Ridge was affected, and detection was positively influenced by canopy cover at or surrounding the camera station. This atypical tropical pine forest supports a mosaic of ecosystems that range from closed to open habitat types, and open habitat has been shown to decrease puma detectability and use (Riley et al. 2021). Our results suggest that pumas may key in on fine-scale habitat in areas with higher canopy cover that is more aligned to typical tropical broadleaf forest (i.e., evergreen deciduous forest), which is less open relating to less perceived risk and increased movement (Riley et al 2021).

Additionally, these areas with high canopy may support prey populations, and provide access to water sources, which would increase puma use and hence increase their detection in such areas. This tropical pine forest is similar to other coniferous and mixed conifer-broadleaf forest types in temperate regions in the U.S. Southeast states. Studies from these areas support that puma occupancy increased with primary productivity (Martin et al. 2023), therefore pumas in MPR may likely frequent areas of higher canopy increasing their detection.

Manual habitat surveys allowed us to gather microhabitat data (i.e., understory density) at site level to use as covariates in occupancy models. The habitat surveys themselves, cost us extensive time, effort, and physical exertion. These covariates did not emerge in any top models except for canopy cover at station or within 100m of the station, both of which take much less time and effort to collect compared to the other microhabitat covariates (i.e., tree density, basal area, and understory density). GIS layers and photo data (see below) were more important in top models suggesting that manual data collection aside from canopy cover, could be discontinued to promote efficiency in fieldwork.

Macrohabitat

Of the 19 covariates on detection, distance to road appeared the most (5 times) across 3 study sites in top models, but direction of the relationship varied across the sites. In two instances, puma detection increased with closeness to main roads (GBMF). The subtropical broadleaf areas of the GBMF have continuous forest with dense understories and holds a large network of historical logging roads. These logging roads are easier paths and create a funnel-like effects throughout the forest and make it is easier to “capture” felids on cameras, which has been noted in other studies (Sollmann et al. 2013). These finding suggest that roads in low impact areas like the GBMF will increase a mobile species’ (i.e., puma) detection due to its facilitation through a generally difficult to transverse habitat type. Interestingly, 2 other study sites had positive influences of distance to road. In the Belize Maya Corridor, pumas were found farther from roads, as this area is close to the Western Highway that experiences heavy vehicle traffic use. Pumas most likely avoid heavily used roads as the perceived risk is higher, and presence of humans and settlements is common. Generally, habitat along major highways is successional or agricultural, which would not support puma occupancy well, thus decreasing detection rates. In support from other studies, puma avoidance of heavily used roads has been shown in southern California (Riley et al. 2006, Onorato et. al. 2010, Riley et al. 2014). In Cockscomb, however, distance to road had a positive quadratic effect indicating the highest detection close to the road and at far distances from the road while intermediate distances had lowest detection. For Cockscomb Basin, which also has thick forest understory, there is only one main road into and out of the area, which also funnels wildlife throughout the protected area (Foster et al. 2010). Additional information from GPS collared pumas in the Cockscomb Basin indicated that they tended to frequent the foothills rather than the basin, which are the farthest from the main road (Harmsen, unpublished data), likely leading to higher detection at farther distances. These

overall findings suggest that low impact areas with road networks will support and increased puma detection, as these areas are generally continuous, well-maintained forests within protected areas. Areas with major highways and increased human presence and development, negatively affects puma detection across its distribution in Belize. As infrastructure such as the building of more roads, towns, and expansion of urban centers continues in Belize and other countries in the neotropics, it will be necessary to maintain areas of continuous forest and incorporate safe wildlife crossing structures to promote puma distribution.

The second most important variables on detection were EVI (4 times) and elevation (4 times) each across 2 sites. In the GBMF (once) and MPR (twice), puma detection increased with EVI. Parts of GBMF are similar to the MPR that have more open areas where there is less of a funneling effect on roads, as vegetation become thicker, travel is likely to be constrained to roads/trails where cameras are placed, increasing detection (Sollmann et al. 2012). Other studies have shown either puma detection or occupancy to increase with EVI (Palomares et al. 2016; Martin et al. 2023), but we additionally found, in the GBMF (once), that pumas were more detectable at intermediate EVI levels of 0.45-0.5, indicating a threshold whereby detection by cameras declines when habitat is too open, and it also declines when habitat is too closed. Similar to the above-mentioned effect from canopy cover, increases in overall vegetation in more closed system habitat types decrease perceived risk associated with humans and other predators allowing unrestricted movement (Riley et al. 2021). This supports the need to maintain vegetation typical in broadleaf forest, however, since EVI is a measure of ‘greenness’ it is difficult to ascertain whether this refers strictly to canopy cover from mature trees or understory density, therefore, intermediate EVI could represent intermediate heterogeneity in the ecosystem.

While elevation also influenced detection, the direction of relationship varied across the 2 sites where this variable occurred. In the GBMF, detection was positively influenced by elevation in 3 different years. Elevation is generally low across this study area (0-272 m) and the site is characterized by escarpments that runs from ~north to ~south and that have dirt roads on them where we place cameras. These areas are likely easier to traverse than steep sides of the escarpments and easier than the low-lying swampy areas that occur in this study site, thus increasing detection on top of the escarpments. This coincides with other studies that found pumas move frequently throughout complex mountainous terrain (Beier et al. 1995, Sweanor et al. 2000, Coon et. al. 2020). Interestingly, and opposite to the GBMF, in the MPR, detection decreased at higher elevation. This site has higher elevations in general (334-926 m), with steep mountainous terrain and it abounds with old logging roads at all elevations. Lower elevations in the MPR tend to have more mixed broadleaf jungle and water sources compared to the majority of the tropical pine forest. Therefore, pumas likely frequent lower elevation due to ease of travel, and habitat with more cover and water, potentially increasing their detection. Additionally, mixed broadleaf jungle has more closed habitat, which allows more unrestricted movement than in more open pine forest so maintaining these areas is paramount to sustaining puma movement, which could be important in allowing connectivity within MPR but also to other sites like CFR.

Distance to settlement influenced detection in 3 study areas with varied relationships. In Cockscomb and Belize Maya Corridor, puma detection increased farther away from settlements. In Cockscomb, this could be related to pumas becoming more cryptic in areas closer to human activities to avoid detection in surrounding agriculture and subsistence hunting lands outside the protected area, as has been previously noted in other studies (Harmsen et al. 2009). The BMC area is most heavily impacted by human activities and villages that are adjacent to the corridor,

and the heavier perceived risk of human encounters also likely causes pumas to become more cryptic (Riley et al 2014). However, in the Manatee Forest Reserve, where there is lower human activity, detection increased closer to settlements (2020, 2021). While it seems counterintuitive that pumas are detected closer to human settlements, this area is larger in size than the corridor and it seems that human activity is not negatively affected puma detection and perhaps their curiosity causes them to investigate areas closer to humans. Alternatively, there could be higher intraspecific competition within MFR causing pumas to move more in these less desirable areas while jaguars maintain a stronghold in less risky areas. Further analysis occupancy modeling of jaguars and co-occurrence modeling of jaguars and pumas, is necessary to answer this question.

Closer distances to water led to increased detection in the GBMF and Manatee Forest Reserve. Both of these sites have less available water than the other sites and thus pumas are likely to more frequently visit areas in closer proximity to water, as has been shown in other studies where water is a valuable resource (Beier et al. 1995, Sweanor et al. 2000, Grey et al. 2016, Coon et. al. 2020). In many of our study areas, water is readily available and plentiful during the rainy season (June-November), which has been shown to lead to larger home ranges in pumas since water is on the landscape allowing more movement, while in the dry season (December-May) home range decreases higher activity near water (Nunez-Perez and Miller 2019). This need for available water drives puma movement especially in areas with lower water availability, especially in the dry season. As climate change continues to increase temperatures and lengthen the dry season, it may be necessary to add artificial water sources to continue support predator and prey communities as has been done in nearby Guatemala (Perera-Romero et al. 2020).

Biotic

There was much variation among the 14 instances where biotic covariates affected puma detection. Interestingly we found no negative relationships between sympatric felid species, and instead jaguar trap rates (twice) positively affected detection across 2 study areas (GBMF and MPR). Additionally, ocelot trap rates (2 times) were positively associated with puma detection in the GMBF. Likely due to plentiful resources and space within protected areas, jaguar activity may not cause pumas to display more cryptic behaviors or spatial avoidance as suggested in several other studies (Polisar et al. 2003, Harmsen et al. 2009, Ramesh et al. 2012). Likewise, ocelots do not appear deter pumas. This is expected as the ocelot is thought to be the subordinate to the puma (Donadio and Buskirk 2011), and we suspect that ocelots are not negatively affected by pumas in these areas due to spatial coexistence findings noted previously in the MPR (Davis et al. 2011). Additionally, ocelots tend to be more nocturnal than either pumas or jaguars, perhaps as a niche partitioning strategy (Davis et al. 2011) Thus, the 3 felids do not appear deterred by one another's sign (i.e. scent, scrapings) and continue to exhibit similar traveling behaviors by using pathways in front of camera stations, increasing detection.

Agoutis increased detection (twice) in 2 study areas, the MPR and Cockscomb. Agoutis are known to be a common prey species for pumas in the tropics (Karandikar et al 2022), and we photographed pumas with agouti prey in their mouths. Based on the optimal foraging theory, when agoutis are plentiful, they have enough mass worthy of exerting effort, they may be a favored prey species, which is noted in scat analysis from Karandikar et al. (2022). Thus, pumas may track agoutis increasing detection by cameras in areas with high agouti activity. Trap rates of different ground bird species (3 times) in the MPR only, had varied effects. Detection decreased strongly with increases in plain chachalaca trap rates in 2004 and weakly in 2020, most likely because they are a sentinel species that makes loud alarm calls when they perceive

risk (Mariyappan et al. 2023), which could ward off pumas and cause them to avoid areas where they are detected by these birds (Klump and Shalter 1984). Also, in the MPR, detection increased with crested guan trap rates. The crested guan, a common ground bird weighing on average about 2 kg (Gilbert and Schulenberg 2020), is thought to be a potential prey species as they are large, unagile birds that require similar effort to catch as other prey species, therefore, pumas could be tracking these species increasing detection on cameras. To date, we have not found references in the literature of pumas keying in on ground birds, which may be a novel finding. Finally, in the MPR, detection declined with small prey trap rates, but effect size was somewhat small, and it is unclear as to why this would occur.

For white-tailed deer (once), white-lipped peccary (once), and combined ungulate trap rates (once) across 2 study sites, there were varied effects on detection. In the MPR, puma detection increased with white-tail deer trap rates. Previous diet and evolutionary studies show that pumas specialize on deer (Trani et al. 2007), therefore pumas are likely to track this prey species when in an area, thus increasing their detection by cameras in areas with high deer activity. However, in Cockscomb, puma detection decreased with white-lipped peccary and with ungulates combined (i.e., red brocket deer, white-tailed deer, red brocket deer, white-lipped peccary, collared peccary) trap rates. White-lipped peccaries travel in large groups and are known to be aggressive (Taber et al. 2011, Noguira et al. 2017), which could deter pumas from areas with high peccary activity. Other studies have noted that jaguars prefer larger prey species and suggest pumas avoid such prey to prevent competition with jaguars (Donadio & Buskirk 2006, Karandikar et al. 2022), but we only found positive associations with jaguars, however not at this study site. Alternatively, since Cockscomb had the highest levels of white-lipped peccaries out of

all study sites, they dominated the “all ungulates” category and thus this response could be due to avoidance of perceived risk of white-lipped peccaries.

In the GBMF, detection increased with human trap rates (once), which may seem counter-intuitive, but this protected area has relatively few tourists, low vehicle traffic, and gated and protected borders, with the majority of human activity resulting from researchers, non-invasive tourism (birdwatching), and community members. Felids, unlike canids, are not as behaviorally wary and tend to be inquisitive towards humans or human objects in the environment (Gartner et al. 2014). We have anecdotally noted pumas investigating, smelling, biting, and pawing at camera traps or their shiny metal hoods in our study. Thus, human activity may not cause pumas to become more cryptic in well-protected areas but instead, their curiosity in such areas may lead to increased detection.

Occupancy-macrohabitat

Out of the 3 macrohabitat covariates that affected occupancy, the MPR was affected twice, and Cockscomb, once. In the MPR, puma occupancy increased closer to water sources, while it decreased with elevation in 2020. This area is mountainous with a more dramatic elevation gradient than most other sites, and lower elevations generally have more water with mixed mesic riparian forest areas that have higher densities of fruiting trees (Terborgh et al. 2015). This area, therefore, may also have higher prey and cover preferable for ambush hunting and avoidance of other predators (Williams et al. 2014, Gray et al. 2016). While pumas are occupying many areas in atypical tropical pine forest, they are likely exhibiting fine-scale choice of typical broadleaf habitat at lower, riparian elevations due to availability of resources and rather than selecting pine forest habitat itself. This is an interesting finding considering that pumas occupy numerous coniferous forest habitats North America.

Puma occupancy in Cockscomb (2019) was affected quadratically by EVI such that occupancy peaked at intermediate EVI. Cockscomb does have thick vegetation and thus there appears to be a threshold at which vegetation is too dense to travel or hunt in, and puma occupancy drops to 0 beyond 5100 (0.51) EVI. On the lower end of EVI, puma occupancy drops to about 0.42, indicating that less dense EVI is also avoided, but not to the same extent as caused by high EVI. While an increase in occupancy with EVI has been seen in other studies (Palomares et al. 2016, Martin et al 2023), we have not found such a quadratic effect on puma occupancy in the literature. Vegetation structure is known to drive prey species distribution (Thoisy et al. 2016) and since pumas are generalists with a wide-ranging diet that can exploit a variety of habitats, they could shift their distribution to more ideal EVI for their common prey species, to hunt, and cache while avoiding other predators. Therefore, pumas can exploit different vegetation structures that other species cannot as easily, allowing coexistence on the overall landscape. This could explain why puma occupancy is high throughout non-logged and logged protected areas.

Occupancy-biotic

In the GBMF, puma occupancy increased with ocelot trap rates suggesting that both species use the same areas, perhaps because there are ample resources supporting similar niche requirements (Gonzales Borrajo et al 2016) and that niches likely are divergent in diet items, even though there is some overlap (Donadio & Buskirk 2006, Karandikar et al. 2022). In the MPR, occupancy decreased with human trap rates. Human activity is high in the MPR and includes local and international tourism and recreation (including off-roading motorcycles and ATVs) in addition to yearly sustainable logging and research activities. Also, hurricane Earl in August 2016, and the subsequent clean-up of down trees in 2017, may have added additional

negative stress to pumas making them more sensitive to human activity this particular year. Other studies have shown pumas to be sensitive to human activities due to perceived risk (Hornocker and Negri 2010) and a previous study in this same study area also found negative influence of humans on puma trap rates in 2007 (Davis et al. 2011).

Overall Occupancy

In the GBMF, puma space use was relatively high throughout 12 years (point estimates 0.78-0.96) except in 2009 (0.41) likely due to the small number of film camera stations (n=20) in Rio Bravo Hill Bank (RBHB). Thus, lower occupancy for 2009 is likely an outlier compared to the overall trend in subsequent years where camera stations covered more area and pumas used much more of a forested landscape that is characterized as “ideal” subtropical moist forest habitat for jungle felids (Sanderson et al. 2002). Indeed, pumas were observed at nearly all stations suggesting they are ubiquitous on the northern landscape.

In the Chiquibul Forest Reserve, occupancy is not affected by any covariates. We were only able to obtain 2 occupancy estimates out of the 5 years due to convergence errors due to small sample sizes mainly caused by high numbers of stolen camera stations in 2006-2008, in conjunction with use of film cameras that take fewer pictures than digital (Trolliet et al. 2013). Naïve occupancy estimates ranged from 0.11 to 0.47, however, and those models that did converge resulted in fairly high occupancy ranging from 0.75-0.79. Better protection of this area has been underway for the last 10+ years making this area a future target for resurveying to determine if puma occupancy has increased with increased border enforcement.

Overall puma occupancy in the Mountain Pine Ridge Forest Reserve (MPR) ranged from 0.30-0.92. It is most likely that this pine forest habitat, which has less palatable vegetation for prey species (Davis et al. 2011), has lower predator and prey populations than the subtropical

broadleaf forest. Nevertheless, in some years the area had high occupancy and given its position between broadleaf areas to the north and south, it likely represents an important area that many cats pass through as they disperse, if they do not live there year-round. It will be particularly important to continue to monitor the MPR as the main road into and out of the area is currently undergoing paving from 2022 to 2024, thus increasing traffic, tourism, and poaching.

Cockscomb had the highest occupancy ranging from 0.80 to 0.95 and was not affected by any covariates for 4 out of 7 survey years, which was most likely due to widespread puma occupancy across the area, and thus little variation to model. Cockscomb has a stereotypical broadleaf forest that is preferred habitat for tropical felids, with low to medium elevation and plentiful prey and water sources (Harmsen et al. 2011).

Puma occupancy from 2009-2013 in the BMC varied considerably from year to year ranging from 0.46-0.88. This variation could be due to the fact that the corridor sites had relatively fewer camera traps (as few as 15 stations some years) that were placed in different areas throughout the corridor from year to year. Habitat is variable from broadleaf jungle, to shrubland, to coastal marshes, contains mixed uses including farming and is located near a large highway, which also contributes to variation in covariate effects. This recently protected area was established to link continuous, protected areas south and north of the main highway (Rewild 2024), to allow for wildlife movement. Therefore, it is not surprising that puma occupancy was lowest in this human-impacted area. Nevertheless, pumas were still using over 45% of the landscape and in some years, much more. This is encouraging and indicates the area is likely accomplishing its goal as a steppingstone facilitating large mammal movement from north to south and visa versa (i.e. Greater Belize Maya Forest to Manatee Forest Reserve). There are current efforts to protect more land in the Belize Central Corridor to prevent deforestation, so our

results showing puma sensitivity to humans on this landscape suggests that these efforts are necessary. Manatee Forest Reserve is a larger, more continuous patch than the BMC, occurring at the coastal end of a patchy corridor network, south of the main highway. Overall, it has fairly high occupancy estimates (0.72-0.88) that were less variable than the BMC, perhaps due to its larger size and lower human impacts.

Compared to literature, we used the most expansive spatial and temporal camera trap dataset for pumas and generally obtained markedly higher occupancy estimates than other studies from the Latin American Neotropics, which averaged 0.48 across sites (see Table 10). These studies also found that macrohabitat features such as canopy cover, EVI, and distance to roads had positive influences on occupancy and detection. However, not all other studies were conducted solely in protected areas, partially explaining their lower occupancy estimates and further exemplifying that protected areas, particularly large ones, with management plans that use patrols and border enforcement including gated systems for entry/exit are vital in supporting large felids like pumas (Naughton-Treves et al. 2010). Despite the protected status of the protected areas in our study, our heat maps showed occupancy to be lower in more human impacted, smaller sites like BMC and at protected area boundary edges (even for large, protected areas) where human development is more prevalent, and poaching is known to occur. Thus, pumas may avoid edges and use interior areas more as suggested in another study in Cockscomb (Foster et al. 2010). This is noteworthy because much of the interior (GBMF, Chiquibul, and Mountain Pine Ridge) experienced annual selective logging, and one has a small cattle ranch and coffee growing operation, none of which appeared to result in lower occupancy estimates than other sites. It is likely that the low human traffic, manned gates, border patrols, and hunting restrictions make the interior of many of these private protected areas (especially the GBMF,

Chiquibul, and Cockscomb) more attractive for pumas. While puma occupancy varied across sites and years, all larger protected areas (GBMF, MPR, CBWS, MFR, CFR) have relatively high (over 50% space use and up to 96%) and stable occupancy over time. We found no evidence of a decline in occupancy over time at any site - positive news for conservation of pumas in Belize. Also compared to other countries in the neotropics, Belize seems to be a stronghold for pumas based on their widespread distribution.

Even though pumas are generalists (Karandikar et al. 2022), our findings indicate it is important to maintain large, protected areas as strongholds (Zanon Martinez et al. 2023) where there is relatively low human activity and there is protection from poaching, as well as maintain steppingstones between them. More research outside protected areas would enable us to gain better insight into impacts caused by human dominated landscapes, as noted in other studies (Zanon Martinez et al. 2023). Outside several of our areas there is intense clear-cutting and ranchland where potential for negative human-wildlife interaction is high so studying these multifaceted, human dominated landscapes, including people's perception of pumas, is another important aspect of overall conservation measures. Research in these areas could more directly inform the Forest Department of Belize that oversees wildlife in these spaces.

Our findings of high occupancy indicate that the subordinate puma, is not likely suppressed by the dominant jaguar on protected landscapes in Belize, indicating perhaps ample resources to allow resource partitioning. In fact, other studies have described jaguars as having narrower habitat preferences than pumas (Astete et al. 2017) and that pumas are more versatile in exploitation of resources than jaguars (Craighead et al. 2022). Jaguars and pumas, therefore, may use fine-scale microhabitat shifting to decrease competition and thus maintain coexistence (Foster et al. 2010, Santos et al. 2019, Craighead et al. 2022). Additionally, temporal partitioning

could be a mechanism enabling pumas and jaguars to avoid direct contact and would be another avenue to explore in future research as has been shown in other studies on felids (Romero-Munoz et al. 2010; Sunarto et al. 2015). Therefore, despite land managers using data mostly from jaguars to affirm management decisions, it appears the puma is benefiting, likely because jaguars are more sensitive than pumas to human impacts and the current use of the jaguar as the umbrella species for overall wildlife health appears suitable for the puma. Future work on jaguar space use in Belize could provide support for this supposition, however more research is needed on other species and guilds, especially those that are less plastic than pumas (i.e. arboreal species and specialists) using various forms of analysis like co-occurrence, density estimation, and temporal overlap to better assess the jaguar as an umbrella species.

From a management perspective, it appears most important to preserve quality habitat that is good for prey species, which has been noted in studies as an important predictor of space use for other jaguars and tigers (Karanth 1995, Harmsen et al. 2011). Overall, it seems that many of the protected areas have relatively high prey activity however when there are more human stressors on the landscape that could affect felid guild behavior by increases in competition to avoid less desirable areas and in turn cause more competition for prey. But in areas with less human influence, there are no negative influences from common prey species. Additionally, we see varied prey species in top models supporting that pumas have a wide breadth diet and the ability to adapt to different areas and shift movement and distribution to follow more prevalent species depending on site which also helps with persistence and coexistence.

However, it should be noted that habitat within protected areas could decline as climate change affects seasonality and major weather events (i.e., frequency and intensity of fires and hurricanes). The UNDP Country Profiles (UNFCCC 2022), are projecting a 2-4° C air

temperature increase and 10% decrease in annual rainfall by 2100. Additionally, they found there will be an increase in sea levels and natural disasters like hurricanes and fires (UNFCCC 2022). For example, in the MPR pumas are sensitive to changing habitat structure as seen in occupancy estimates tied to EVI, therefore an increase in fires would thin understory, but if there were too many intense fires, would destroy all vegetation, which of course would be detrimental to the puma. Measures such as strengthening training to fight and prevent fires in tropical forests is important while also considering controlled burns in the pine forest habitat to prevent catastrophic.

Interestingly, several of our study sites (GBMF, MPR, CFR) practice reduced impact or sustainable logging, and we found no indication that these sites had lower occupancy than those without. Therefore, it appears that this level of sustainable resource extraction has minimal impact on puma occupancy. This is in line with the literature review by Naughton-Treves et al. (2010) that found resounding evidence of the benefits of protected areas on wildlife across 49 protected areas, but there were conflicting results on the socio-economic benefits to the communities and country at large. Belize perhaps provides an example of how to protect wildlife and benefit local economics of the area through sustainable logging, ecotourism, and research. However, human dimensions and economics impact studies are needed to offer evidence of financial benefits to local people, especially those surrounding the protected areas.

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Figures/Tables

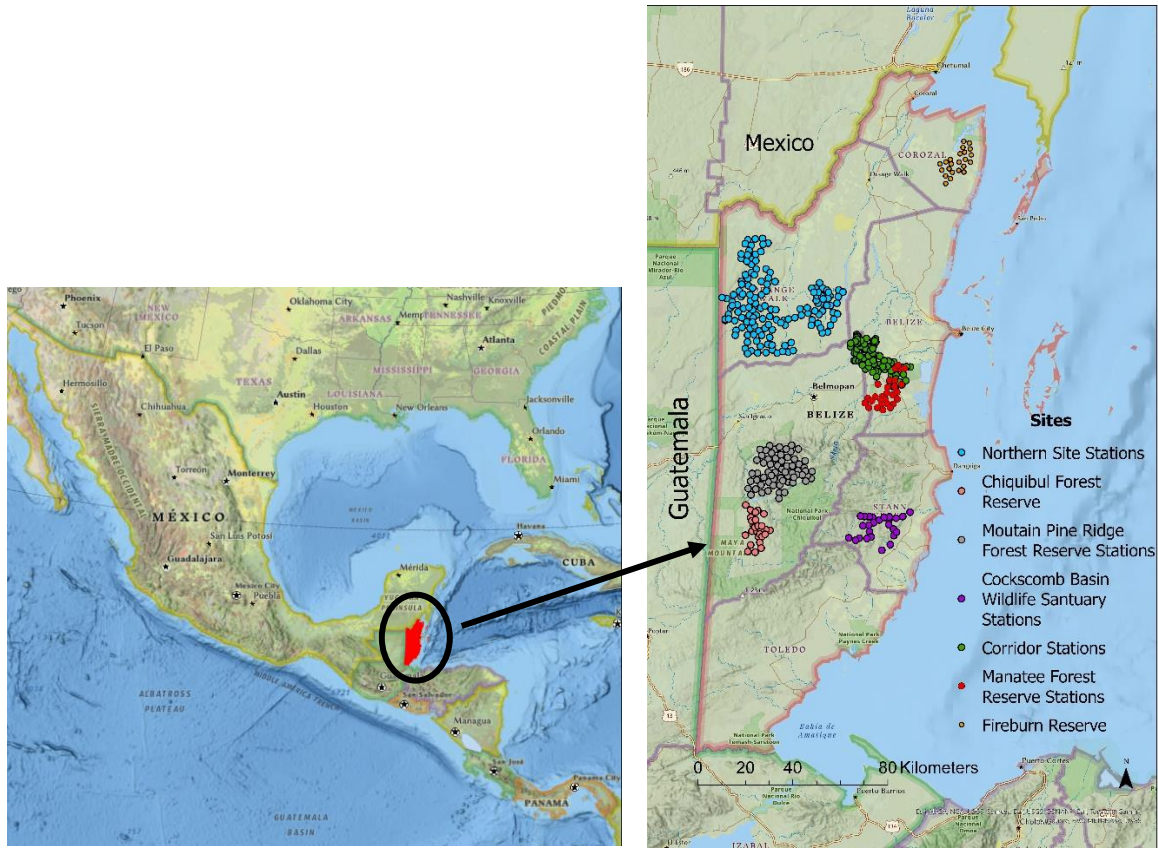


Figure 1. Belize in red and camera trapping survey sites (different colored dots) throughout Belize, Central America: Central Belize Corridor site station (green), Cockscomb Basin Wildlife Sanctuary (purple), Fireburn Reserve (orange), Greater Belize Maya Forest (light blue), Mountain Pine Ridge Forest Reserve (grey), and Manatee Forest Reserve (red), Chiquibul Forest Reserve (pink).

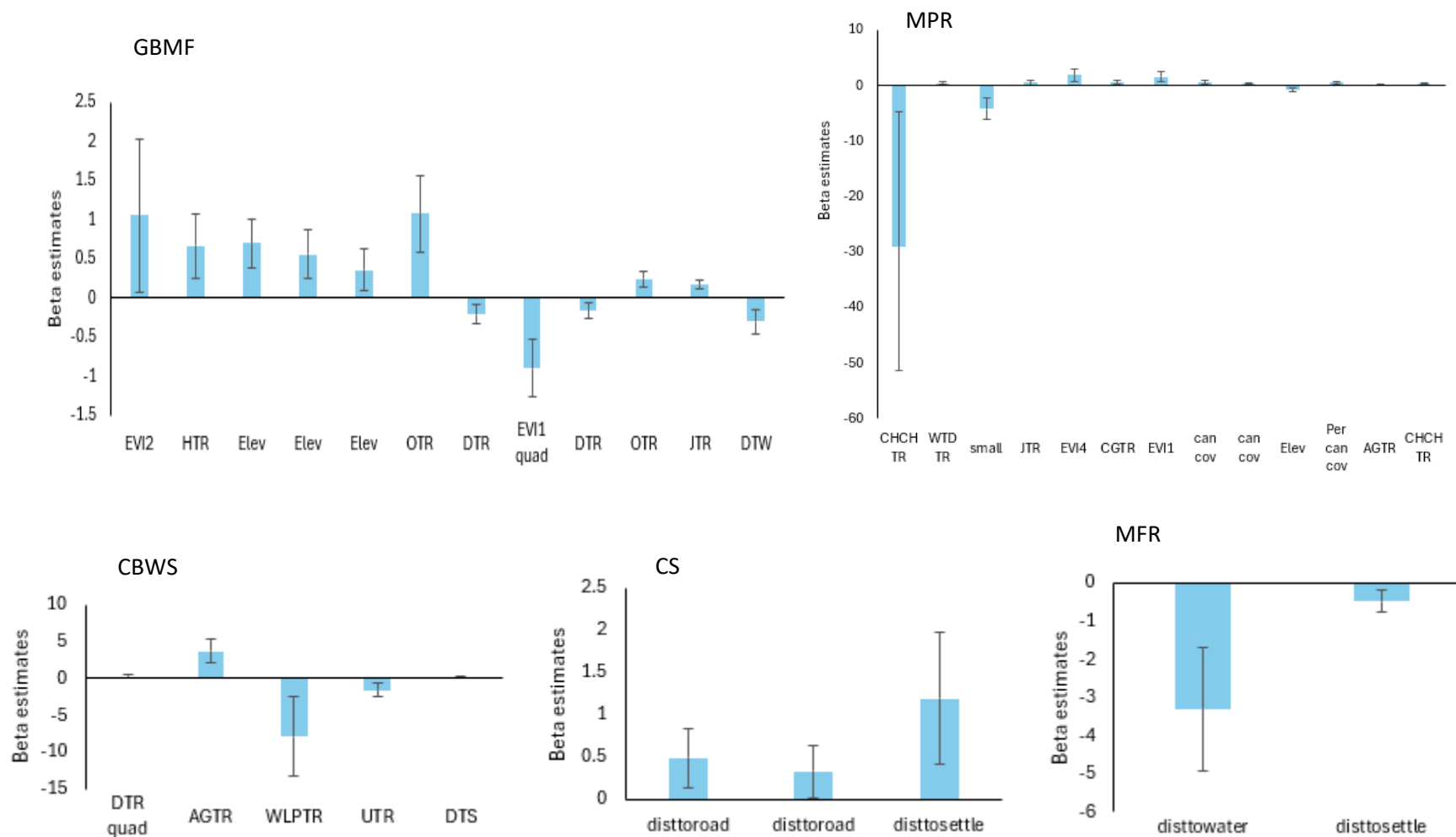


Figure 2. Magnitude of detection beta estimates of covariates from top single-season models. Estimates are from the Greater Belize Maya Forest (GBMF) 11 years, Mountain Pine Ridge (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years, Belize Maya Corridor sites (BMC) 4 years, and Manatee Forest Reserve (MFR) 3 years. Covariates are: Enhanced Vegetation Index (EVI), human trap rate (HTR), elevation (Elev), ocelot trap rate (OTR), distance to road (DTR), quadratic effect on EVI (EVI quad), jaguar trap rate (JTR), distance to water (DTW), chachalaca trap rate (CHCHTR), white-tailed deer trap rate (WTDTR), small prey (small), crested guan trap rates (CGTR), canopy cover at station (can cov), percent canopy cover in 100m radius (per can cov), agouti trap rate (AGTR), white-lipped peccary trap rate (WLPTR), ungulate trap rate (UTR), distance to road (disttoroad), distance to settlements (disttosettle), distance to water (disttowater).

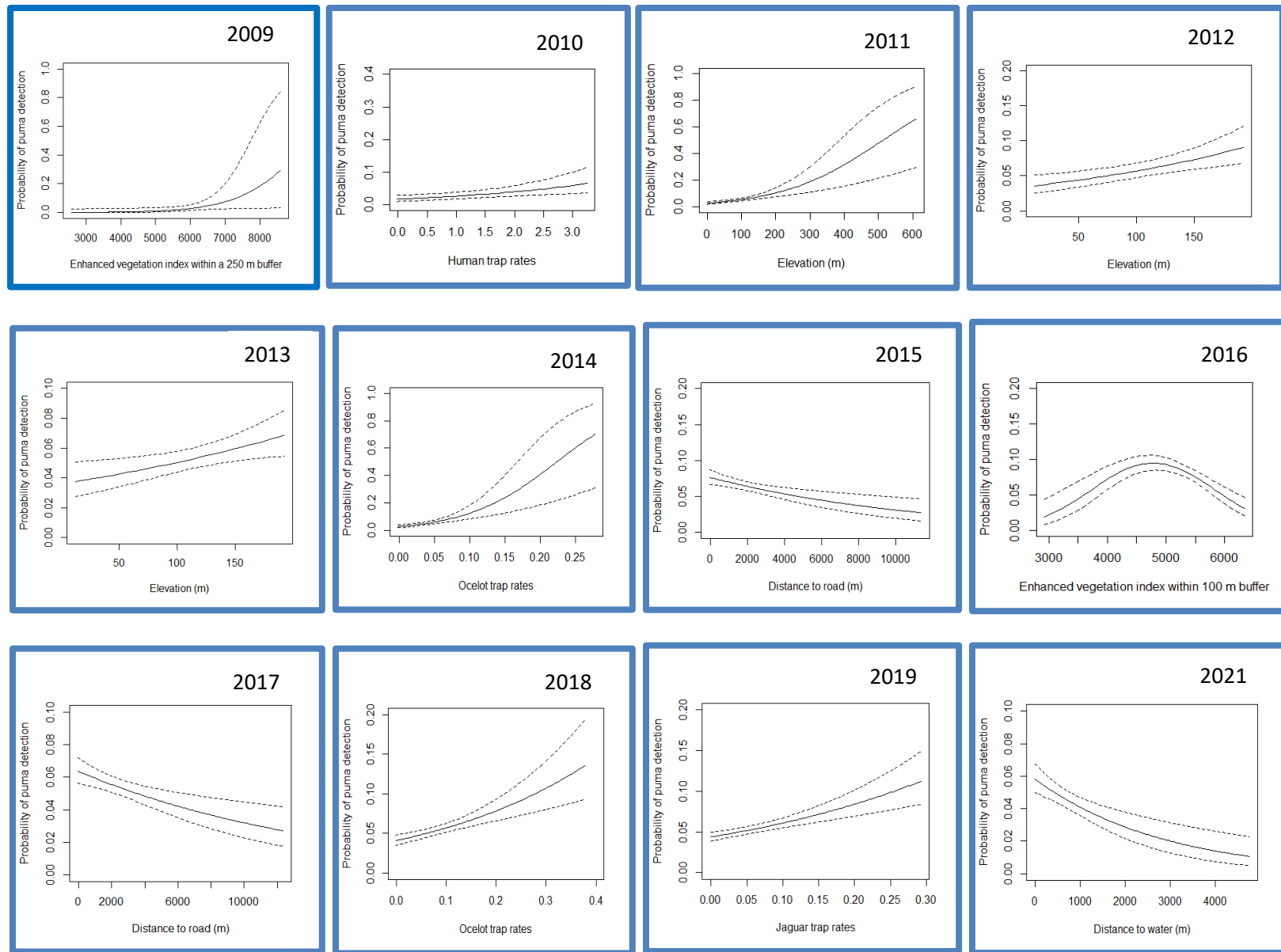


Figure 3. Detection (p) estimates as solid line with confidence intervals in dotted lines for pumas from top models in RPresence plotted chronologically with covariates that affected detection in the Greater Belize Maya Forest in Belize, Central America from 2009-2019, 2021. Data from remote camera traps.

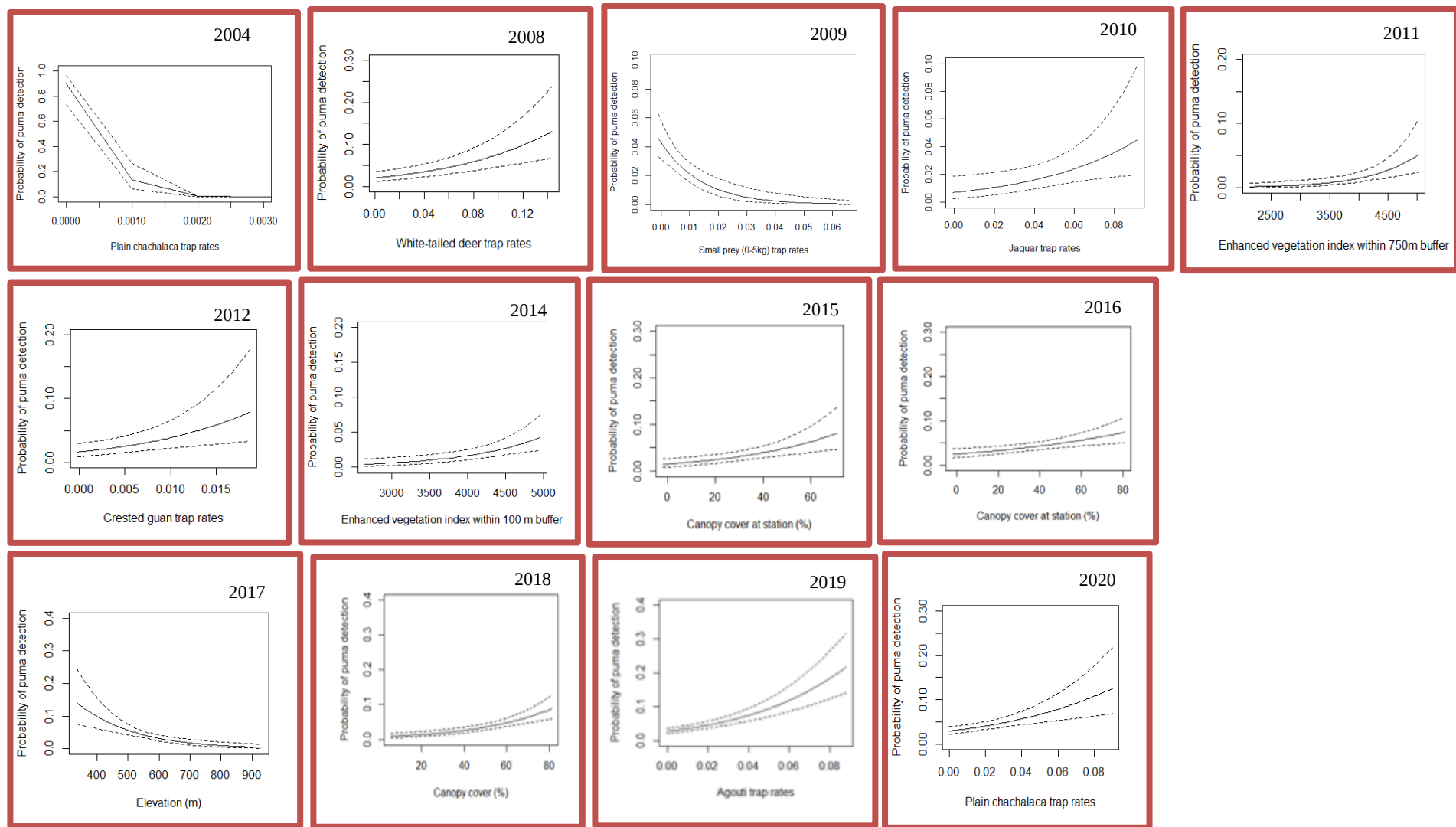


Figure 4. Detection (p) estimates as solid line with confidence intervals in dotted lines for pumas from top models in RPresence plotted chronologically with covariates that affected detection in the Mountain Pine Ridge Forest Reserve in Belize, Central America from 2009-2019, 2021. Data from remote camera traps.

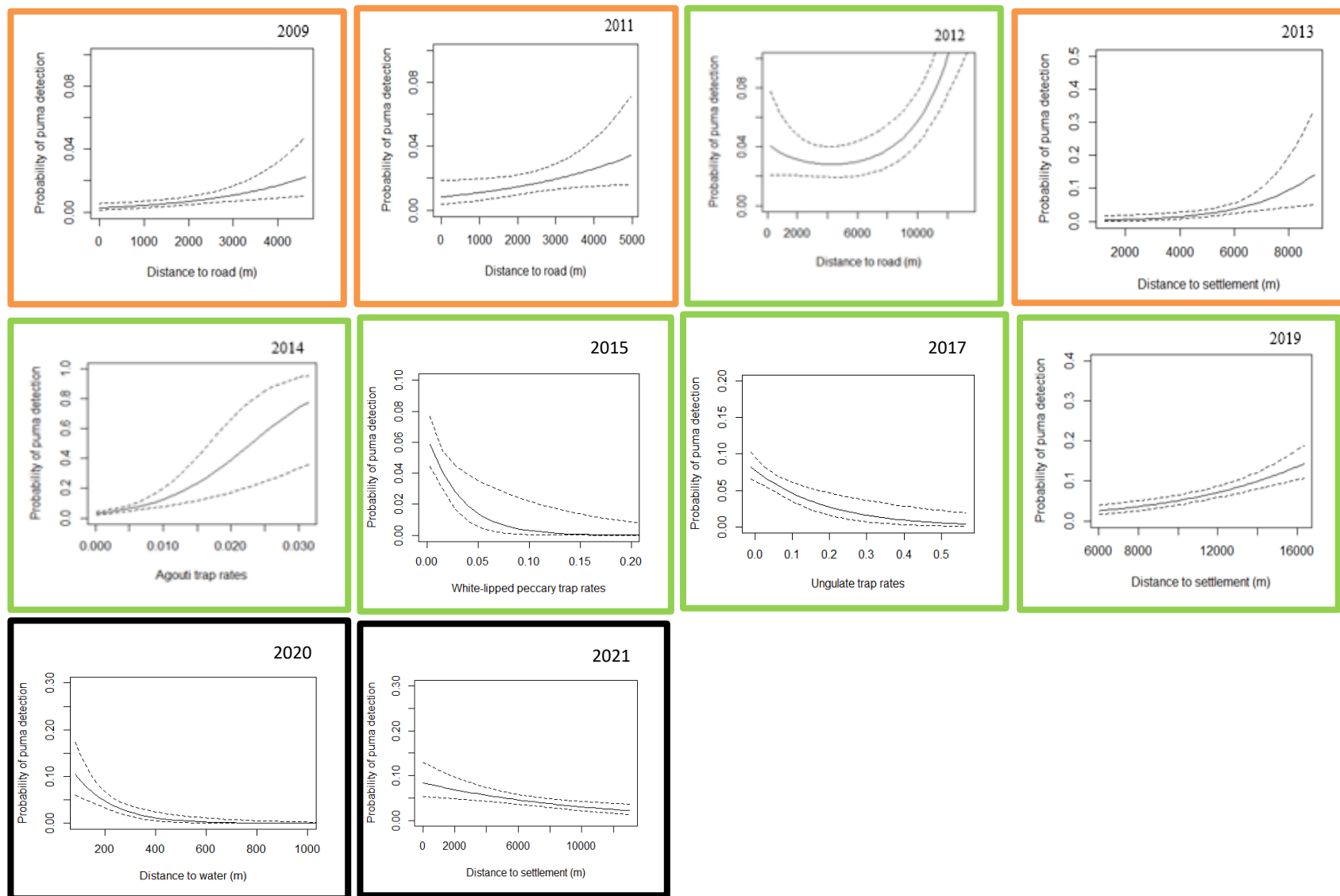


Figure 5. Detection (p) estimates as solid line with confidence intervals in dotted lines for pumas from top models in RPresence plotted chronologically displaying covariates that affected detection in the Central Corridor sites from 2009, 2011, 2013 (orange), Cockscomb Basin Wildlife Sanctuary (green) and Manatee Forest Reserve (black) in Belize, Central America from 2012-2017, 2019, 2021. Data from remote camera traps.

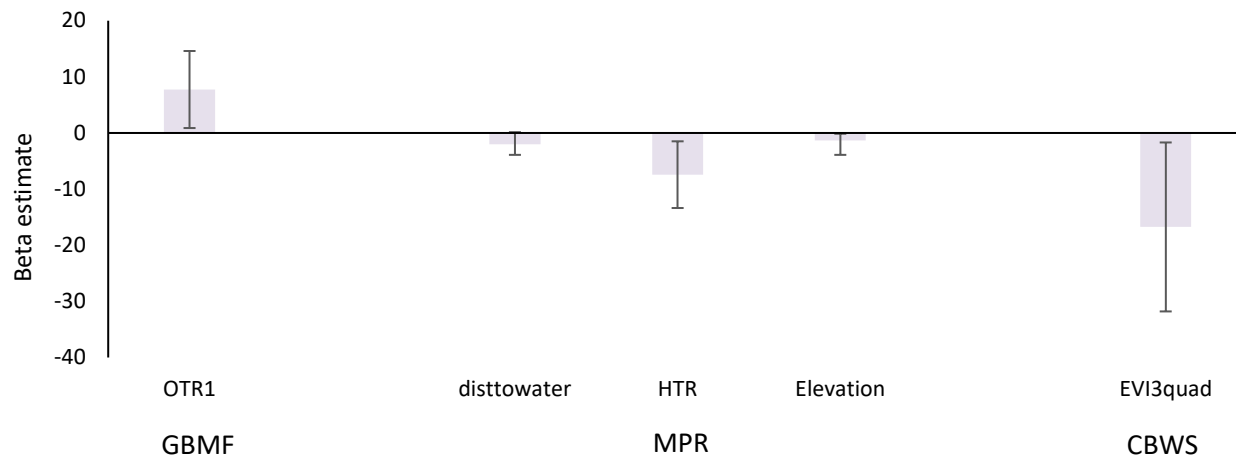


Figure 6. Occupancy beta estimates and confidence intervals of covariates from top single-season models. Estimates are from the Greater Belize Maya Forest (GBMF) 11 years, Mountain Pine Ridge (MPR) 18 years, and Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years.

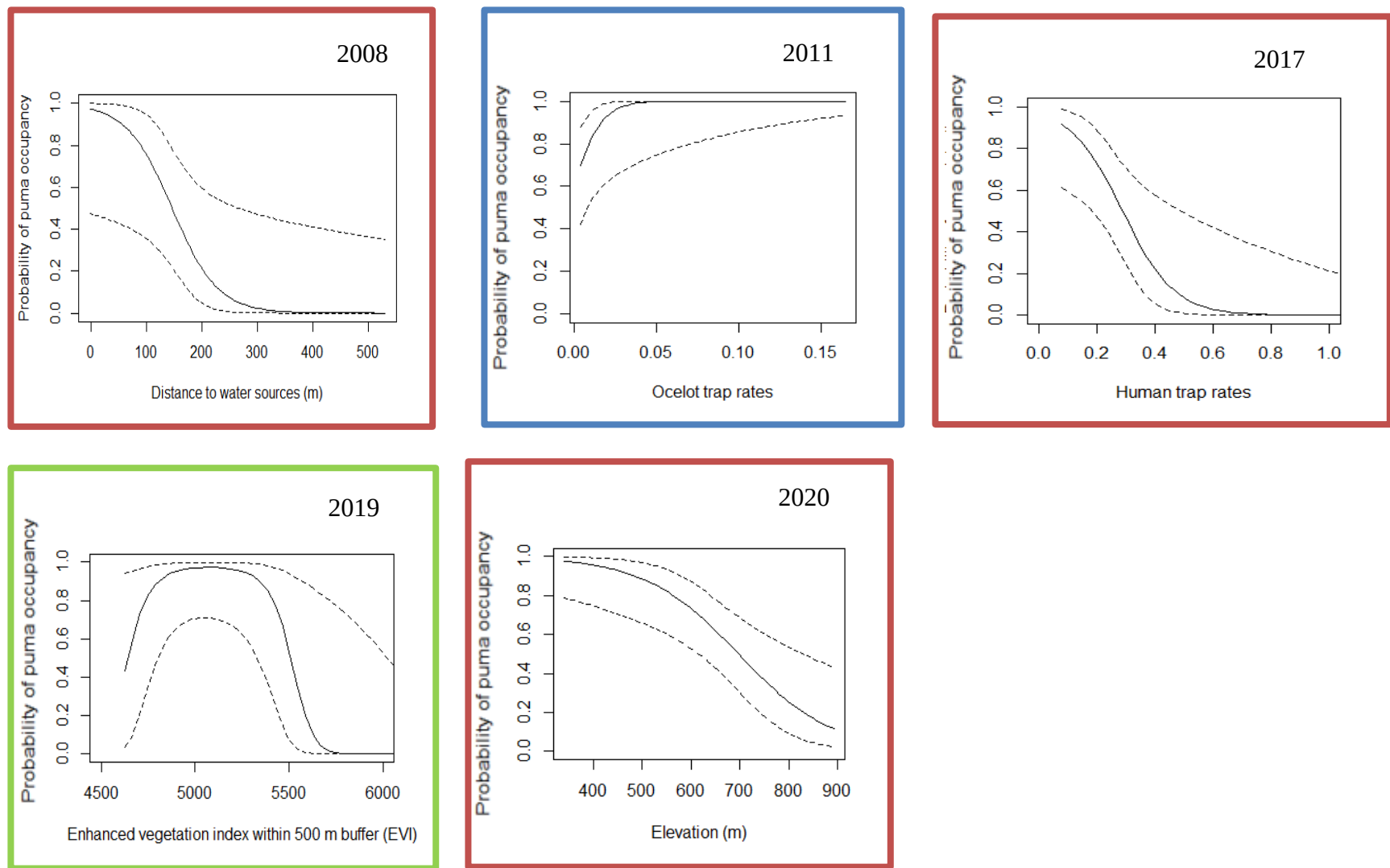


Figure 7. Puma occupancy (ψ) estimates as solid line with confidence intervals in dotted lines from selected top models run in RPresence plotted chronologically with covariates that affected occupancy in the Mountain Pine Ridge (red) 2004-2021; Greater Belize Maya Forest (blue) 2009-2019, 2021, Cockscomb Basin Wildlife Sanctuary 2012-2017, 2019, 2021 (green), in Belize, Central America. Data from remote camera traps.

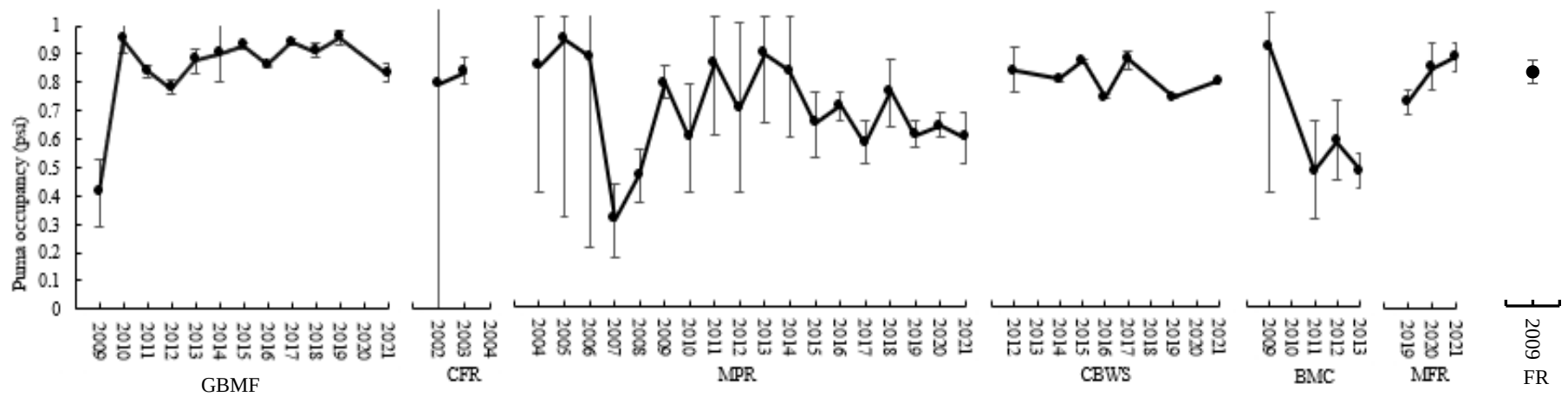


Figure 8. Puma occupancy (ψ) estimates (y-axis) from the Greater Belize Maya Forest combined from 2009-2021 consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, Gallon Jug; the Chiquibul Forest Reserve (CFR); Mountain Pine Ridge (MPR) 2004-2021; Cockscomb Basin Wildlife Sanctuary (CBWS); the Belize Maya Corridor (BMC), Manatee Forest Reserve (MFR) from 2004 to 2021; and Fireburn Reserve in 2009 in Belize, Central America. Most sites were not surveyed (with the exception of MPR) during 2020 due to COVID19. Error bars represent confidence intervals.

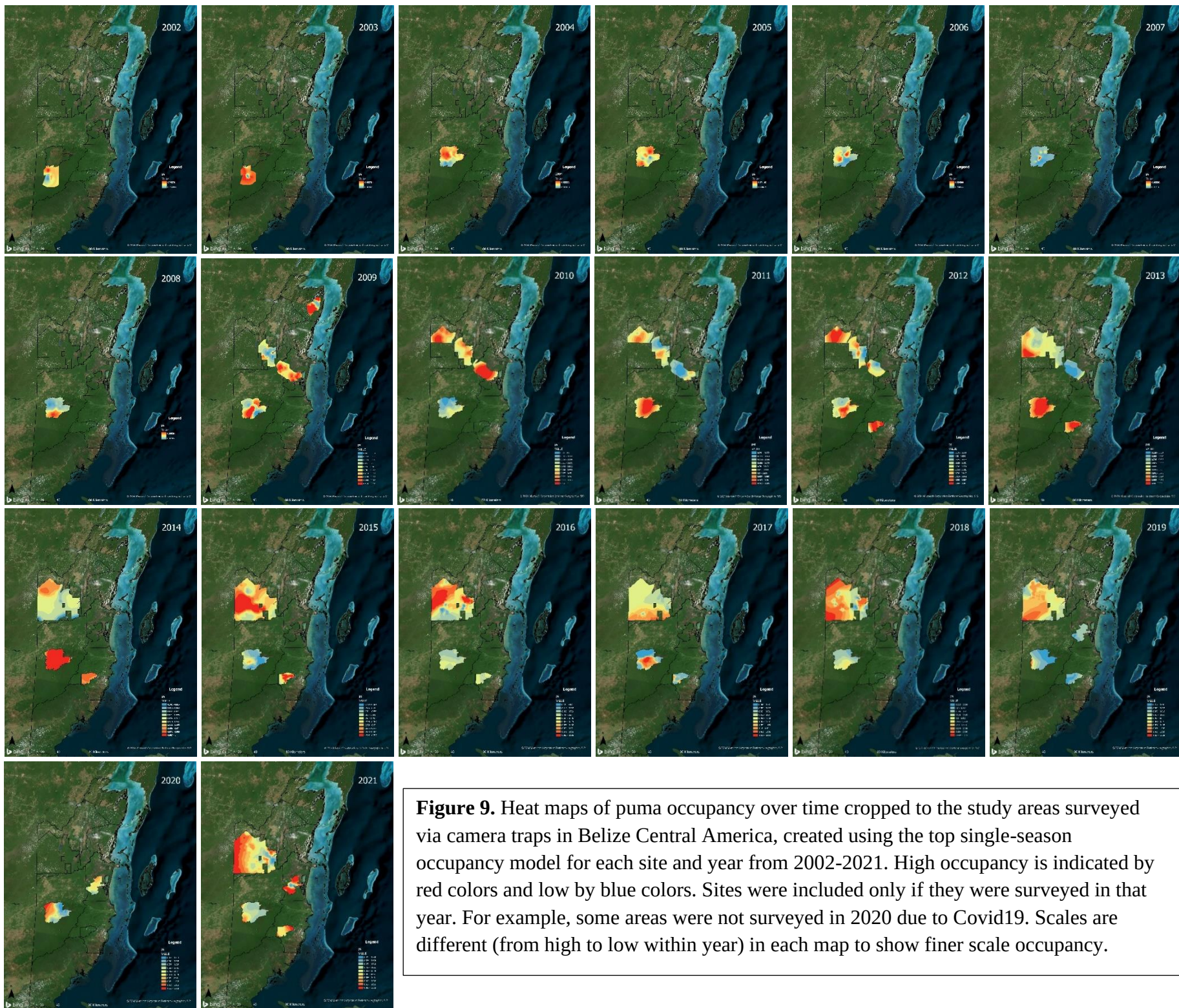


Figure 9. Heat maps of puma occupancy over time cropped to the study areas surveyed via camera traps in Belize Central America, created using the top single-season occupancy model for each site and year from 2002-2021. High occupancy is indicated by red colors and low by blue colors. Sites were included only if they were surveyed in that year. For example, some areas were not surveyed in 2020 due to Covid19. Scales are different (from high to low within year) in each map to show finer scale occupancy.

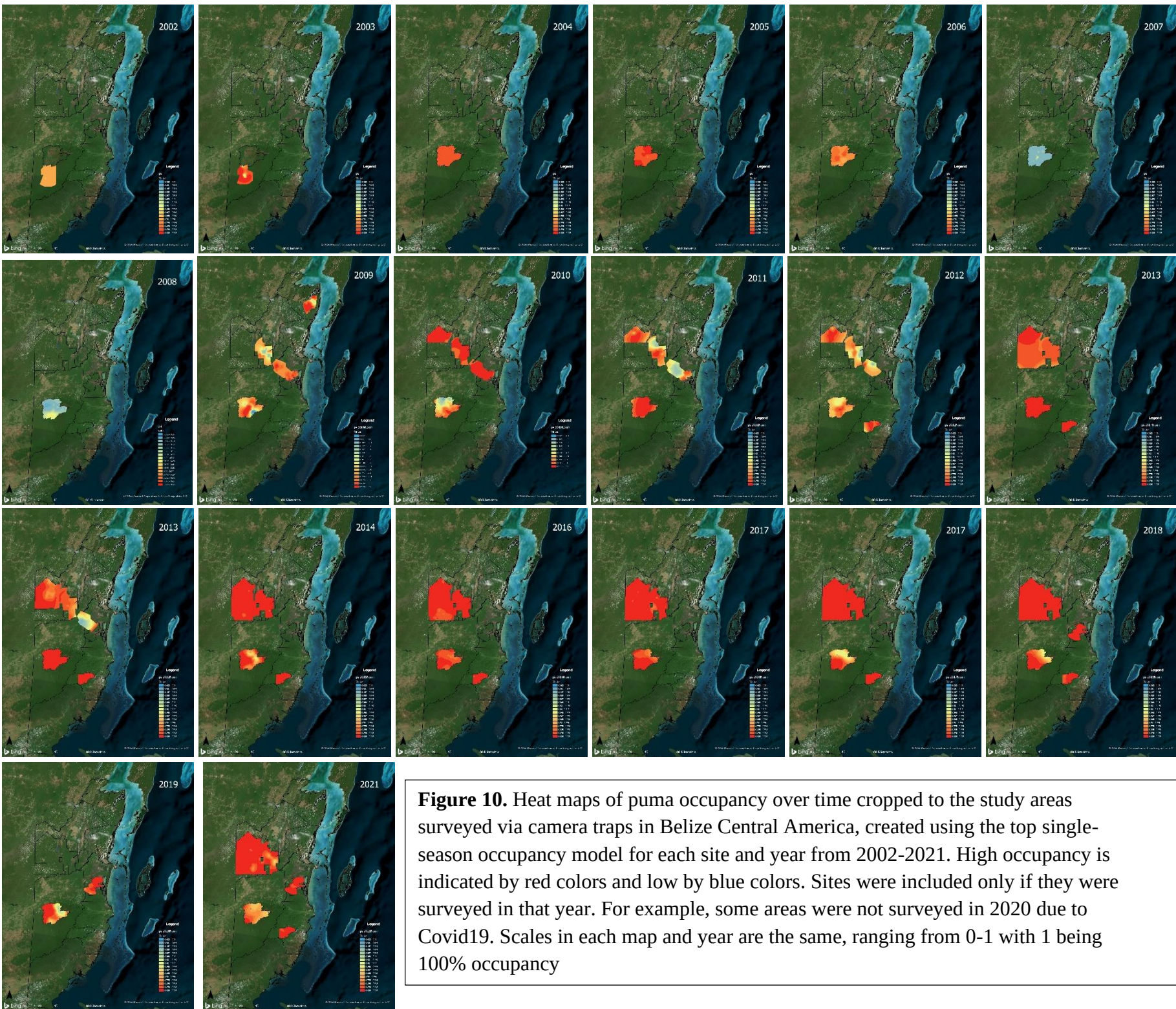


Figure 10. Heat maps of puma occupancy over time cropped to the study areas surveyed via camera traps in Belize Central America, created using the top single-season occupancy model for each site and year from 2002-2021. High occupancy is indicated by red colors and low by blue colors. Sites were included only if they were surveyed in that year. For example, some areas were not surveyed in 2020 due to Covid19. Scales in each map and year are the same, ranging from 0-1 with 1 being 100% occupancy

Table 1. All study sites with total years running from the beginning to the present with total trap nights functioning and current number of stations in each site in Belize, Central America used in the analysis.

Site	Years Running	Total Trap Nights	Stations
Greater Belize Maya Forest	2009-2019, 2021	72,585	20-147
<i>Yalbac</i>	2014-2019, 2021	10,036	9-35
<i>Gallon Jug</i>	2013-2019, 2021	21,226	29-42
<i>La Milpa</i>	2010-2019, 2021	17,497	20-27
<i>Hillbank</i>	2009-2019, 2021	23,826	20-43
Chiquibul Forest Reserve	2002-2008	3,540	10-30
Mountain Pine Ridge Forest Reserve	2004-2008, 2009-2021	50,654	19-65
Cockscomb Basin Wildlife Sanctuary	2012-2017, 2019, 2021	14,400	20-22
Belize Central Corridor	2009, 2011-2013	28,254	32-100
<i>Big Falls</i>	2009, 2012-2013	8,370	29-32
<i>Bonzana</i>	2009, 2011	4,080	20
<i>Cox Lagoon</i>	2009, 2011	2,852	31
<i>Cox Logging Road</i>	2012	1,012	11
<i>Runaway Creek</i>	2009, 2011	2,100	20-21
<i>LCJCWS</i>	2012	1,380	15
Manatee Forest Reserve	2019-2021	8,460	20-37
Fireburn Reserve	2009	1704	23
Total	2002-2021	181,025	2,221

Table 2. Summary of numbers of camera stations, stations with puma captures, naïve occupancy (stations with pumas/total stations per site/year) within each site and year for Greater Belize Maya Forest (Belize Maya Forest and Rio Bravo combined), Chiquibul Forest Reserve (CFR), Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), Belize Maya Corridor (BMC), Manatee Forest Reserve (MFR), and Fireburn (FB) from camera trap data collected in Belize, Central America.

GBMF	Stations	Stations with Puma captures	Naïve occupancy
2009	20	7	0.35
2010	40	22	0.55
2011	40	33	0.83
2012	40	30	0.75
2013	76	65	0.84
2014	90	83	0.89
2015	97	90	0.93
2016	112	95	0.85
2017	117	106	0.91
2018	123	105	0.85
2019	140	132	0.94
2021	147	121	0.82
CFR			
2002	18	4	0.22
2003	17	12	0.71
2006	15	7	0.47
2007	19	2	0.11
2008	32	7	0.22
MPR			
2004	22	9	0.41
2005	23	7	0.30
2006	24	10	0.42
2007	47	2	0.04
2008	27	10	0.37
2009	30	17	0.57
2010	33	12	0.36
2011	35	15	0.43
2012	40	19	0.48
2013	40	26	0.65
2014	40	21	0.53
2015	40	22	0.55
2016	50	32	0.64
2017	50	24	0.48
2018	50	29	0.58
2019	54	26	0.48
2020	56	30	0.54
2021	65	29	0.45
CBWS			
2012	20	18	0.90
2013	15	15	1.00
2014	15	13	0.87
2015	15	14	0.93
2016	20	16	0.80

2017	20	18	0.90
2019	20	16	0.80
2021	21	19	0.90
CS			
2009	72	23	0.32
2011	75	22	0.29
2012	26	7	0.27
2013	24	9	0.38
MFR			
2019	20	14	0.70
2020	25	13	0.52
2021	28	24	0.86
FB			
2009	22	14	0.64

Table 3. Top, competing (within 2 delta AICs), chosen models (*), number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Greater Belize Maya Forest that consists of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug from 2009-2019, 2021 in Belize, Central America. Ψ is occupancy while p is detection. Data from camera traps.

2009 models	npar	AIC	DeltaAIC	weight	ML
$\Psi \sim \text{PATR } p \sim \text{small}$	4	129.968	0.000	0.083	1.000
$\Psi \sim \text{PATR } p \sim \text{birds}$	4	130.193	0.225	0.074	0.894
$\Psi \sim \text{PATR } p \sim \text{OTTR}$	4	130.586	0.619	0.061	0.734
$\Psi \sim \text{PATR } p \sim \text{deer}$	4	131.083	1.115	0.048	0.573
$\Psi \sim \text{PATR } p \sim \text{WTDTR}$	4	131.127	1.159	0.047	0.560
$\Psi \sim \text{PATR } p \sim \text{HTR}$	4	131.142	1.175	0.046	0.556
$\Psi \sim \text{PATR } p \sim \text{ungulates}$	4	131.149	1.181	0.046	0.554
$\Psi \sim \text{PATR } p \sim \text{CHCHTR}$	4	131.153	1.185	0.046	0.553
$*\Psi \sim \text{PATR } p \sim \text{EVI2}$	4	131.575	1.607	0.037	0.448
$\Psi \sim \text{PATR } p \sim \text{EVI1}$	4	131.725	1.757	0.035	0.415
$\Psi \sim \text{PATR } p \sim \text{small}$	4	131.765	1.797	0.034	0.407
2010 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{HTR}$	3	475.364	0.000	0.433	1.000
2011 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim \text{OTR } p \sim \text{elevation}$	4	948.172	0.000	0.991	1.000
2012 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim \text{elevation } p \sim \text{elevation}$	4	996.053	0.000	0.781	1.000
2013 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{elevation}$	3	1959.481	0.000	0.213	1.000
$\Psi \sim 1 \text{ } p \sim \text{disttowater}$	3	1959.724	0.243	0.189	0.886
$\Psi \sim 1 \text{ } p \sim \text{JTR}$	3	1959.895	0.414	0.173	0.813
$\Psi \sim 1 \text{ } p \sim \text{GCTR}$	3	1961.321	1.840	0.085	0.399
2014 models	npar	AIC	DeltaAIC	weight	ML
$\Psi \sim \text{GCTR } p \sim \text{OTR}$	4	3032.519	0.000	0.991	1.000
$*\Psi \sim 1 \text{ } p \sim \text{OTR}$	3	3033.185	9.718	0.008	0.008
2015 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{disttoroad}$	3	3022.526	0.000	0.545	1.000
$\Psi \sim 1 \text{ } p \sim \text{disttoroadquad}$	3	3024.485	1.959	0.204	0.375
2016 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{EVI1quad}$	4	3536.082	0.000	0.878	1.000
2017 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{disttoroad}$	3	3731.269	0.000	0.597	1.000
$\Psi \sim 1 \text{ } p \sim \text{disttoroadquad}$	3	3732.928	1.660	0.260	0.436
2018 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{OTR}$	3	3363.055	0.000	0.967	1.000
2019 models	npar	AIC	DeltaAIC	weight	ML
$*\Psi \sim 1 \text{ } p \sim \text{JTR}$	3	4077.442	0.000	0.993	1.000
2021 models	npar	AIC	DeltaAIC	weight	ML
$\Psi \sim \text{EVI1quad } p \sim \text{EVI1quad}$	6	2722.295	0.000	0.505	1.000
$\Psi \sim \text{EVI1quad } p \sim \text{EVI2quad}$	6	2722.627	0.332	0.428	0.847
$*\Psi \sim 1 \text{ } p \sim \text{disttowater}$	3	2727.769	5.475	0.033	0.065

~ 1 = constant model, PATR= paca trap rates, small= agouti, armadillo, crested guan, greater curassow, ocellated turkey, plain chachalaca trap rates, HTR= human trap rates, OTR=ocelot trap rates, OTTR= ocellated turkey trap rate, disttowater= distance to water, WTDTR = white-tailed deer trap rates, ungulates= white-tailed deer, red brocket deer, white-lipped peccary, and collared peccary trap rates, JTR=jaguar trap rates, CHCHTR= plain chachalaca trap rates, GCTR=Greater Currasow trap rates, disttoroad=distance to nearest road, disttoroadquad=distance to nearest road with quadratic function, EVI1quad=enhanced vegetation index at 100 m buffer with a quadratic formula, EVI2quad=enhanced vegetation index at 250 m buffer with a quadratic formula

Table 4. Top, competing (within 2 delta AICs), chosen models*, number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from a priori (in italics) and post hoc (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Chiquibul Forest Reserve 2006-2008 in Belize, Central America.

2002 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
psi~disttoroad p~EVI4quad	5	68.43	0.00	0.20	1.00
psi~roadwidth p~EVI4quad	5	70.16	1.73	0.08	0.42
<i>*psi~1 p~EVI4quad</i>	4	74.53	6.10	0.01	0.05
2003 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
psi~OTR p~roadwidth	4	190.47	0.00	0.78	1.00
<i>*psi~1 p~1</i>	2	213.37	22.90	0.00	0.00
2006 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
Data does not fit					
2007 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
Data does not fit					
2008 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
Data does not fit					

Table 5. Top and competing models (within 2 delta AICs), number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Mountain Pine Ridge, Belize, Central America from 2004-2021. Ψ is occupancy while p is detection.

2004 models	npar	AIC	DeltaAIC	weight	ML
psi~EVI4quad p~CHCHTR	5	167.810	0.000	0.147	1.000
<i>*psi~1 p~CHCHTR</i>	3	169.647	1.837	0.059	0.399
2005 models	npar	AIC	DeltaAIC	weight	ML
psi~EVI4quad p~EVI5quad	6	123.559	0.000	0.371	1.000
<i>psi~EVI4quad p~1</i>	4	123.877	0.318	0.316	0.853
<i>*psi~1 p~EVI4quad</i>	4	122.738	7.179	0.010	0.028
2006 models	npar	AIC	DeltaAIC	weight	ML
psi~1 p~disttoroadquad	4	162.73	0.00	0.13	1
psi~1 p~EVI3quad	4	163.28	0.55	0.1	0.76
psi~1 p~EVI4quad	4	164.21	1.48	0.06	0.48
psi~EVI3quad p~1	4	164.46	1.73	0.06	0.42
<i>*psi~1 p~1</i>	2	168.63	5.90	0.00	0.05
2007 models	npar	AIC	DeltaAIC	weight	ML
<i>psi~EVI3quad p~1</i>	4	199.86	0.00	0.24	1.00
<i>psi~CGTR p~1</i>	3	202.93	3.07	0.05	0.22
2008 models	npar	AIC	DeltaAIC	weight	ML
*Ψ~disttowater p~WTDTR	4	242.510	0.000	0.393	1.000
Ψ~ disttowater p~deer	4	242.789	0.279	0.342	0.870
Ψ~ disttowater p~ungulates	4	243.562	1.052	0.232	0.591
2009 models	npar	AIC	DeltaAIC	weight	ML
<i>*Ψ~1 p~small</i>	3	554.926	0.000	0.203	1.000
Ψ~JTR p~small	4	554.967	0.042	0.199	0.980
Ψ~EVI2quad p~small	5	555.389	0.463	0.161	0.793
<i>Ψ~1 p~birds</i>	3	555.165	0.639	0.147	0.726
Ψ~HTR p~small	4	556.165	1.239	0.109	0.538
Ψ~ARMTR p~small	4	556.767	1.841	0.081	0.398
2010 models	npar	AIC	DeltaAIC	weight	ML
Ψ~HTR p~EVI3	4	261.031	0.000	0.380	1.000
<i>*Ψ~1 p~JTR</i>	3	261.934	0.903	0.242	0.637
<i>Ψ~1 p~roadwidth</i>	3	262.382	1.351	0.193	0.509
2011 models	npar	AIC	DeltaAIC	weight	ML
Ψ~EVI1quad p~EVI4	5	263.667	0.000	0.125	1.000
Ψ~EVI1quad p~1	4	263.919	0.252	0.111	0.882
<i>*Ψ~1 p~EVI4</i>	3	263.944	0.277	0.109	0.871
Ψ~EVI2quad p~EVI5	5	264.253	0.587	0.093	0.746
Ψ~EVI2quad p~EVI4quad	6	264.367	0.700	0.088	0.705
<i>Ψ~1 p~EVI5</i>	3	264.508	0.841	0.082	0.657
2012 models	npar	AIC	DeltaAIC	weight	ML
Ψ~elevation p~elevation	4	319.747	0.000	0.590	1.000
<i>Ψ~1 p~elevation</i>	3	321.808	2.061	0.211	0.357
<i>Ψ~elevation p~1</i>	3	324.220	4.473	0.063	0.107
<i>*Ψ~1 p~CGTR</i>	3	324.706	4.959	0.050	0.084
2013 models	npar	AIC	DeltaAIC	weight	ML
<i>Ψ~1 p~ungulates</i>	3	430.127	0.000	0.295	1.000

$\Psi \sim 1$ $p \sim \text{deer}$	3	430.991	0.863	0.189	0.649
$\Psi \sim 1$ $p \sim \text{WTDTR}$	3	431.163	1.036	0.174	0.596
$*\Psi \sim 1$ $p \sim 1$	2	437.788	7.660	0.006	0.022
2014 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim 1$ $p \sim \text{EVI1}$	3	405.903	0.000	0.166	1.000
$\Psi \sim 1$ $p \sim \text{EVI4}$	3	407.768	1.866	0.065	0.394
$\Psi \sim 1$ $p \sim \text{EVI1quad}$	3	407.829	1.926	0.063	0.382
2015 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim 1$ $p \sim \text{cancovst}$	3	480.908	0.000	0.455	1.000
$\Psi \sim 1$ $p \sim \text{WLPTR}$	3	481.806	0.898	0.290	0.638
2016 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$\Psi \sim 1$ $p \sim \text{EVI5quad}$	4	874.666	0.000	0.138	1.000
$\Psi \sim 1$ $p \sim \text{EVI4quad}$	4	875.882	1.216	0.075	1.216
$\Psi \sim 1$ $p \sim \text{EVI3quad}$	4	875.985	1.319	0.072	1.319
$\Psi \sim \text{EVI1}$ $p \sim \text{EVI5quad}$	5	876.666	2.000	0.051	0.368
$*\Psi \sim 1$ $p \sim \text{cancovst}$	3	876.999	2.333	0.043	0.311
2017 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim \text{HTR}$ $p \sim \text{elevation}$	4	618.923	0.000	0.993	1.000
2018 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim 1$ $p \sim \text{per_can_cov}$	3	743.605	0.000	0.776	1.000
2019 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim \text{ungulates}$ $p \sim \text{AGTR}$	4	792.154	0.000	0.340	1.000
$\Psi \sim \text{CHCHTR}$ $p \sim \text{AGTR}$	4	792.593	0.440	0.321	0.803
$\Psi \sim \text{elevation}$ $p \sim \text{AGTR}$	4	793.277	1.123	0.228	0.570
2020 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim \text{elevation}$ $p \sim \text{CHCHTR}$	4	804.286	0.000	0.454	1.000
$\Psi \sim \text{elevation}$ $p \sim \text{jag}$	4	805.071	0.785	0.307	0.675
$\Psi \sim \text{elevation}$ $p \sim \text{roadwidthquad}$	5	805.638	1.352	0.231	0.509
2021 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$*\Psi \sim \text{EVI1quad}$ $p \sim \text{EVI5}$	5	668.850	0.000	0.026	1.000
$\Psi \sim \text{EVI3quad}$ $p \sim \text{EVI5}$	5	668.950	0.101	0.025	0.951
$\Psi \sim \text{EVI4quad}$ $p \sim \text{EVI5}$	5	669.113	0.263	0.023	0.877
$\Psi \sim 1$ $p \sim \text{disttoroadquad}$	4	669.135	0.286	0.023	0.867
$\Psi \sim \text{EVI3quad}$ $p \sim \text{EVI5quad}$	6	669.194	0.344	0.022	0.842
$\Psi \sim \text{EVI5quad}$ $p \sim \text{OTTR}$	5	669.235	0.385	0.021	0.825
$\Psi \sim 1$ $p \sim \text{OTTR}$	3	669.258	0.408	0.021	0.815
$\Psi \sim \text{EVI1quad}$ $p \sim \text{EVI5quad}$	6	669.316	0.467	0.021	0.792
$\Psi \sim \text{EVI5quad}$ $p \sim \text{elevation}$	5	669.356	0.507	0.020	0.776
$\Psi \sim \text{EVI5quad}$ $p \sim \text{EVI5}$	5	669.395	0.546	0.018	0.761
$\Psi \sim \text{EVI5}$ $p \sim \text{OTTR}$	4	669.599	0.749	0.018	0.688
$\Psi \sim \text{EVI4quad}$ $p \sim \text{OTTR}$	5	669.639	0.789	0.017	0.674
$\Psi \sim 1$ $p \sim \text{elevation}$	3	669.654	0.804	0.017	0.669
$\Psi \sim \text{EVI4quad}$ $p \sim \text{EVI5quad}$	6	669.667	0.818	0.017	0.665
$\Psi \sim \text{EVI1quad}$ $p \sim \text{OTTR}$	5	669.879	1.030	0.016	0.598
$\Psi \sim \text{EVI5quad}$ $p \sim 1$	4	670.053	1.204	0.014	0.548
$\Psi \sim \text{EVI4quad}$ $p \sim \text{elevation}$	5	670.069	1.220	0.014	0.544
$\Psi \sim \text{EVI3quad}$ $p \sim \text{OTTR}$	5	670.143	1.294	0.014	0.524
$\Psi \sim \text{EVI5}$ $p \sim 1$	3	670.252	1.403	0.013	0.496
$\Psi \sim \text{cancovst}$ $p \sim \text{OTTR}$	4	670.282	1.433	0.013	0.489
$\Psi \sim 1$ $p \sim \text{disttowater}$	3	670.317	1.468	0.013	0.480

$\psi \sim \text{EVI1quad } p \sim \text{elevation}$	5	670.363	1.513	0.012	0.469
$\psi \sim \text{EVI2quad } p \sim 1$	4	670.364	1.514	0.012	0.469
$\psi \sim 1 \text{ } p \sim \text{CGTR}$	3	670.375	1.526	0.012	0.466
$\psi \sim \text{EVI1quad } p \sim 1$	4	670.414	1.565	0.012	0.457
$\psi \sim \text{EVI4quad } p \sim 1$	4	670.416	1.566	0.012	0.457
$\psi \sim \text{EVI1quad } p \sim \text{EVI4quad}$	6	670.438	1.588	0.012	0.452
$\psi \sim \text{EVI5quad } p \sim \text{small}$	5	670.547	1.697	0.011	0.428
$\psi \sim 1 \text{ } p \sim \text{AGTR}$	3	670.573	1.723	0.011	0.422
$\psi \sim \text{cancovst } p \sim 1$	3	670.624	1.774	0.011	0.412
$\psi \sim \text{cancovst } p \sim \text{disttoroadquad}$	5	670.625	1.775	0.011	0.412
$\psi \sim \text{EVI5quad } p \sim \text{AGTR}$	5	670.669	1.819	0.011	0.403
$\psi \sim \text{EVI3quad } p \sim \text{elevation}$	5	670.695	1.846	0.010	0.397
$\psi \sim \text{EVI5quad } p \sim \text{CGTR}$	5	670.708	1.859	0.010	0.395
$\psi \sim \text{cancovst } p \sim \text{EVI4quad}$	5	670.765	1.916	0.010	0.384
$\psi \sim 1 \text{ } p \sim \text{roadwidthquad}$	4	670.772	1.923	0.010	0.382
$\psi \sim \text{EVI5quad } p \sim \text{EVI5quad}$	6	670.790	1.941	0.010	0.379
$\psi \sim \text{EVI3quad } p \sim 1$	4	670.802	1.952	0.010	0.377
$\psi \sim 1 \text{ } p \sim \text{small}$	3	670.827	1.977	0.010	0.372

~1= constant model, AGTR=agouti trap rates, CGTR= crested guan trap rates, small= agouti, armadillo, crested guan, greater curassow, ocellated turkey, plain chachalaca trap rates, HTR= human trap rates, OTTR=ocellated turkey trap rates, WTDTR = white-tailed deer trap rates, deer= white-tailed and red brocket deer trap rates, UTR=ungulate (white-tailed deer, red brocket deer, white-lipped peccary, and collared peccary) trap rates, JTR=jaguar trap rates, CHCHTR= plain chachalaca trap rates, ARMTR=armadillo trap rates, cancovst= canopy cover at station, disttowater=distance to nearest water source, EVI1quad=enhanced vegetation index at 100 m buffer with a quadratic formula, EVI2quad=enhanced vegetation index at 250 m buffer with a quadratic formula, EVI3quad=enhanced vegetation index at 500 m buffer with a quadratic formula, EVI4quad=enhanced vegetation index at 750 m buffer with a quadratic formula, EVI5quad=enhanced vegetation index at 1000 m buffer with a quadratic formula

Table 6. Top and competing models (within 2 delta AICs), number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Cockscomb Basin Wildlife Sanctuary throughout all survey time periods in Belize, Central America. Ψ is occupancy while p is detection.

2012 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
<i>*$\Psi \sim 1$ $p \sim \text{disttoroadquad}$</i>	4	623.234	0.000	0.786	1.000
2013 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
Data does not fit					
2014 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{EVI2}$ $p \sim \text{AGTR}$	4	403.024	0.000	0.923	1.000
2015 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
<i>*$\Psi \sim 1$ $p \sim \text{disttoroadquad}$</i>	4	476.052	0.000	0.778	1.000
2016 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$\Psi \sim \text{OTR}$ $p \sim \text{elevation}$	4	737.575	0.000	0.959	1.000
<i>*$\Psi \sim 1$ $p \sim \text{elevation}$</i>	3	744.158	6.583	0.036	0.037
2017 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$\Psi \sim \text{PATR}$ $p \sim \text{ungulates}$	4	758.006	0.000	0.309	1.000
$\Psi \sim \text{PATR}$ $p \sim \text{WLPTR}$	4	759.015	1.009	0.186	0.604
<i>*$\Psi \sim 1$ $p \sim \text{ungulates}$</i>	3	766.486	8.481	0.004	0.015
2019 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{EVI3quad}$ $p \sim \text{disttosettlement}$	5	704.304	0.000	0.653	1.000
$\Psi \sim \text{EVI1quad}$ $p \sim \text{disttosettlement}$	5	706.003	1.700	0.279	0.428
2021 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{CGTR}$ $p \sim \text{disttoroadquad}$	5	622.163	0.000	0.566	1.000
$\Psi \sim \text{CGTR}$ $p \sim \text{disttoroad}$	4	623.702	1.539	0.262	0.463

~ 1 = constant model, disttoroadquad= distance to the nearest road with a quadratic equation, ungulates=ungulates (white-tailed deer, red brocket deer, white-lipped peccary, collared peccary) trap rates, EVI1quad=enhanced vegetation index with 100 m buffer with a quadratic equation, EVI2=enhanced vegetation index within 250 m buffer, AGTR=agouti trap rates, OTR=ocelot trap rates, JTR=jaguar trap rates, PATR=paca trap rates, WLPTR=white-lipped peccary trap rates, EVI3quad=enhanced vegetation index with 500 m buffer with a quadratic equation, disttosettlement= distance to nearest settlement, CGTR=crested guan trap rate

Table 7. Top and competing models (within 2 delta AICs), number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Central Belize Corridor throughout all survey time periods in Belize, Central America. Ψ is occupancy while p is detection.

<i>2009 models</i>	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
$\Psi \sim \text{JTR } p \sim \text{disttoroadquad}$	5	344.712	0.00	0.552	1.000
<i>$\Psi \sim \text{JTR } p \sim 1$</i>	3	347.752	3.041	0.121	0.219
<i>*$\Psi \sim 1 \text{ } p \sim \text{disttoroad}$</i>	3	349.636	4.925	0.047	0.085
<i>2010 models</i>	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
Data does not fit					
<i>2011 models</i>	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{disttoroad } p \sim \text{JTR}$	4	500.705	0.000	0.643	1.000
<i>2012 models</i>	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{AGTR } p \sim \text{EVI2quad}$	5	117.470	0.000	0.064	1.000
$\Psi \sim \text{AGTR } p \sim \text{JTR}$	4	117.642	0.171	0.059	0.918
$\Psi \sim \text{OTR } p \sim \text{EVI2quad}$	5	117.924	0.454	0.051	0.797
$\Psi \sim \text{rodents } p \sim \text{EVI2quad}$	5	117.994	0.524	0.049	0.770
$\Psi \sim \text{AGTR } p \sim \text{OTR}$	4	117.997	0.527	0.049	0.769
$\Psi \sim \text{AGTR } p \sim \text{deer}$	4	118.366	0.915	0.041	0.633
<i>$\Psi \sim 1 \text{ } p \sim \text{OTR}$</i>	3	118.438	0.968	0.040	0.616
$\Psi \sim \text{AGTR } p \sim \text{RBDTR}$	4	118.472	1.002	0.039	0.606
$\Psi \sim \text{AGTR } p \sim \text{ungulates}$	4	118.472	1.002	0.039	0.606
$\Psi \sim \text{AGTR } p \sim \text{CPTR}$	4	118.550	1.079	0.037	0.583
$\Psi \sim \text{OTR } p \sim \text{JTR}$	4	118.868	1.398	0.032	0.497
$\Psi \sim \text{OTR } p \sim \text{RBDTR}$	4	119.011	1.541	0.030	0.463
$\Psi \sim \text{OTR } p \sim \text{ungulates}$	4	119.011	1.541	0.030	0.463
<i>$\Psi \sim 1 \text{ } p \sim \text{JTR}$</i>	3	119.217	1.746	0.027	0.418
$\Psi \sim \text{OTR } p \sim \text{deer}$	4	119.453	1.982	0.024	0.371
<i>2013 models</i>	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{OTR } p \sim \text{disttosettle}$	4	247.914	0.000	0.742	1.000

~1= constant model, disttoroad=distance to nearest road, RBDTR=red brocket deer trap rates, , EVI4quad=enhanced vegetation index at 750 m buffer with a quadratic formula, birds=combined bird trap rates, small=prey (0-5kg) trap rates, JTR=jaguar trap rates, AGTR= Central American agouti trap rates, EVI2quad=enhanced vegetation index at 250 m buffer with a quadratic formula, OTR=ocelot trap rates, rodents=combined agouti and paca trap rates, deer trap rates=red brocket and white tailed deer trap rates, ungulates= ungulates (white-tailed deer, red brocket deer, white-lipped peccary, collared peccary) trap rates, disttosettle=distance to nearest settlement, CPTR=collared peccary trap rates *chosen model

Table 8. Top and competing models (within 2 delta AICs), number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold) single season occupancy models run in RPresence for the puma (*Puma concolor*), in the Manatee Forest Reserve throughout all survey time periods in Belize, Central America. Ψ is occupancy while p is detection.

2019 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
<i>*$\Psi \sim 1$ $p \sim \text{EVI1quad}$</i>	4	510.188	0.000	0.402	1.000
$\Psi \sim \text{deer} \sim \text{EVI1quad}$	5	510.206	0.017	0.399	0.992
2020 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
<i>*$\Psi \sim 1$ $p \sim \text{disttowater}$</i>	3	271.137	0.000	0.976	1.000
2021 models	<i>npar</i>	<i>AIC</i>	<i>DeltaAIC</i>	<i>weight</i>	<i>ML</i>
*$\Psi \sim \text{EVI5}$ $p \sim \text{disttosettle}$	3	636.435	0.000	0.670	1.000

~ 1 = constant model, JTR=jaguar trap rates, CPTR=Collared peccary trap rates, disttoroad=distance to nearest road, disttoroadquad=distance to nearest road with quadratic formula, disttosettle=distance to settlement *chosen mode

Table 9. Literature review of other puma single-season occupancy studies within Latin America from 2006-2024

Country	Years	Stations	Trap Nights	Occupancy	Reference cited
Argentina	2003-2008	216	13,929	0.62	Di Bitetti et al 2010
Brazil	2005-2007	10-22	7,929	0.35-0.39	Negroes et al. 2010
Brazil	2008	119	NA	0.47	Sollmann et al. 2012
Brazil	2013-2014	274	13,347	0.55	Paviolo et al. 2018.
Ecuador	2009-2010	119	2,800	0.22-0.28	Zapata-Ríos, G. and L.C. Branch 2018.
Brazil Peru Suriname Ecuador	2008-2016	480	72,835	0.34-0.45 0.37- 0.50 0.47 0.62	Santos, F. et al. 2019.
Mexico	2008, 2010-2012	113	7,159	0.68	Ávila-Nájera, D. M. et al. 2020.
Colombia	2014	47	3,069	0.45	Boron, V. et al. 2020.
Panama	2012-2017	418	43,294	0.02	Meyer, Ninon FV. et al. 2020.
Argentina	2018-2022	149	4,877	0.40-1.00	Nanni, A. S. et al. 2023.
Chile	2012-2013, 2015	100	5,953	0.51	Osorio, C. et al. 2020.
Panama	2014-2015	103	4,057	0.23-0.50	Fort, J.L. et al. 2022.
Brazil	2013-2014	205	6,358	0.65	Pônzio, M do C. et al. 2023
Argentina	2014-2015	45	5,040	0.35-0.88	Zanón Martínez, J I. et al. 2023
Belize - Pine Forest Belize - Broadleaf Forest Belize - Mixed	2002-2021	2,221	181,025	0.30-0.92 0.78*-0.96 0.46-0.88	McPhail et al. 2024

*Indicated one anomalous year in 2004 that had an estimate of 0.41 most likely due to only surveying in one site with mostly film cameras

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Table 10. Covariates that had strong influences on puma detection and occupancy across 20 years (2002-2021) and 6 sites in Belize, Central America, using single season occupancy models from remote camera trap data.

Sites and years surveyed	Detection			Occupancy		
	Microhabitat covariates	Macrohabitat covariates	Biotic Covariates	Microhabitat covariates	Macrohabitat covariates	Biotic Covariates
GBMF Total years 2009-2019, 2021	0	elevation (+) 2011, 2012, 2013 dist roads (-) 2015, 2017 dist water (-) 2021 EVI (-) 2009 EVI2 (-) 2016	human TR (+) 2010 ocelot trap rates (+) 2014, 2018 jaguar trap rates (+) 2019	0	0	ocelot TR (+), 2009
CFR Total years: 2002-2008	-	0	0	-	0	0
MPR Total years: 2004-2008, 2009-2021	canopy cover at station (+), 2015, 2016 %canopy cover in 100 m radius (+), 2018	EVI (+) 2011, 2014 elevation (+) 2017	white-tailed deer TR (+), 2008 jaguar TR (+), 2010 crested guan TR (+), 2012 agouti TR (+), 2019 plain chachalaca TR (+), 2020 plain chachalaca TR (-), 2004 small prey TR (+), 2009	0	dist water (-), 2008 elevation (-), 2019	human TR (-), 2017
CBWS Total years: 2012-2017, 2019, 2021	-	dist settlement (+), 2019 dist roads2 (+), 2012, 2021	agouti TR (+), 2014 white-lipped peccary (-), 2015 ungulate trap rate (-), 2017	-	EVI3 (-), 2019	0
BCC Total years: 2009, 2011-2013	-	dist roads (+), 2009, 2011 dist settlement (+), 2013	0	-	0	0
MFR Total years: 2019-2021	-	dist water (-) 2020 dist settlement (-), 2021	0	-	0	0
Total site/years with covariate effect	3	19	14	0	3	2

Supplementary Materials

S1. Landscape variables extracted from geographic information system (GIS) layers obtained from the Biodiversity and Environmental Resource Data System of Belize (BERDS) site in Belize, Central America and from Moderate Resolution Imaging Spectroradiometer (MODIS). Anthropogenic variables were extracted from GIS or camera trap data or measured manually in the field. Microhabitat variables come from manual surveys surrounding each camera trap. Trap rates come from photo data. Covariates listed were used in *a priori* and *post hoc* models on both parameters: occupancy (ψ) and detection (p). Negative (-) and positive (+) signs indicated the hypothesized direction of the effect with justification and sources.

Local variables microhabitat data collected within 100 m around camera traps

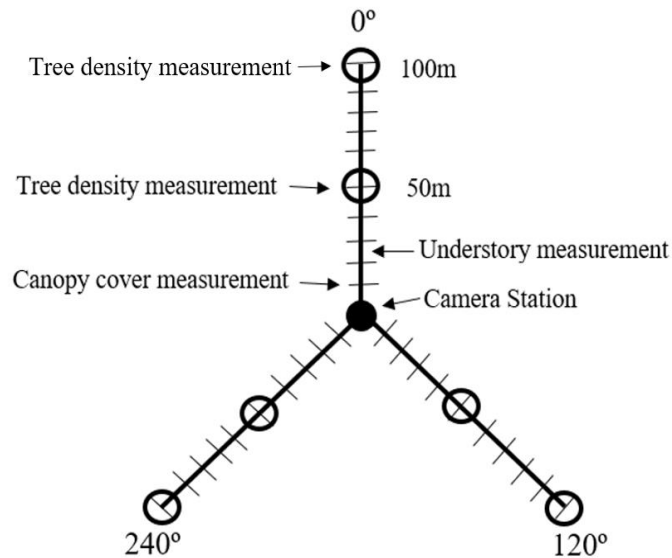
Canopy cover at station (cancovst)	$\Psi +, p +$	Higher canopy cover at the station itself may provide more hiding cover allowing for ambush hunting and caching areas (Gray et al. 2016) and cover for lower perceived risk allowing more unrestricted movement (Gray et al. 2016).
Percentage of canopy cover (percancov)	$\Psi +, p +$	Higher canopy cover within the general area (within 100 m of camera) may provide more hiding cover allowing for ambush hunting and caching areas (Terborgh et al. 2015) and cover for lower perceived risk allowing more unrestricted movement (Gray et al. 2016).
Understory density 0-0.5 m (average1)	$\Psi +, p +$	Since short understory is needed for small prey species (Terborgh et al. 2015), it will draw pumas into the area, but as it increases, becomes harder to penetrate funneling pumas on the trails where cameras are located increasing detection.
Understory density 0.5-1 m (average2)	$\Psi +, p +$	Same as above.
Understory density 1-2 m (average3)	$\Psi +, p +$	Same as above.
Understory density 0-2 m (average4)	$\Psi +, p +$	Same as above.
Coefficient of variation on understory density 0-0.5 m (CoOvar1)	$\Psi +, p o -$	Coefficient of variation can represent habitat heterogeneity or patchiness (Terborgh et al. 2015). Patchiness at ground level could lead to more microhabitats and fruiting vines for small prey (Terborgh et al. 2015) drawing pumas in. Patchiness would make it easier to traverse leading to either no effect or decreases in detection as pumas are not necessarily funneled in front of cameras.
Coefficient of variation on understory density 0.5-1 m (CoOvar2)	$\Psi +, p o -$	Same as above.
Coefficient of variation on understory density 1-2 m (CoOvar3)	$\Psi +, p o -$	Same as above.

Coefficient of variation on understory density 0-2 m (CoOvar4)	$\Psi +$, p o -	Same as above.
Basal area without station (BasalAreaNC)	$\Psi +$, p +	Higher basal area indicates there are potentially more and/or older trees in the area that can provide larger fruit for larger prey (Terborgh et al. 2015) and provide cover for prey and pumas increasing occupancy and detection.
Road width	$\Psi +$, p +	Pumas will use areas with larger roads to move more easily and larger roads will allow easier detection as it funnels animals in front of the station (Gray et al. 2016).
Road width (quadratic)	$\Psi +$, p + then $\Psi -$, p -	Same as above however if roads are too wide, pumas will avoid the area due to heavier vehicle traffic and very wide roads make it more difficult to detect pumas due to limits on camera detection distance (Gray et al. 2016).
Landscape variables – macrohabitat	<i>A priori</i>	Justification and sources
Distance to sources of water (distantwater)	$\Psi -$, p -	Water sources are a vital resource so pumas will choose, and be detected, in areas near water (Gray et al. 2016).
Elevation	$\Psi +$, p +	Pumas are known to inhabit higher elevation areas and it is easier to transverse the paths along ridges where many of our cameras are located in higher elevation areas (Ironside et al. 2017).
Enhanced vegetation index at 100m, 250m, 500m, 750m, 1000m buffers (EVI1, EVI2, EVI3, EVI4, EVI5)	$\Psi +$, p +	Higher vegetation index (i.e. canopy and ground vegetation) may also provide more ambush/caching cover and more resources for prey species (Ironside et al. 2017), while avoiding other predators (Ironside et al. 2017), and increases likelihood of detection while moving through area.
Enhanced vegetation index at 100m, 250m, 500m, 750m, 1000m buffers (EVI1quad, EVI2quad, EVI3quad, EVI4quad, EVI5quad) (quadratic)	$\Psi +$, p + then $\Psi -$, p -	Same as above but if EVI gets too dense, it gets harder to see prey and move (Ironside et al. 2017), resulting in higher occupancy detection at intermediate EVI levels.
Distance to settlements	$\Psi +$, p -	Perceived risk is higher around humans leading to higher occupancy farther from settlements (Gray et al. 2016) but detection close to settlements may go up due to fewer choices of natural areas where cameras are placed (Gray et al. 2016).

Distance to roads	$\Psi +, p +$	Roads present risks as above, including risk of vehicles (Gray et al. 2016) so occupancy will be higher farther away from roads, but they are easier to travel on leading to higher detection (Solloman et al 2015).
Biotic variables		
White-tail deer trap rates (WTDTR)	$\Psi +, p +$	Pumas are deer specialists (Novack et al. 2005) so they will choose areas with higher WTD activity and will track/follow them causing increased camera detections.
Red brocket deer trap rates (RBDTR)	$\Psi +, p +$	Same as above but more so because the smaller deer species will be in a better weight range for the puma (Novack et al. 2005).
Agouti trap rates (AGTR)	$\Psi +, p +$	As a common prey species (Novack et al. 2005), pumas will choose areas with higher AG activity and will follow AG signs causing increased camera detections.
Paca trap rates (PATR)	$\Psi +, p +$	Same as above.
Armadillo trap rates (ARMTR)	$\Psi +, p +$	Same as above.
Ocellated turkey trap rates (OTTR)	$\Psi +, p +$	Same as above.
Great curassow trap rates (GCTR)	$\Psi +, p +$	Same as above.
Crested guan trap rates (CGTR)	$\Psi +, p +$	Same as above.
Chachalaca trap rates (CHCHTR)	$\Psi +, p +$	Same as above.
White-lipped peccary trap rates (WLPTR)	$\Psi +, p +$	Same as above (Foster et al. 2010).
Collared peccary trap rates (CPTR)	$\Psi +, p +$	Same as above (Foster et al. 2010).
Deer trap rates (DTR) – WTD and RBD combined	$\Psi +, p +$	Same as above.
Ungulates (white-tailed and red brocket deer and white-lipped and collared peccary) trap rates (UTR)	$\Psi +, p +$	Same as above.
Rodent (Agouti and Paca) trap rates (RTR)	$\Psi +, p +$	Same as above.
Ground Bird (OTTR, GCTR, CGTR, CHCHTR) trap rates (BTR)	$\Psi +, p +$	Same as above (Karandikar et al 2020).
Small prey (0-5kg, OTTR, GCTR, CGTR, CHCHTR, AGTR, ARMTR) trap rates (STR)	$\Psi +, p +$	Same as above (Karandikar et al 2020).
Ocelot trap rates (OTR)	$\Psi +, p +$	As a dominant carnivore, pumas will key in on ocelot sign (scent, markings, sight) as an indicator of good habitat and resources, having increased occupancy in the same areas as ocelots. Therefore, they will follow close behind when an ocelot is caught on camera thus increasing detection (Donadio & Buskirk 2006).

Jaguar trap rates (JTR)	Ψ -, p -	As the subordinate carnivore, pumas will try to avoid general areas with higher jaguar activity (Donadio & Buskirk 2006, Gonzalez-Borrajo et al. 2016) and also will be more cryptic in areas with jaguars and thus will have lower detection (Gray et al. 2016).
Human trap rates (HTR)	Ψ -, p -	Perceived risk is higher around humans due to people and their scents, sounds, and vehicles causing avoidance of area (Gray et al. 2016). They also will be more cryptic in areas with humans and thus will have lower detection (Gray et al. 2016).

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S2. Habitat survey schematic displaying where measurements are recorded at each camera trapping station (black dot). We took bearings (0°, 120°, and 240°) from each station and walked three 100 m transects (bold lines). Every two meters along each transect we recorded presence/absence understory measurements by dropping a 2m pole to the ground and noting whether vegetation touched the pole at heights of 0-0.5m, 0.5-1m, and 1-2m. Additionally, every 10 meters presence/absence canopy cover data was recorded (small perpendicular lines on transects). At the station, and at 50m and 100m along each transect, we used the point-centered quarter technique to measure tree distance and diameter at breast height to calculate tree density and basal area.

S3. Example of a Pearson's correlation matrix from the Greater Belize Maya Forest in Belize, Central America in 2021. Correlation Matrices were made for each year and study site (45 in total) to determine covariates that could be used in the same occupancy/detection models as long as they were uncorrelated ($r < |0.7|$).

	small	birds	rodents	deer	UTR	CHCHTR	CPTR	GCTR	WLPTR	OTTR	CGTR	WTDTR	RBDTR	AGTR	PATR	ARMTR	HTR	OTR	JTR	DTW	DTR	DTS	EV1	EV2	EV3	EV4
small	1.0																									
birds	1.0	1.0																								
rodents	0.2	0.0	1.0																							
deer	0.3	0.3	0.1	1.0																						
UTR	0.3	0.3	0.1	0.9	1.0																					
CHCHTR	0.2	0.2	-0.1	0.0	0.0	1.0																				
CPTR	-0.1	-0.1	0.0	0.0	0.2	0.0	1.0																			
GCTR	0.3	0.3	0.2	0.1	0.1	0.0	0.0	1.0																		
WLPTR	-0.1	-0.1	0.1	-0.1	0.1	0.0	-0.1	0.1	1.0																	
OTTR	0.9	1.0	0.0	0.3	0.2	0.2	-0.1	0.0	-0.1	1.0																
CGTR	-0.1	-0.1	0.0	0.0	0.0	0.1	0.0	0.2	0.2	-0.2	1.0															
WTDTR	0.3	0.3	0.0	0.8	0.7	0.1	0.0	0.1	-0.1	0.2	0.0	1.0														
RBDTR	0.2	0.1	0.2	0.6	0.5	0.0	0.0	0.0	0.0	0.2	0.0	-0.1	1.0													
AGTR	0.3	0.1	0.9	0.1	0.1	-0.1	0.0	0.3	0.1	0.0	0.0	0.0	0.2	1.0												
PATR	0.0	-0.1	0.6	0.0	0.0	-0.1	0.0	0.0	-0.1	-0.1	-0.1	-0.1	0.1	0.2	1.0											
ARMTR	0.1	0.0	0.1	0.0	-0.1	0.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0	0.1	0.0	1.0										
HTR	0.2	0.2	0.2	0.0	0.0	0.0	-0.1	-0.1	-0.1	0.2	-0.1	0.0	0.0	-0.1	0.5	0.0	1.0									
OTR	0.2	0.2	0.1	0.1	0.1	0.0	0.0	0.0	-0.1	0.2	0.0	0.1	0.0	0.1	0.2	-0.1	0.3	1.0								
JTR	0.2	0.2	0.1	0.2	0.1	0.0	0.0	0.1	0.0	0.2	-0.1	0.0	0.2	0.1	0.0	-0.1	0.2	0.2	1.0							
DTW	0.0	0.0	-0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	-0.1	-0.2	-0.1	-0.1	-0.1	0.1	1.0						
DTR	-0.2	-0.1	-0.1	0.0	0.0	0.0	0.1	0.2	0.0	-0.2	0.1	0.0	0.0	-0.1	-0.1	-0.1	-0.3	0.0	0.0	0.1	1.0					
DTS	-0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.2	0.1	-0.1	0.1	0.0	0.1	0.0	0.0	-0.1	-0.1	0.0	0.0	0.4	0.5	1.0				
EV1	0.0	0.0	0.0	-0.1	-0.1	-0.1	0.0	0.2	0.0	-0.1	0.1	-0.1	0.0	0.0	0.1	0.0	0.0	0.2	0.1	0.1	0.3	0.1	1.0			
EV2	0.0	0.0	0.0	-0.1	-0.1	-0.2	0.0	0.2	0.0	-0.1	0.1	-0.1	0.0	0.0	0.1	0.0	0.0	0.2	0.1	0.1	0.3	0.1	1.0	1.0		
EV3	0.0	-0.1	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	-0.1	0.1	0.0	0.0	0.0	0.1	0.1	1.0	
EV4	0.0	0.0	0.0	0.0	0.0	-0.2	0.0	0.1	0.0	0.0	0.1	0.0	0.0	-0.1	0.1	0.0	0.0	0.2	0.1	0.1	0.3	0.2	0.8	0.9	0.1	1.0

Small=CHCHTR, GCTR, CGTR, OTTR, AGTR, ARMTR, birds= CHCHTR, GCTR, CGTR, OTTR, rodents=PATR, AGTR, deer=WTDTR, RBDTR, UTR=, CHCHTR=plain chachalaca trap rates, CPTR=collared peccary trap rates, GCTR=greater curassow, WLPTR=white-lipped peccary trap rates, OTTR=ocellated turkey trap rates, CGTR=crested guan trap rates, WTDTR=white-tailed deer trap rates, RBDTR=red brocket deer trap rates, AGTR=agouti trap rates, PATR=paca trap rates, ARMTR=armadillo trap rates, HTR=human trap rates, OTR=ocelot trap rates, JTR=jaguar trap rates, DTW=distance to nearest water source, DTR=distance to nearest road, DTS=distance to nearest settlement, EVI1=enhanced vegetation index within 100 m buffer, EVI2= enhanced vegetation index within 250 m buffer, EVI3= enhanced vegetation index within 500 m buffer, EVI4= enhanced vegetation index within 750 m buffer, EVI5= enhanced vegetation index within 1000 m buffer

S4. Covariates that affected puma occupancy (ψ), and detection (P), with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Greater Belize Maya Forest combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America from 2009-2019, 2021. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2009	PATR	-1.42 (-4.79, 1.95)	-7.64 (-19.22, 3.94)	0.41 (0.29, 0.53)
2010	NA	NA	NA	0.95 (0.63, 1.00)
2011	OTR	7.03 (1.23, 12.83)	7.74 (0.88, 14.60)	0.84 (0.82, 0.86)
2012	Elevation	2.64 (-0.06, 5.34)	2.93 (-0.95, 6.81)	0.78 (0.75, 0.80)
2013	NA	NA	NA	0.88 (0.84, 0.93)
2014	NA	NA	NA	0.90 (0.79, 1.00)
2015	NA	NA	NA	0.93 (0.92, 0.94)
2016	NA	NA	NA	0.86 (0.86, 0.87)
2017	NA	NA	NA	0.94 (0.93, 0.95)
2018	NA	NA	NA	0.91 (0.88, 0.93)
2019	NA	NA	NA	0.96 (0.94, 0.99)
2021	NA	NA	NA	0.83 (0.79, 0.86)
Year	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p Range (LCL, UCL)
2009	EVI2	-3.89 (-4.65, -3.13)	1.06 (0.08, 2.04)	0.00 (0.00, 0.03)- 0.06 (0.02, 0.13)
2010	HTR	-3.76 (-4.17, -3.35)	0.67 (0.26, 1.08)	0.02 (0.01, 0.03)-0.08 (0.04, 0.16)
2011	Elevation	-2.79 (-2.99, -2.59)	0.70 (0.39, 1.01)	0.03 (0.02, 0.04)- 0.10 (0.07, 0.13)
2012	Elevation	-2.78 (-2.98, -2.58)	0.56 (0.25, 0.87)	0.04 (0.03, 0.05)- 0.09 (0.07, 0.12)
2013	Elevation	-2.92 (-3.06, -2.78)	0.36 (0.09, 0.63)	0.04 (0.03, 0.05)-0.08 (0.06, 0.10)
2014	OTR	-2.51 (-2.78, -2.24)	1.08 (0.59, 1.57)	0.03 (0.02, 0.04)-0.56 (0.24, 0.84)
2015	Disttoroad	-2.70 (-2.80, -2.60)	-0.21 (-0.33, -0.09)	0.03 (0.02, 0.05)- 0.08 (0.07, 0.09)
2016	EVI1quad	-2.63 (-2.77, -2.49)	-0.54 (-0.78, -0.30)	0.01 (0.00, 0.03)-0.09 (0.08, 0.11)
2017	Disttoroad	-2.85 (-2.95, -2.75)	-0.16 (-0.26, -0.06)	0.03 (0.02, 0.04)-0.06 (0.02, 0.04)
2018	OTR	-2.93 (-3.05, -2.81)	0.24 (0.14, 0.34)	0.04 (0.04, 0.05)-0.10 (0.08, 0.13)
2019	JTR	-2.94 (-3.04, -2.84)	0.17 (0.11, 0.23)	0.04 (0.04, 0.05)-0.14 (0.09, 0.19)
2021	disttewater	-3.07 (-3.19, -2.95)	-0.30 (-0.46, -0.14)	0.01 (0.00, 0.02)-0.06 (0.05, 0.07)

PATR= paca trap rates, OTR=ocelot trap rates, EVI2= enhanced vegetation index within 250 m buffer, HTR= human trap rates, disttoroad=distance to nearest road, EVI1quad=enhanced vegetation index within 100 m buffer with a quadratic formula, JTR=jaguar trap rates, disttewater= distance to nearest water source

S5. Covariates that affected puma occupancy (ψ), and detection (P) with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Chiquibul Forest Reserve in Belize, Central America from 2002-2003, 2006-2008. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2002	NA	NA	NA	0.75 (-0.05, 1.55)
2003	NA	NA	NA	0.79 (0.75, 0.84)
Year	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p Range (LCL, UCL)
2002	disttoroad	-5.21 (-6.77, -3.63)	-1.45 (-3.14, 0.24)	0.00 (0.00, 0.03)-0.02 (0.00,0.07)
2003	NA	NA	NA	0.21 (0.16, 0.28)

disttoroad=distance to nearest road

S6. Covariates that affected puma occupancy (ψ), and detection (P), with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Mountain Pine Ridge in Belize, Central America from 2004-2021. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2004	NA	NA	NA	0.83 (0.39, 1.00)
2005	NA	NA	NA	0.92 (0.31, 1.00)
2006	NA	NA	NA	0.86 (0.20, 1.52)
2007	CGTR	-1.14 (-.51)	0.77 (-0.72, 2.26)	0.30 (0.17, 0.42)
2008	disttowater	-0.25 (-1.54, 1.04)	-2.02 (-3.90, -0.14)	0.45 (0.36, 0.54)
2009	NA	NA	NA	0.77 (0.72, 0.83)
2010	NA	NA	NA	0.58 (0.39, 0.77)
2011	NA	NA	NA	0.84 (0.59, 1.00)
2012	NA	NA	NA	0.68 (0.39, 0.98)
2013	NA	NA	NA	0.87 (0.63, 1.00)
2014	NA	NA	NA	0.81 (0.58, 1.00)
2015	NA	NA	NA	0.63 (0.51, 0.74)
2016	NA	NA	NA	0.69 (0.64, 0.74)
2017	HTR	-0.60 (-1.80, 0.60)	-7.43 (-13.37, -1.49)	0.56 (0.49, 0.64)
2018	NA	NA	NA	0.74 (0.62, 0.85)
2019	Ungulates	0.67 (-0.19, 1.53)	2.21 (-0.30, 4.72)	0.59 (0.55, 0.64)
2020	Elevation	0.70 (-0.10, 1.50)	-1.31 (-3.90, -0.14)	0.62 (0.58, 0.67)
2021	NA	NA	NA	0.58 (0.49, 0.67)
Year	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p Range (LCL, UCL)
2004	CHCHTR	-17.58 (-26.52, -8.64)	-28.97 (-51.41, -4.85)	0.00 (0.00,0.00)-0.01 (0.01-0.03)
2005	EVI4quad	-3.97 (-5.09, -2.85)	-2.72 (-5.46, 0.02)	0.00(0.00,0.00)-0.02 (0.01,0.06)
2006	NA	NA	NA	0.01 (0.00,0.02)
2007	NA	NA	NA	0.02 (0.01,0.04)
2008	WTDTR	-3.69 (-4.20, -3.18)	0.40 (0.20, 0.60)	0.02 (0.01,0.04)-0.12 (0.06-0.22)
2009	small	-5.38 (-6.30, -4.46)	-4.25 (-6.19, -2.31)	0.00 (0.00,0.00)-0.04 (0.03,0.06)
2010	JTR	-4.59 (-5.33, -3.84)	0.49 (0.10, 0.88)	0.01 (0.00,0.02)-0.04 (0.02,0.10)
2011	EVI4	-3.49 (-4.06, -2.92)	1.87 (0.75, 2.99)	0.00(0.00,0.01)-0.05 (0.02,0.10)
2012	CGTR	-3.99 (-4.56, -3.42)	0.49 (0.16, 0.82)	0.02 (0.01,0.03)-0.08 (0.03,0.17)
2013	NA	NA	NA	0.02 (0.01,0.03)
2014	EVI1	-3.50 (-3.95, -3.05)	1.56 (0.62, 2.50)	0.00 (0.00,0.00)-0.04 (0.02,0.07)
2015	cancovst	-3.64 (-4.01, -3.27)	0.55 (0.26, 0.84)	0.01 (0.00, 0.01)-0.03 (0.02,0.06)
2016	cancovst	-3.35 (-3.62, -3.08)	0.31 (0.13, 0.49)	0.03(0.02,0.04)-0.07 (0.05,0.11)
2017	elevation	-3.60 (-3.27, -3.27)	-0.76 (-1.13, -0.39)	0.00 (0.00,0.01)-0.14(0.08,0.25)
2018	Per_can_cov	-3.67 (-4.00, -3.34)	0.52 (0.30, 0.74)	0.01(0.00,0.02)-0.09(0.06,0.13)
2019	AGTR	-3.51 (-3.78, -3.24)	0.20 (0.14, 0.26)	0.03 (0.02,0.04)-0.21 (0.14,0.31)
2020	CHCHTR	-3.40 (-3.67, -3.13)	0.30 (0.14, 0.46)	0.03 (0.02,0.05)-0.12 (0.07,0.22)
2021	disttoroadquad	-3.96 (-4.74, -3.18)	0.15 (-0.22, 0.52)	0.01 (0.00,0.08)-0.10(0.00,0.91)

disttowater= distance to nearest water source, HTR= human trap rates, ungulates= ungulate (white-tailed deer, red brocket deer, white-lipped peccary, collared peccary) trap rates, CHCHTR= Plain chachalaca trap rates, EVI4quad=enhanced vegetation index within 750 m buffer with quadratic formula, WTDTR= white-tailed deer trap rates, Small= small (0-5kg) prey (Central American agouti, Nine-banded armadillo, Ocellated turkey, Crested guan, Great curassow, Plain chachalaca) trap rates, JTR=jaguar trap rates, CGTR=crested guan trap rates, EVI1=enhanced vegetation index within 100 m buffer, cancovst=canopy cover at station, per_can_cov=percent canopy cover, AGTR=Central American agouti trap rates, disttoroadquad=distance to nearest road with quadratic formula

S7. Covariates that affected puma occupancy (ψ), and detection (P) with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Cockscomb Forest Reserve in Belize, Central America from 2012-2017, 2019. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ Covar	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2012	NA	NA	NA	0.90 (0.82, 0.99)
2014	EVI2	10.78 (-18.68, 40.24)	10.92 (-18.81, 18.81)	0.87 (0.86, 0.88)
2015	NA	NA	NA	0.94 (0.93, 0.95)
2016	NA	NA	NA	0.80 (0.80, 0.81)
2017	NA	NA	NA	0.95 (0.91, 0.98)
2019	EVI3quad	-2.19 (-6.25, 1.87)	-12.16 (-23.10, -1.22)	0.80 (0.80, 0.81)
2021	CGTR	1.71 (-0.17, 3.59)	-3.79 (-7.59, 0.01)	0.86 (0.85, 0.86)
Year	P Covar	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p range (LCL, UCL)
2012	disttoroadquad	-3.47 (-3.86, -3.08)	0.33 (0.09, 0.57)	0.03 (0.02, 0.04)-0.17 (0.11, 0.25)
2014	AGTR	-2.12 (-2.59, -1.65)	3.72 (2.13, 5.31)	0.03 (0.02,0.04)-0.14 (0.08,0.23)
2015	WLPTR	-5.19 (-6.78, -3.60)	-7.84 (-13.33, -2.35)	0.00 (0.00,0.03)-0.06 (0.04,0.08)
2016	elevation	-2.76 (-3.00, -2.52)	0.42 (-0.24, 0.60)	0.04 (0.03,0.06)-0.15 (0.11,0.20)
2017	ungulates	-3.34 (-2.77, -2.91)	-1.55 (-2.41, -0.69)	0.01 (0.00, 0.03)-0.08 (0.06-0.09)
2019	disttosettle	-2.94 (-3.04, -2.84)	0.17 (0.11, 0.23)	0.03 (0.02-0.04)-0.14 (0.11,0.19)
2021	disttoroadquad	-2.93 (-3.24, -2.62)	-0.09 (-0.33, 0.15)	0.02 (0.01,0.05)-0.08 (0.05,0.14)

EVI2=enhanced vegetation index within a 250 m buffer, EVI3quad=enhanced vegetation index at 500 m buffer with a quadratic formula, CGTR= Crested guan trap rate, disttoroadquad=distance to nearest road with quadratic formula, AGTR= Central American agouti trap rates, WLPTR= white-lipped peccary trap rate, ungulates= ungulate (white-tailed deer, red brocket deer, white-lipped peccary, collared peccary) trap rates, disttosettle=distance to nearest settlement, disttoroadquad=distance to nearest road with quadratic formula

S8. Covariates that affected puma occupancy (ψ), and detection (P), with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Central Belize Corridor in Belize, Central America from 2009-2013. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2009	NA	NA	NA	0.88 (0.39, 1.00)
2011	NA	NA	NA	0.46 (0.30, 0.63)
2012	AGTR	0.12 (-2.90, 3.14)	4.97 (-3.69, 13.63)	0.56 (0.43, 0.70)
2013	OTR	-0.51 (-1.63, 0.61)	0.96 (-0.16, 2.08)	0.46 (0.40, 0.52)
Year	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p range (LCL, UCL)
2009	disttoroad	-5.20 (-5.96, -4.44)	0.49 (0.14, 0.84)	0.00 (0.00,0.01)-0.02 (0.01,0.05)
2011	disttoroad	-4.44 (-4.44, -3.89)	0.33 (0.02, 0.64)	0.01 (0.00,0.02)-0.03 (0.02,0.07)
2012	NA	NA	NA	0.01 (0.00,0.02)
2013	disttosettle	-4.21 (-4.87, -3.54)	1.19 (0.41, 1.97)	0.00 (0.00,0.02)-0.14 (0.05,0.34)

AGTR=Central American agouti trap rates, OTR=ocelot trap rates, disttoroad=distance to nearest road, disttosettle=distance to nearest settlement

S9. Covariates that affected puma occupancy (ψ), and detection (P), with intercept and lower and upper confidence limits (Int. (LCL, UCL)), beta estimate and confidence limits (Beta Est. (LCL, UCL)), average occupancy estimates and lower and upper confidence limits (Ave. ψ (LCL, UCL)), and detection range with confidence limits (p Range LCL, UCL), in the Manatee Forest Reserve in Belize, Central America from 2019-2021. Estimates obtained from top/chosen models, run in RPresence. Supported relationships for covariates (CLs do not overlap 0) are *italicized*.

Year	Ψ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	Ave. Ψ (LCL, UCL)
2019	NA	NA	NA	0.72 (0.68, 0.76)
2020	NA	NA	NA	0.84 (0.76, 0.93)
2021	EVI5	0.66 (-1.18, 2.50)	3.76 (-1.36, 8.88)	0.88 (0.83, 0.93)
Year	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)	p Range (LCL, UCL)
2019	EVI1quad	-6.57 (-12.65, -0.49)	-3.06 (-7.72, 1.60)	0.00 (0.00, 0.46)-0.09 (0.05, 0.16)
2020	disttowater	-5.29 (-6.43, -4.15)	-3.30 (-4.93, -1.67)	0.00 (0.00, 0.00)-0.10 (0.06, 0.16)
2021	disttosettle	-2.97 (-3.22, -2.72)	-0.48 (-0.77, -0.19)	0.02 (0.01, 0.04)-0.08 (0.05, 0.13)

EVI5=enhanced vegetation index within 1000 m buffer, EVI1quad=enhanced vegetation index within 100 m buffer with a quadratic formula, disttowater= distance to nearest water source, disttosettle=distance to nearest settlement

III. Assessing changes in landscape and biotic factors over 20 years driving puma distribution through multi-season occupancy modeling within 5 sites in Belize, Central America.

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Abstract

Understanding long-term puma distribution and dynamic processes affected by changes in landscape features, habitat, and biotic factors can inform land management decisions since pumas influence, and are influenced by, sympatric carnivore populations, lower trophic levels, and habitat. While pumas (*Puma concolor*) are well studied in North America, there is relatively scant information on their habitat use in the tropics and there are no multi-season occupancy studies. Using microhabitat (e.g. tree/understory density, canopy cover, etc.), macrohabitat (enhanced vegetation index, distances to water, settlements, roads, etc.), and biotic (prey and sympatric species trap rates) covariates, we used single-species, multi-season occupancy modeling in the first and fourth parameterizations to explore factors influencing puma distribution and the dynamic processes driving long term changes across the country of Belize. We collated camera trapping data across 5 protected areas of varying habitats (interior to coastal habitat, pine to tropical broadleaf forest, low to high elevation) and management, culminating in 20 years, and 2,093 camera stations covering ~4,000 km² of private and public protected areas. Occupancy was generally high and ranged from 0.55-0.90 while daily detection ranged from 0.02-0.06, colonization ranged from 0.31-0.70, and extinction ranged from 0.08-0.39 across the landscapes over time. Top models indicated that mostly macrohabitat influenced occupancy and detection parameters while biotic factors influenced colonization and extinction. Generally, occupancy was positively affected by denser vegetation and tree cover, supporting puma ambush style hunting, and lower perceived risk due to more cover from humans. Colonization was the most strongly positively affected by increased deer activity, a known preferred prey species. Occupancy and colonization were usually higher in tropical broadleaf forest sites compared to the tropical pine forest habitat and compared to the broadleaf habitat with higher human impacts. Due to relatively high occupancy and colonization across areas, and the occasional positive influence of jaguar trap rate on pumas, spatial coexistence is occurring, thus supporting the use of the jaguar as an umbrella species for management of sympatric felids. However, the puma's generalist lifestyle allows it to shift distribution throughout the years, so it is important to study less plastic species of conservation concern such as the threatened Baird's tapir, crested guan, black howler monkey, and smaller felids, the margay and jaguarundi, using occupancy, co-occurrence, and density modeling to further understand population dynamics on the landscape and further test the effectiveness of the umbrella species concept.

Keywords: multi-season occupancy, detection, covariates, maximum likelihood estimation, competition, niche partitioning, *Puma concolor*, Belize

Potential Journals: Wildlife Research, Wildlife Biology, Journal of International Wildlife Law and Policy, Journal of Fish and Wildlife Management, Journal of Animal Ecology, Mammal Review, Journal of Zoology, Journal of Wildlife Management

Introduction

Understanding long-term changes in landscape features, habitat, and biotic factors that affect plant and animal distributions is perhaps the greatest tool in combating threats to important ecosystems and wildlife therein (Lindenmayer et al. 2012, Roseblatt et al. 2014). Conservation efforts aim to create a sustainable future for wildlife species, and thus we need tools that can better gauge the efficiency and effectiveness of such efforts. Through multi-year or multi-season modeling of target wildlife species across large landscapes, not only can we determine demographic processes such as colonization and extinction (MacKenzie et al. 2017), we can gain further insight by linking changing features of climate, human encroachment, habitat, and competing species, to these dynamic processes to understand what promotes species persistence across ecosystems (Pereira et al. 2010, Parmesan et al 2011, Bellard et al 2012, Rybicki and Hanski 2013).

While multi-year surveys and analyses are necessary to understand dynamic process driving species persistence (Lindenmayer 2012, Dickman 2013), there is a lack of long-term data on most species of conservation concern mostly due to lack of funding for rigorous monitoring programs. Additionally, this problem is compounded when studying elusive, wide-ranging species in developing nations, and especially in the tropics, which harbor high-levels of biodiversity yet are poorly studied (Dickman 2013, Beaudrot et al. 2016). However, it is vital to close this knowledge gap in dynamic processes as tropical forest ecosystems, especially in Latin America, are an integral part of biodiversity conservation, carbon sequestration, ecotourism,

acquisition of resources, culture (CEPF accessed 2021) and are rapidly being altered, diminished, and destroyed due to increasing human populations and resource demands (Hansen et al. 2013, Ripple et al. 2014). Forests are converted to agricultural, livestock, and urban lands leading to habitat loss, fragmentation and degradation, increases in bushmeat hunting and expansion of exotic species (Laurance 2015, Farris et al. 2017), which increases potential for negative human-wildlife interactions (Ripple et al. 2014).

To develop conservation action plans, scientists, managers, and local communities often lean on shorter-term analyses that represent only a snapshot in time, and do not have the capability to account for dynamic processes. While single year estimates of population parameters are important to establish a baseline occupancy or density for example, they can potentially lead to misinformed management plans by failing to identify impending population declines (Krauss et al. 2010; Sales et al. 2015) or failing to document ongoing declines (Farris et al. 2017). Furthermore, conservation management plans in the tropics tend to focus efforts on single target species like top felids because such charismatic megafauna garner conservation attention as flagship species (Simberloff 1998) and they have large spatial requirements and exert top-down control in ecosystems through maintaining biodiversity and structuring ecological communities (Soule et al. 1999, Terborgh 2001, Terborgh et al. 2015). The umbrella species concept (Fleishman et al. 2000) has been used as a common management strategy to combat high extinction rates and climate change accelerated threats, assuming that protecting land for species with large area requirements will protect all others within that range (Maslo et al. 2016).

Felids tend to disappear first due to their large home ranges, naturally low densities, and conflicts with humans. For instance, as the human population has grown, landscapes have been

altered, prey availability has declined, and hunting of pumas has led to widescale decline reducing range by two-thirds of its original size (Sunquist and Sunquist 2002). This loss is exacerbated by climate change in tropical areas through a combination of increasing frequency and intensity in weather patterns like hurricanes and a shift in seasonality, with longer dry seasons and shorter rainy seasons (Pascale et al. 2015, Knutson et al. 2019), thus negatively affecting tropical predator and prey populations. Losing biodiversity in biodiversity hotspots can be detrimental to ecosystem function and stability needed to provide sustainable future resources for both people and animals, making these areas targets for conservation.

In the Neotropics, the jaguar (*Panthera onca*) is typically used as an umbrella species however, there are mixed results across the literature on whether this is an efficient strategy (Schoener 1974, Roberge and Angelstam 2004, Branton and Richardson 2014) due to interspecific competition that can result in negative distribution and abundance relationships between top- and meso-predators (Crooks and Soule 1999, Ritchie & Johnson 2009). Therefore, using the jaguar as an umbrella species can be problematic for the puma where potential for interspecies conflict is high due to similarities in diet, hunting strategies, and size (Donadio and Buskirk 2006). Pumas, as well as jaguars, use ambush, stalking behaviors to hunt opportunistically, correlating with their preference for habitat with concealment cover (Emmons 1987, Sunquist and Sunquist 2002).

Due to pumas' generalist lifestyle (Logan and Sweanor 2004), they can shift movement, diet, and temporal behaviors to possibly avoid the dominant jaguar enabling coexistence. For instance, while some studies have shown a large degree of dietary overlap (Iriarte et al. 1990, Harmsen et al. 2009), Karandikar et al. (2022) found that despite body size similarities, pumas chose more medium sized prey over larger prey species as they are more energetically profitable

according to optimal foraging theory and possibly avoid competition over prey species of jaguars. Spatially, pumas occupy a myriad of habitats; studies from the Nearctic suggest that pumas commonly prefer dense vegetation, higher elevation, and rugged terrain, which most likely correlates with the pumas' stalk and pounce (ambush) type hunting strategy (Beier et al. 1995, Sweanor et al. 2000). However, due to their adaptability, pumas may avoid higher quality habitat preferred by jaguars (Harmsen et al. 2009, Romero-Munoz et al. 2010). For instance, Sollmann et al. (2012) found that jaguars primarily stayed within the protected area, Emas National Park in Brazil, while the puma would go outside the boundaries to search for resources. Romero-Munoz et al. (2010) also found that pumas could avoid competition via temporal partitioning. But these studies do not directly incorporate dynamic long-term processes such as colonization and extinction of sites due to difficulties associated with felids' elusive, wide-ranging nature (Crawshaw and Quigley 1991, Noss et al. 2006, Harmsen et al. 2011) and lack of long-term data on multiple predators simultaneously.

Since conservation measures tend to focus on the jaguar, pumas are generally more understudied within tropical forest ecosystems. For example, we found no multi-season occupancy analyses conducted on pumas in the tropics. However, we did find 11 single-season occupancy studies on tropical pumas (Chapter 2), many of which assessed overlap with jaguars to better understand interspecific competition (Avila et al. 2020, Boron et al. 2020; Pônzio, M do C., et al. 2023), rather than address puma status and conservation. Thus, there is a lack of species-specific knowledge on puma occupancy and especially changes in occupancy over time.

Our goal was to provide the first multi-year puma occupancy assessment in the Neotropics. We used a multi-season occupancy modeling framework to analyze data from ongoing remote camera-trap surveys and from collaborative efforts among multiple stakeholders. This

culminated in up to 20 years of data across 5 areas (over 4,000 km²) in Belize, Central America making it one of the longest running and largest scale camera trapping projects globally. We aimed to assess important microhabitat features collected manually around camera stations, macrohabitat factors extracted from geographic information systems, and biotic factors such as trap rates of co-occurring species, that influenced occupancy. Our multi-season framework enabled us create “memory” within the system to elucidate whether changing micro-habitat, macro-habitat, and biotic factors could influence underlying dynamic processes of occupancy, detection, and local colonization and extinction over time (Mackenzie et al. 2018). Our objectives were to 1) estimate occupancy over time and evaluate changes in occupancy, local colonization, and extinction across multiple sites 2) evaluate the influence of microhabitat, macrohabitat, and biotic factors on these dynamic processes and 3) compare our results to our previous analysis using single season occupancy models to determine congruence between methods and evaluate precision and 4) evaluate how knowledge of parameter dynamics can influence long-term management. Filling this knowledge gap is integral to making well-informed management decisions to determine puma population status over time and to clarify whether jaguars are an effective umbrella species for sympatric felid species.

Methods

Study area

In our previous single-season analysis (Chapter1) we were able to use 7 different study sites, however two of those sites only had 1 year of data and hence, we were able to include 5 field sites across the country of Belize, Central America (Figure 1). These sites included the Greater Belize Maya Forest consisting of Rio Bravo La Milpa, Rio Bravo Hill Bank, Gallon Jug

Estates, and Belize Maya Forest that we collectively call the Greater Belize Maya Forest (2,543 km²), Chiquibul Forest Reserve (CFR-598 km²), Mountain Pine Ridge Forest Reserve (MPR-430 km²), Cockscomb Basin Wildlife Sanctuary (488 km²), and Manatee Forest Reserve (MFR-469 km²) (Figure 1; Table 1). The GBMF consist of moist broadleaf forest areas, pine savannah, and wetlands (Rio Bravo 2016, Laguna Seca 2020), Chiquibul Forest Reserve consists of variants of lowland and submontane tropical broadleaf forest (Penn et al. 2004), Mountain Pine Ridge consists of tropical pine forest (Kesler et al. 1974), Cockscomb consists of tropical rainforest (Harmsen et al. 2017), and Manatee Forest Reserve consists of a variety of broadleaf and pine trees, shrubs, grasses (Guy and Eitniear 2012). All sites are on private and/or protected lands, some of which allow sustainable extraction of timber or have active farming/ranching and tourism, and some of which do not. These areas contain a wide array of fauna and flora species. More details on the sites can be found in Chapter 1.

Photographic sampling

We used camera trapping, a standard, non-invasive wildlife research technique to gather data on puma occurrence across the landscape (Kelly et al. 2012). Our original camera trapping grid design was intended for jaguars, setting camera traps approximately 30-40 cm above the ground and on average at 1.5-3 kilometers intervals based on the smallest estimated jaguar home range in Belize of 10 km² to ensure that no home range of a jaguar can be located entirely between cameras (Rabinowitz and Nottingham 1986). Fortunately, this design is appropriate for pumas as they are similar enough in body size (Harmsen et al. 2011). Cameras were set on trails, game trails, old logging roads, and active logging roads to improve detection rates since cameras originally placed off trails in the early years of this project resulted in capture probabilities of felid captures around zero (Kelly et al 2012). Most stations had two opposing cameras to capture

both sides of jaguars for positive identification, but all other animals (including pumas) were captured as well. Across sites and surveys cameras operated 24 hours a day for ~3 months with no bait or lure used. All sites were set up for a minimum of 3 years, and most study sites expanded over time to increase sample size (at least 30 camera stations per grid) (Table 1).

Multi-season occupancy

We used single-species, multi-season occupancy modeling to assess micro-habitat, macro-habitat, and biotic factors influencing puma distribution across the landscape over a minimum of 3 and maximum of 20 years, depending on site. Multi-season refers to multi-year in our study. Multi-season occupancy modeling extends single season modeling by linking together each survey season (i.e. year) thus incorporating changes in covariates throughout years into the estimates (MacKenzie et al. 2003). This enables us to estimate and incorporate dynamic processes of local colonization and extinction from year to year, in addition to site occupancy and probability of detection, while also incorporating covariates on all of these parameters (Mackenzie et al. 2006). Local colonization refers to the probability that an unoccupied site (i.e. camera station) in one year will become occupied in the next year, and local extirpation is the probability that a site that was occupied in one year will become unoccupied in the following year (MacKenzie et al., 2006). This approach allows occupancy, detection, colonization, and extinction to change between years but within years the parameter state cannot change. For example, a species migrating out of the study area during a survey violates the geographic closure. In this way multi-season occupancy models are equivalent to robust design mark-recapture models that estimate detection and abundance within year, and survival from one year to the next (Pollock 1982).

There are 4 parameterizations of multi-season occupancy models and we used the first and fourth parameterizations, which vary in what parameters are estimated or derived (MacKenzie et al. 2006). The first parameterization is the more commonly used in the multi-season framework (MacKenzie et al. 2006) and it uses a first order Markov process, which accounts for occupancy changes from previous seasons such that occupancy in the current season relies on occupancy from the previous season following this formula:

$$\psi_{t+1} = \psi_t (1 - \epsilon_t + (1 - \psi_t) \gamma_t)$$

ψ is occupancy, ϵ is extinction of previously occupied sites, γ is colonization at previously unoccupied sites. This modeling focuses on parameters gamma and epsilon, the underlying dynamic processes, and estimates detection (p) each year and estimates occupancy in each current year to derive occupancies for subsequent years by the formula above. For example, the proportion of sites occupied in season 2 is derived from the proportion of sites that were occupied but failed to go extinct in season 1, plus the proportion of empty sites in season 1 that became occupied (Donovan and Hines 2007). Thus, each year over multiple years, occupancy depends on the previous year. The benefit of this parameterization is that you can constrain ψ_1 , ϵ , γ , and p to be functions of covariates to explore their impacts on different parameters.

The 4th parameterization modeling framework is similar to the first in that it estimates ψ_1 only, but it forces extinction to be equal to 1 minus colonization ($\epsilon_1 = 1 - \gamma_1$) and thus rearranges the equation used in the first parameterization and not allowing covariates on extinction. This method still explicitly incorporates gamma, γ , and epsilon, ϵ , however they are the parameters that are only calculated for the first season to allow for occupancy and detection to be calculated for each season (MacKenzie et al. 2006). We tried this parameterization because it had fewer parameters, and we thought might lead to better model convergence with using large numbers of covariates.

For both modeling strategies, we incorporated covariates on the parameters, where possible. As in single-season occupancy modeling, the same holds true for multi-season occupancy modeling, where incorporating covariates in relation to the locations of target species across camera stations can clarify factors influencing parameters and is likely to result in more precise estimates (MacKenzie et al. 2006). In first parameterization, covariates were placed on γ and ϵ and not ψ and p . While in the fourth parametrization γ and ϵ are explicitly accounted for in the models, however covariates cannot be placed on them because the probability equation underlying the modeling was reparametrized to explicitly estimate ψ so only detection probabilities (p) and the proportion of sites occupied (ψ) can hold covariates. Accounting for changes across years can reveal more about dynamic systems that exhibit changes between seasons and is ideal for long-term monitoring data sets (Donovan and Hines 2007).

We used remote cameras as detectors and then created detection histories for pumas at each camera station to create a matrix of detections and non-detections (1s and 0s respectively) for each day a given survey at each site. We used these detection histories combined with covariates to estimate four population parameters: detection probabilities (p) and the proportion of sites occupied (ψ), colonization (γ), and extinction(ϵ); all of which are bounded by 0 and 1, with 0 being never detected, occupied, colonized, or gone extinct, and 1 being 100% detection, occupancy, colonization, or extinction at a site.

Covariates

Covariates were site-specific and averaged over the survey season to give one estimate per site. We z-scored all continuous variables throughout all years together across all study sites combined to standardize them to be centered on zero to improve maximum likelihood convergence for models (Ragazzini and Zadeh 1952) and to compare the magnitude of beta (β)

coefficients across all sites. Correlated variables ($|r|=0.7$) via Pearson correlation matrix were not used in the same model (see supplemental materials Figure S2).

Micro-habitat and macro-habitat covariates

In our previous analysis (Chapter 2), we found the only habitat variables collected manually at the camera stations themselves (microhabitat covariates) were canopy cover at the station or in a 100 m radius. Additionally, another study found road width to influence felid species (Davis et al. 2011). Thus, we only included canopy cover and road width as microhabitat covariates.

Macrohabitat covariates were calculated from GIS layers obtained from the Biodiversity and Environmental Resources Data System of Belize website (BERDS 2016), maintained by Jan Meerman and derived GIS products from MODIS (USGS-MODIS 2021), for all sites and survey years. We used ArcGIS Pro to estimate the following macro-habitat covariates: distance from each station to water sources, human settlements, roads, and logging blocks as well as enhanced vegetation index (EVI) which is a measure of greenness that eliminates noise such as humidity making it better for the tropics and presence of fire. For EVI and presence of fire, we only included layers within the survey period. We calculated distance to roads and settlements and EVI using both a linear and quadratic functions. For example, pumas might choose habitat or be detected more initially, as vegetation gets denser as it is beneficial for hunting behavior (Ironsides et al. 2017), but then might decrease in occupancy and/or detection if the vegetation gets too dense making it harder to see prey or be seen on camera.

To better understand the influence of spatial scale, we also created circular buffers surrounding each camera trap at 100 m, 250 m, 500 m, 750 m, and 1,000 m to link GIS layers containing the enhanced vegetation index (EVI) to the buffers. For the 100 m and 250 m buffer, we had to use spatial interpolation within GIS to set the original resolution for EVI layers,

231.65 m, to 50 m to create an artificially smaller resolution by using surrounding cells whose center fell within the buffer and averaging those cells.

Biotic covariates

Trap rates, an index of activity, were used as biotic covariates. We calculated trap rates at each station for each survey time by dividing the number of capture events by the total number of trap nights. A capture event is delineated by 30-minute intervals after initial capture unless there are distinctly different individuals captured within that 30-minute period and a trap night is a 24-hour period the camera is functioning (Di Bitetti et al. 2006). We calculated trap rates for sympatric predators (jaguars, ocelots), to better understand coexistence or competition on the landscape. We calculated trap rates for prey species (white-tailed deer [*Odocoileus virginianus*], red brocket deer [*Mazama temama*], white-lipped peccary [*Tayassu pecari*], collared peccary [*Dicotyles tajacu*], Central American agouti [*Dasyprocta punctata*], paca [*Cuniculus paca*], nine-banded armadillo [*Dasypus novemcinctus*], plain chachalaca [*Ortalis vetula*], great curassow [*Crax rubra*], crested guan [*Penelope purpurascens*], ocellated turkey [*Meleagris ocellata*]), as they are potentially important prey resources (Karandikar et al. 2022). Prey were also grouped into size categories (small <5 kg, medium 5-10 kg and large >10kg) as that is an important factor for hunting (Karandikar et al. 2022). They were also grouped by similar species (i.e. red brocket and white-tailed deer combined) for one deer estimate. Finally, we calculated human rap rates (researchers, tourists, loggers, workers, poachers, unknown) since the areas vary in human use.

These biotic covariates were placed individually and in groupings on parameters ψ and p in multi-season alternative occupancy models to better understand sympatric species and prey availability interplaying with puma space use and detection on the landscape. For instance, jaguar trap rates could shift or lessen space use or decrease detection due to avoidance behavior (Donadio and Buskirk 2011).

Biotic covariates were also placed on parameters gamma and epsilon in multi-season first parameterization occupancy models to better understand sympatric species and prey availability interplaying with colonization and extinction across years on the landscape. For instance, increasing deer activity throughout years across the landscape could increase colonization due to more abundant prey as seen in optimal foraging theory (Cooley et al. 2008). Similarly, increasing agouti trap rates could increase colonization throughout years (Krandikar et al 2022). Conversely, lowered prey activity could increase extinction.

Maximum Likelihood Estimation

We created *a priori* models by considering the ecology of pumas and the covariates that might influence occupancy, detection, colonization, and extinction, as well as the scale at which the influence might extend by defining appropriate buffer sizes (see supplemental materials Table S2). Since we already created *a priori* models for single season models (see Chapter 1 Supplement S1) we focused our *a priori* on expectations for extinction and colonization. For example, we expected intermediate range of EVI to positively affect colonization (γ), but too dense of ranges of EVI could increase extinction (ϵ). For both parameterizations, we first added covariates to detection (p) while keeping proportion of sites occupied (ψ) constant. Similarly, for first parameterization, we first added covariates to colonization (γ) while keeping extinction (ϵ) constant. We then ran those models through the R package Rpresence, version 4.0.4 (R Core Team 2021) and ranked models using Akaike Information Criterion (AIC) to determine the best model for p and separately the best model for γ . If there were competing models (i.e. those within two delta AIC) we considered model weights and model likelihoods (Burham and Anderson 2002) to choose the best model. After determining the best model for p and γ , we placed covariates on ψ and separately for ϵ and followed the same AIC approach to determine

the best models for ψ . We then created post hoc models with covariates that emerged from top models for parameters p and ψ and for parameters γ and ϵ to ultimately determine the best overall model. For instance, if covariates were not correlated and were within 2 $\Delta AICs$, we created post-hoc models with interactive and additive effects using those top and competing covariates.

Results

Overall, we used 20 years of data, spanning over 3,750 km² across 5 areas in Belize, with a total of 2,093 camera traps, accumulating 149,639 trap nights (Table 1). The puma, the target species and sympatric species, the jaguar and ocelot, were “captured” within all study areas. However, not all target prey species were captured within all study areas. Each field site was modeled separately using all available years per site.

Single-species, multi-season, fourth parameterization

Generally, results are from top models that achieved convergence in the MLE framework (Table 2). Occupancy of pumas was affected by 1 micro-habitat, 3 macro-habitat, and 3 biotic covariates. Occupancy in the Greater Belize Maya Forest, Chiquibul Forest Reserve, Mountain Pine Ridge Forest Reserve, Cockscomb Basin Wildlife Sanctuary, and Manatee Forest Reserve was respectively affected by EVI within a 750 m buffer with a quadratic relationship ($\beta = -0.10$; LCL = -0.14; UCL = -0.06), positively by jaguar trap rates ($\beta = 0.59$, LCL = -0.37, UCL = 1.55), positive by canopy cover at station ($\beta = 0.34$, LCL = 0.14, UCL = 0.54), additive effect of distance to settlement and armadillo trap rates ($\beta = -1.14$, UCL = -0.04, UCL = 2.45), and an interactive effect of distance to water and jaguar trap rates ($\beta = 1.20$; LCL = -0.17 UCL = 2.57) (Tables 2 and 3). However, the only supported covariates (CIs did not cross zero) were in the GBMF where

puma occupancy was highest at intermediate EVI, in the MPR where puma occupancy increased with canopy cover, and in CBWS where occupancy increased further from settlements (Figures 2A and 3). Occupancy (Ψ) ranged from 0.24-0.93 across all sites with averages ranging from 0.85-0.92 in the GBMF, 0.43-0.86 with an average of 0.55 in the CFR, 0.60 with an average of 0.55 in the MPR, 0.66- 1.00 with averages ranging from 0.86-0.91 in CBWS, 0.07 -1.00 with averages ranging from 0.74-0.75 in MFR (Figure 4, Tables 4 and 5).

Detection was affected by 1 micro-habitat, 2 macro-habitat, and 2 biotic covariates. All covariates had supported effects (Figure 2B). In the GBMF, CFR, MPR, CBWS, and MFR detection was respectively influenced by EVI within a 250 m buffer with a quadratic relationship ($\beta = -0.03$, LCL=-0.04, UCL=-0.02), positively by crested guan trap rates ($\beta = 0.21$, LCL= 0.07, UCL=0.35), positively by canopy cover at the station ($\beta = 0.22$, LCL=0.14, UCL=0.30), positively by elevation ($\beta = 0.23$, LCL=0.15, UCL=0.31), and positively by jaguar trap rates ($\beta = 0.25$, LCL=0.13, UCL=0.37) (Table 3; Figures 2B and 5). Puma daily detection ranged from 0.03-0.06 with an average of 0.05 in the GBMF, 0.02-0.07 with an average of 0.021 in the CFR, 0.03-0.06 with an average of 0.03 in the MPR, 0.04-0.09 with an average of 0.058 in CBWS, 0.03-0.10 with an average of 0.040 in MFR (Figure 6, Tables 4 and 5).

Colonization ranged from 0.34-0.93 with an average of 0.90 in the GBMF, 0.43-0.87 with an average of 0.57 in the CFR, 0.55 with an average of 0.55 in the MPR, 0.66- 1.00 with an average of 0.88 in CBWS, 0.09-1.00 with an average of 0.75 in MFR (Tables 4 and 5). Epsilon ranged from 0.07-0.66 with an average of 0.10 in the GBMF, 0.13-0.57 with an average of 0.43 in the CFR, 0.20-0.55 with an average of 0.47 in the MPR, 0.00- 0.34 with an average of 0.12 in CBWS, 0.00-0.91 with an average of 0.25 in MFR (Tables 4 and 5).

Single-species, multi-season, first parameterization

Puma occupancy ranged from 0.16-0.95 in the GBMF, 0.76 in the CFR, 0.22-0.88 in the MPR, 0.77-0.99 in CBWS, 0.48-0.90 in MFR (Table 4). Averaged occupancy estimates were 0.89 in the GBMF, 0.76 in the CFR, 0.50 in the MPR, 0.88 in CBWS, 0.77 in the MFR (Table 5). Puma daily detection was 0.05 in the GBMF, 0.02 in the CFR, 0.03 in the MPR, 0.06 CBWS, 0.04 in MFR (Tables 4 and 5).

Colonization of pumas was affected by 1 macro-habitat and 3 biotic covariates. Colonization (y) in the GBMF, CFR, MPR, and MFR was respectively affected by EVI within a 100 m buffer ($\beta = 0.39$, UCL=0.01; LCL=0.78), agouti trap rate ($\beta = -4.23$, LCL=-15.05, UCL= 6.59), deer trap rate ($\beta = -2.26$, LCL=-3.67, UCL= -0.85), and deer trap rate ($\beta = 135.90$, LCL=89.04, UCL= 182.76) (Table 3). For supported covariates (CIs do not cross zero), in the GBMF as EVI increased puma colonization increased, in the MPR, puma colonization decreased as deer activity increased but this effect was weak, and in the MFR, colonization increased strongly as deer activity increased (Figures 7A and 8). Puma colonization(y) ranged from 0.15-0.95 with an average of 0.70 in the GBMF, 0.00-0.75 with an average of 0.54 in the CFR, 0.00-0.42 with an average of 0.31 in the MPR, 0.59 in CBWS, 0.00-1.00 with an average of 0.64 in MFR (Figure 9; Tables 4 and 5).

Extinction of pumas was affected by 2 macro-habitat and 4 biotic covariates. Extinction in the GBMF, CFR, MPR, CBWS, and MFR was respectively affected quadratically (positively) by EVI within a 500 m buffer ($\beta = 0.32$, LCL=0.15, UCL=0.49), agouti trap rate ($\beta = 3.49$, LCL=-5.94, UCL= 12.92), additive effect of collared peccary and rodents ($\beta = -1.78$, LCI=-3.67, UCI= 0.09), EVI within a 500 m buffer with a negative quadratic relationship ($\beta = -4.81$, LCL=-10.71, UCL= 1.09) and was constant (Table 3). None of these relationships were supported as the CIs

overlapped zero (Figure 7B). Puma extinction (ϵ) ranged from 0.05-0.94 with an average of 0.08 in the GBMF, 0.20-1.00 with an average of 0.39 in the CFR, 0.00-0.40 with an average of 0.32 in the MPR, 0.00-0.18 with an average of 0.08 in CBWS, and 0.17 in MFR (Tables 4 and 5).

In the GBMF, CBWS, and MFR, colonization was always much higher than extinction indicated that if a site was unoccupied in one year – it was highly likely to become occupied in the following year, although CBWS has large CIs (Figure 9). The CFR had variable rates and had CIs from 0-1 in several instances, while the MPR had similar colonization and extinction rates that hovered around 50% (Figure 9).

First versus fourth parameterization

For multi-season fourth and first parameterization averages, there were no significant differences between estimates of parameters ψ ($p=0.38$, test stat=-0.33), p ($p=0.33$, test stat=-0.47), γ ($p=0.06$, test stat=1.74), and ϵ ($p=0.26$, test stat=0.66) in the GBMF, CFR, MPR, CBWS and MFR, respectively (Figure 10). However, trends show lower estimates on γ and ϵ in the first parameterization where covariates are placed directly on the parameters. (Figure 10).

Single versus multi-seasons occupancy

Multi season occupancy estimates were less variable and more precise than single season estimates, especially for the GBMF and the MPR (Figure 11). They were also less variable for Cockscomb and the MFR, but less precise. For the Chiquibul multi-season estimates were lower and less precise (Figure 11).

Discussion

We used multi-season occupancy modeling over multiple years across 5 sites to better understand the utility of estimating dynamic processes that capture changes in occupancy while

investigating factors influencing puma persistence. This is the first study we found to use multi-season occupancy modeling for pumas in the Neotropics. Puma occupancy was notably high and stable over time within most sites, although it did vary across habitat types and was lower in areas more heavily human dominated or in more atypical tropical pine forest (MPR) indicating that pumas prefer areas of broadleaf habitat within the neotropics, possibly due to more abundant water sources, vegetation structure, and prey. However, persistence in these more atypical and human dominated landscapes indicate pumas are able to adapt outside their preferred areas and these areas are still important for connectivity. Local colonization was higher than local extinction in all sites except the MPR where pumas appeared to shift distribution spatially across years. This micro-scale shifting resulting in similar annual colonization and extinction rate, combined with occupancy consistently over 50% exemplifies pumas' plasticity and ability to utilize additional habitat types. CFR had highly variable colonization and extinction rates, likely due to low sample sizes at that site due to stolen camera stations.

Occupancy and detection

Using the fourth parameterization, for occupancy throughout all sites, there was only 1 microhabitat, 3 macrohabitat, and 3 biotic covariates in all top models. One site had microhabitat, 3 sites had macrohabitat and 3 sites had biotic covariate effects on occupancy. For detection throughout all sites, there was 1 microhabitat, 2 macrohabitat, and 2 biotic covariates across top models. One site had microhabitat, 2 sites had macrohabitat, and 2 sites had biotic covariates that affected detection. Based on *a priori* models and hypotheses for occupancy covariates, we were correct 1 out of 1 time for microhabitat, 2 out of 3 times for macrohabitat, and 1 out of 3 times for biotic covariates. As for detection covariates, we were incorrect for microhabitat, correct for 2 out of 2 times for macrohabitat, and 1 out of 2 times for biotic covariates. Overall, macrohabitat covariates were the most influential on puma occupancy and

detection, similar to our findings from single season modeling (Chapter 2). We generally found similar effects of covariates and similar trends in our single season occupancy (i.e. year to year snapshots) as our long-term, multi-season occupancy modeling results, corroborating our previous results and signifying that pumas within these public and private protected areas appear widespread and stable over time.

The GBMF and CBWS had the highest occupancy estimates followed by MFR. MPR and CFR had the lowest occupancy however pumas still used over 50% of the landscape even in these sites. The first parameterization resulted in similar estimates of occupancy as the fourth. Occupancy was higher in GBMF at intermediate EVI, peaking at EVI of around 0.6 (range 0-1), but this effect was somewhat weak, while the positive influence of canopy cover was stronger in the MPR where there is a more open habitat. These results coincide with other puma studies including from our single season occupancy analysis that stress the importance of habitat cover throughout their range, because it promotes preferred prey, and puma hunting and caching behavior (Beier et al. 1995, Sweanor et al. 2000, Gray et al. 2016). Interestingly, both GBMF and MPR allow extraction of timber, yet human activity did not appear to negatively influence pumas in top models. The GBMF has some of the highest occupancy values indicating that well-protected, broadleaf habitat, despite sustainable logging, promotes puma space use across this landscape suggesting that pumas can occupy these areas and the sustainable extraction of resources can be compatible with puma conservation. The MPR is a unique tropical pine habitat (Davis et al. 2011) with the lowest average occupancy, yet pumas still use over 50% of the landscape and occupancy has remained stable over 20 years, potentially resulting from a less productive habitat type, rather than logging impacts, as has been suggested by other studies (Hutchison 1976, Colatski 2011).

Daily detection was low ranging from 0.00-0.10 throughout all years and sites and was affected by 1 microhabitat, 2 macrohabitat, and 1 biotic covariates. As canopy cover increased, detection increased in the MPR, which was expected as thicker areas could funnel pumas in front of cameras and cause more movement due to less perceived risk (Solloman et al. 2015) and allow unrestricted movement due to lower perceived risk (Riley et al. 2021). Puma occupancy increased with elevation in Cockscomb, and this corroborates other research on GPS collared pumas in the area that showed they frequented the mountain sides of basin the rather than the flat basin itself (Harmsen, unpublished data). This is in line with US studies showing pumas move through rugged mountainous terrain (Dunford and Marks 2019). Additionally, there are many water sources in CBWS, and it receives the most rain of all of our study areas annually (2500 – 4000 mm), causing seasonal flooding of lower-lying areas, which likely results in pumas frequenting higher, rugged terrains that they are ecologically adapted use. Surprisingly, in the Manatee Forest Reserve, puma detection increased as jaguar activity increased, perhaps due to following signs such as scat, scent, or markings to key in on prime habitat or prey (Solloman et al. 2015). Several other occupancy studies have found positive associations between pumas and jaguars (Harmsen et al. 2009, Davis et al. 2011, Gutierrez-Gonzalez and Lopez-Gonzalez 2017). This is further support that the jaguar and puma can coexist on the landscape and that current wildlife management based on the jaguar as the umbrella species appears beneficial for puma use of such areas.

Colonization and extinction

Using the first parameterization, for colonization throughout all sites, there were 0 microhabitat, 1 macrohabitat and 3 biotic covariates in all top models. One site had macrohabitat covariates and 3 sites had biotic covariates that affected colonization. For extinction throughout

all sites, there were 0 microhabitat, 2 macrohabitat, and 3 biotic covariates in all top models, but no covariates were supported. Based on *a priori* models and hypotheses for covariates affecting colonization, we were correct 1 out of 1 times for macrohabitat, and 1 out of 3 times for biotic covariates. Overall, biotic covariates were the most influential on puma colonization.

Colonization increased in previously unoccupied areas as EVI increased within 100 m around the station in the GBMF. The small scale EVI of 100 m around the stations suggests that pumas were colonizing these areas at a fine scale potentially for better hunting cover, and a higher probability of prey species being present (Donadio & Buskirk 2006). By far the strongest influence on puma colonization occurred in the Manatee Forest Reserve where colonization rate strongly increased as deer activity increased. Pumas are known as deer specialists, capitalizing on a larger preferred prey species (Polisar et al. 2003, Karandikar et al. 2023). Other studies justify puma habitat preference by linking it to prey availability (REFS), but our results explicitly link deer activity explicitly to pumas' movement into such areas, indicating how influential prey, especially deer, are on puma distribution, and suggesting the importance bottom-up control in driving puma space use rather than top down control from sympatric carnivores.

The MPR, with its high local extinction rate, lower occupancy and colonization rates, is a dynamic ecosystem that has mostly pine forest, some typical broadleaf jungle in riverine areas, and also experiences frequent fires especially in the dry season (Hutchinson 1976) changing habitat structure. This combined with sustainable logging and creation of roads has led to changes throughout the landscape that could contribute to the constantly shifting dynamics of puma distribution in the MPR, which can also be seen in yearly single-season occupancy heat maps. The changes in distribution highlight puma plasticity and generalist ecology allowing puma occupancy to remain stable, albeit at lower occupancy, even in this changing environment

(Donadio and Buskirk 2006) perhaps adhering to optimal foraging theory (Pyke 2010) where they can shift their locations in response to dynamic annual habitat changes to survive.

Multi-season modeling comparison of first and forth parameterization

Despite different parameterizations of multi-season occupancy models (MacKenzie et al. 2006), the long-term trends do not differ between the two analyses. Allowing covariates to be placed on parameters ψ and p in fourth parameterization allows us to estimate occupancy throughout all years, while still accounting for dynamic processes. Additionally, placing covariates on parameters γ and ϵ in first parameterization allows us to explicitly examine the driver of dynamic processes underlying long-term changes, gaining further insight into when pumas may abandon a site versus move to a new site on the landscape (MacKenzie et al. 2006). This combination allowed us to show that long term puma occupancy is relatively high and stable in all sites with the majority of sites high in colonization rates of previously unoccupied sites, all of which we linked to macrohabitat (EVI and canopy cover), and biotic (deer and jaguar trap rates) factors. This highlights important features for land managers to consider when designing sustainable landscape management, supported from analysis across a variety of tropical habitats.

Single-season vs. multi-season occupancy

We found single-season occupancy estimates were similar to multi-season occupancy estimates, however, single-season estimates had a larger range and larger confidence levels for some sites. For the GBMF, MPR, and CBWS precision increased by 0.48, 0.62, and 0.11 respectively using multi-season models. Additionally, multi-season models allowed us to obtain occupancy estimates for 5 years from the Chiquibul while we were only able to obtain 2

estimates using single-season models, demonstrating the power of multi-season occupancy models in the face of sparse data (Makenzie et al. 2006).

We were able to incorporate more covariates in single season models because we had microhabitat covariates for some sites only, thus potentially allowing more insight into specific years that could not be incorporated in long term trends. Thus, the coupling of our snapshots from single season models combined with long-term trends in from multi-season occupancy models, revealed multiple layers of effects on puma space use. However, most of our microhabitat covariates (except canopy cover) did not appear in any top models, indicating that an approach of collecting canopy cover measurements at each camera station while using macrohabitat covariates extracted from GIS layers is perhaps the most efficient for occupancy modeling of large predators in general. However, microhabitat data could be informative in modeling occupancy of other species such as prey or smaller carnivores and could be the subject of future research.

Hierarchical, occupancy modeling has opened many avenues for ecologists to address concerning spatial distribution and habitat selection for numerous wildlife species, areas of major ecological and management interest. This is especially important for species like pumas that are not easily uniquely identifiable to the individual level. Additionally, there are limited studies in the neotropics on pumas and no long-term studies. Occupancy analysis allowed us to gain insight into puma distribution, and stability in that distribution, across a large landscape and provided good news for puma conservation in Belize. Additionally, since research techniques are an approximation and simplification of the real world, adjusting for inaccuracies such as imperfect detection allows for more accurate and precise estimates of distribution, leading to better available science upon which to base management decisions (Donovan et al. 2024).

Management

Considering relatively high, stable occupancy and dynamic processes of colonization and extinction gathered from multi-season modeling, the public and protected area management system seems effective for pumas despite the general focus in Belize on jaguar conservation and management. It should be noted, however, that many areas surveyed are remote and/or have gated systems patrolled by rangers to minimize illegal human impacts like poaching and resource extraction. While poaching is still present, it tends to occur on the boundaries of the protected areas. Spatially, the areas cover large swaths of land with the smallest being 430 km². It has been shown that large continuous areas are beneficial for wildlife communities (Watson et al. 2014), which holds true in our study. Habitat and biotic factors were the most commonly supported covariates influencing pumas indicating that intact habitat and prey populations lead to high occupancy in most study areas. Thus, the combination of management strategies designed to protect habitat for jaguars and prey, along with pumas' generalist behaviors, allows coexistence of this tropical predator guild (Ruth & Murphy 2010). While all estimates from our occupancy methods show that the puma distribution is widespread in current management strategies that mostly focuses on the jaguar, it is important to note that further population studies should be investigated to ensure pumas numbers are not being suppressed. Since pumas have large home ranges and cover large areas, we cannot rule out that widespread distribution results from a few individuals covering large areas. Additionally, pumas live up to 9 years in the wild (Gay and Best 1995) and despite our long-term study, this may represent only 2-3 puma generations, thus continuing long-term monitoring is essential to track distributional change. Studies of puma density through more recently developed spatial mark-resight (Efford and Hunter 2018) or spatial partial identity modeling (Augustine et al. 2018) would enable us to determine numbers

of pumas over time, which is likely a more sensitive indicator of puma long term population status.

Additionally, it is important to stress that analyses are needed on other wildlife species that may not have as much plasticity or a generalist lifestyle like the puma. Thus, research is required on other species of conservation concern such as threatened tapirs, crested guans, black howler monkeys, and the smaller cat species, margay and jaguarundi, through species-specific occupancy modeling, co-occurrence modeling, density modeling, and other forms of analysis such as temporal overlap and movement modeling, to fully understand the species-specific population dynamics and repercussions of using the umbrella species concept for management of all wildlife species.

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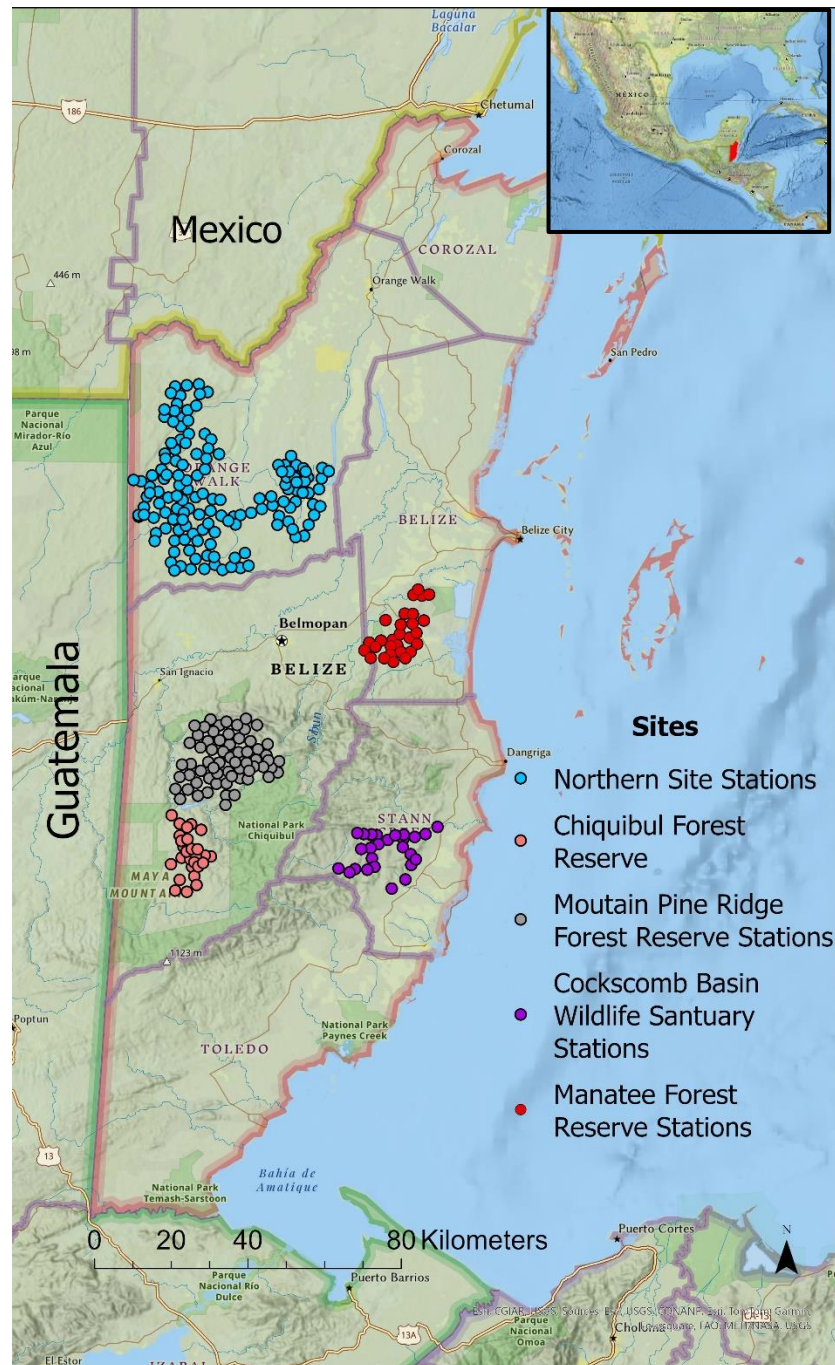


Figure 1. Camera trapping survey sites (different colored dots) throughout Belize, Central America from Cockscomb Basin Wildlife Sanctuary, Greater Belize Maya Forest, Mountain Pine Ridge Forest Reserve, and Manatee Forest Reserve.

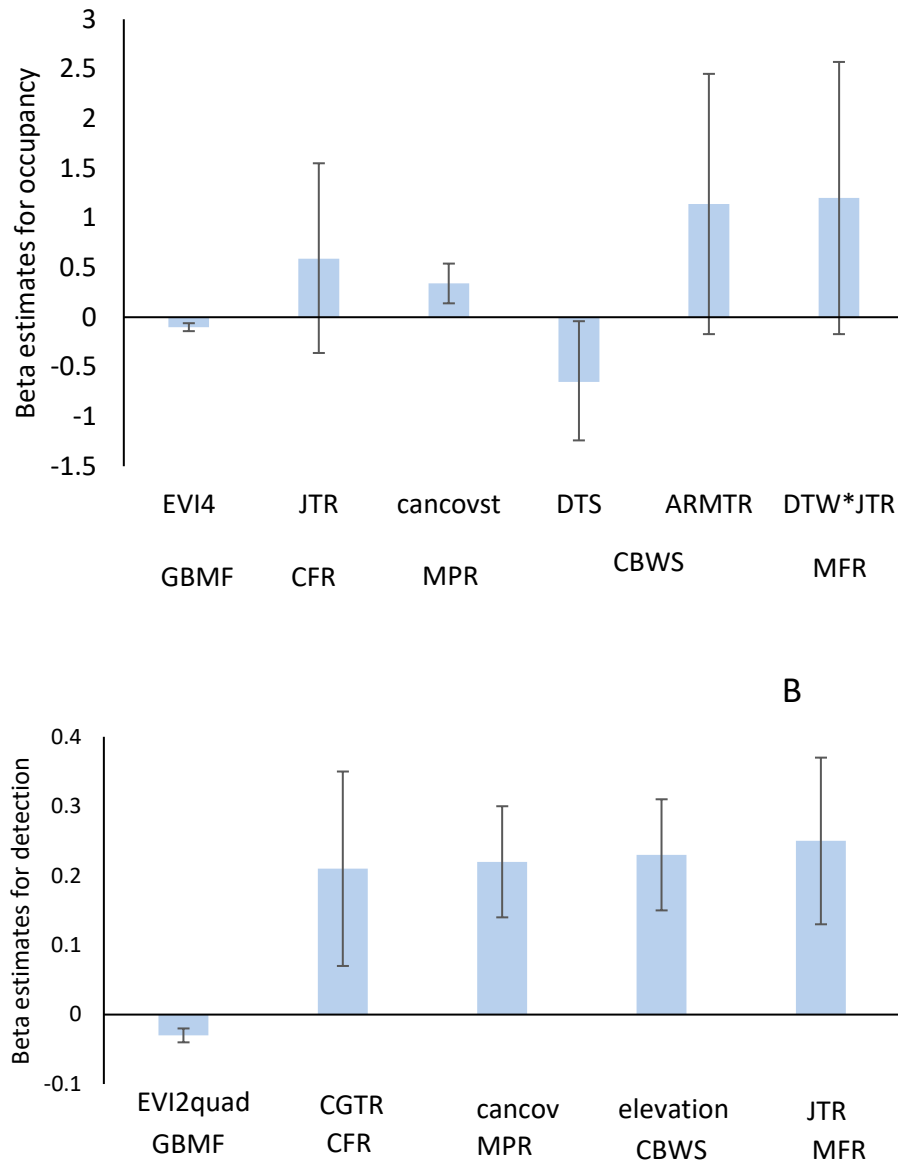


Figure 2. Magnitude of beta estimates of covariates on ψ (A) and p (B) from top multi-season alternative parameterization models. Estimates are from the Greater Belize Maya Forest (GBMF) 11 years, Chiquibul Forest Reserve (5 years), Mountain Pine Ridge Forest Reserve (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years, and Manatee Forest Reserve (MFR) 3 years. Data are from camera trapping surveys.

*EVI4=enhanced vegetation index within 750 m buffer, EVI2=within 250 m buffer, quad=quadratic formula, JTR=jaguar trap rates, cancov=canopy cover at station, ARMTR=armadillo trap rates, DTS=distance to settlements, DTW=distance to water, CGTR=crested guan trap rates

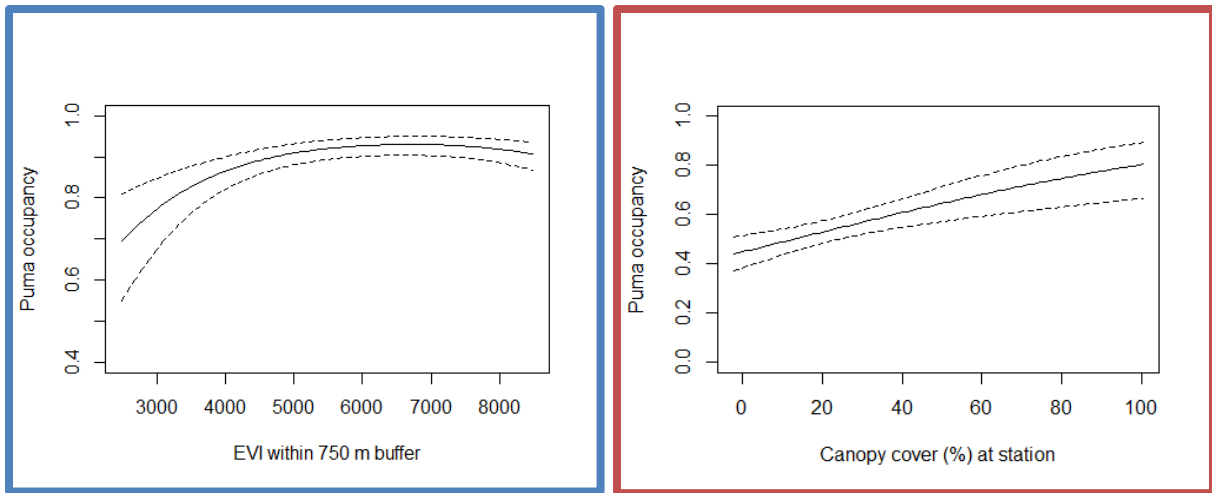


Figure 3. Puma occupancy (ψ) estimates (y-axis) from selected multi-season fourth parameterization occupancy models implemented in RPresence for pumas (*Puma concolor*) from top models with supported covariates (CIs do not cross zero) that influenced occupancy in the Greater Belize Maya Forest (blue) over 11 years, and Mountain Pine Ridge Forest Reserve (red) 18 years, in Belize, Central America. Data come from camera trap surveys.

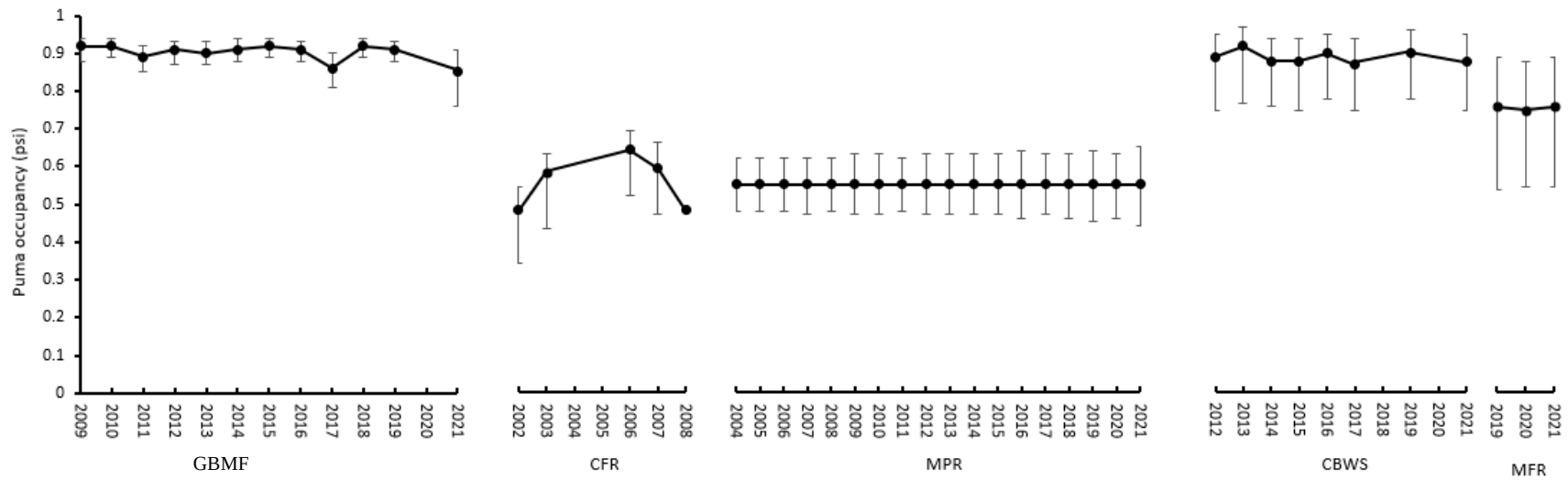


Figure 4. Averaged yearly occupancy (ψ) estimates (y-axis) from selected multi-season fourth parameterization occupancy models implemented in RPresence for pumas (*Puma concolor*) over time (x-axis) for Greater Belize Maya Forest over 11 years, Chiquibul Forest Reserve over 5 years, Mountain Pine Ridge Forest Reserve over 18 years, Cockscomb Basin Wildlife Sanctuary over 8 years, and Manatee Forest Reserve over 3 years in Belize, Central America from camera trapping data.

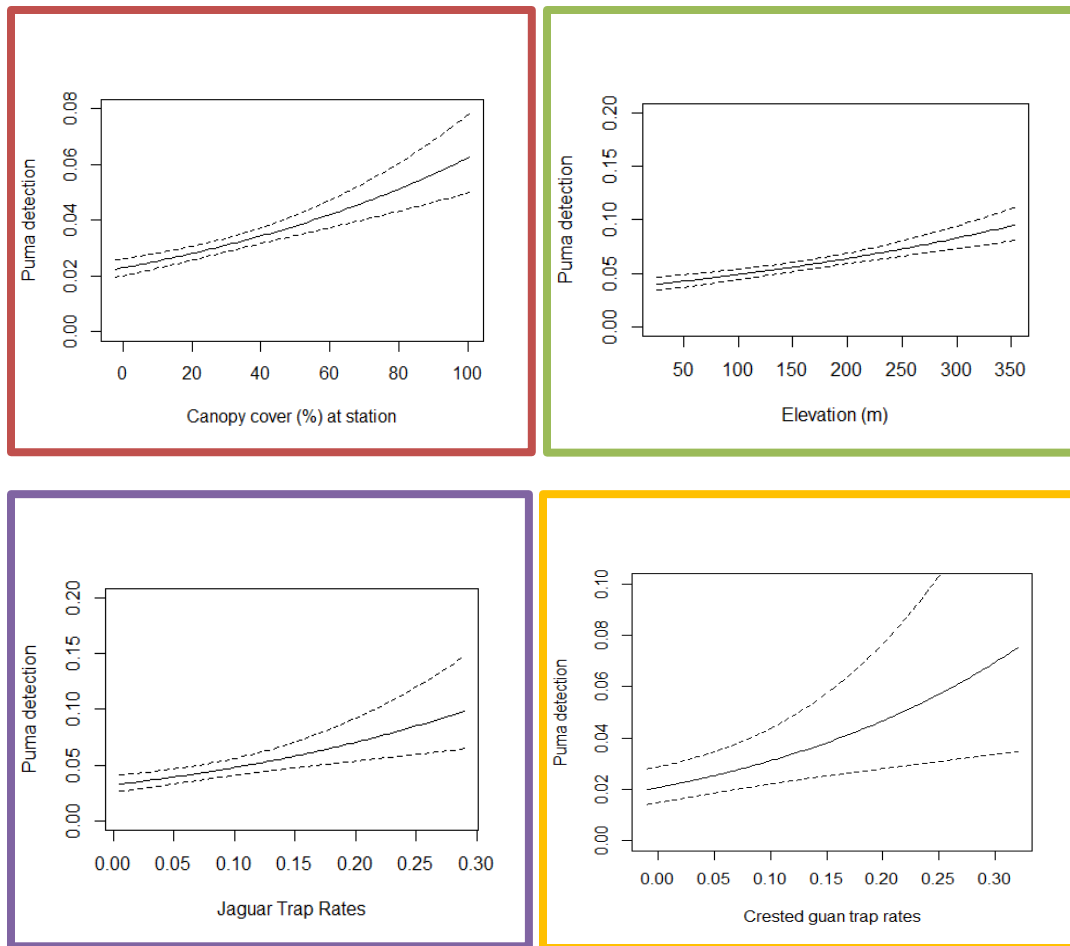


Figure 5. Puma detection (p) estimates (y-axis) from selected multi-season, fourth-parameterization occupancy models implemented in RPresence for pumas (*Puma concolor*) plotted from top models with supported covariates (CIs did not cross zero) that influenced detection in the Mountain Pine Ridge Forest Reserve (red) over 18 years, Cockscomb Basin Wildlife Sanctuary (green) over 8 years, Manatee Forest Reserve (purple) over 3 years, and Chiquibul Forest Reserve (yellow) over 5 years in Belize, Central America. Data come from camera trap surveys.

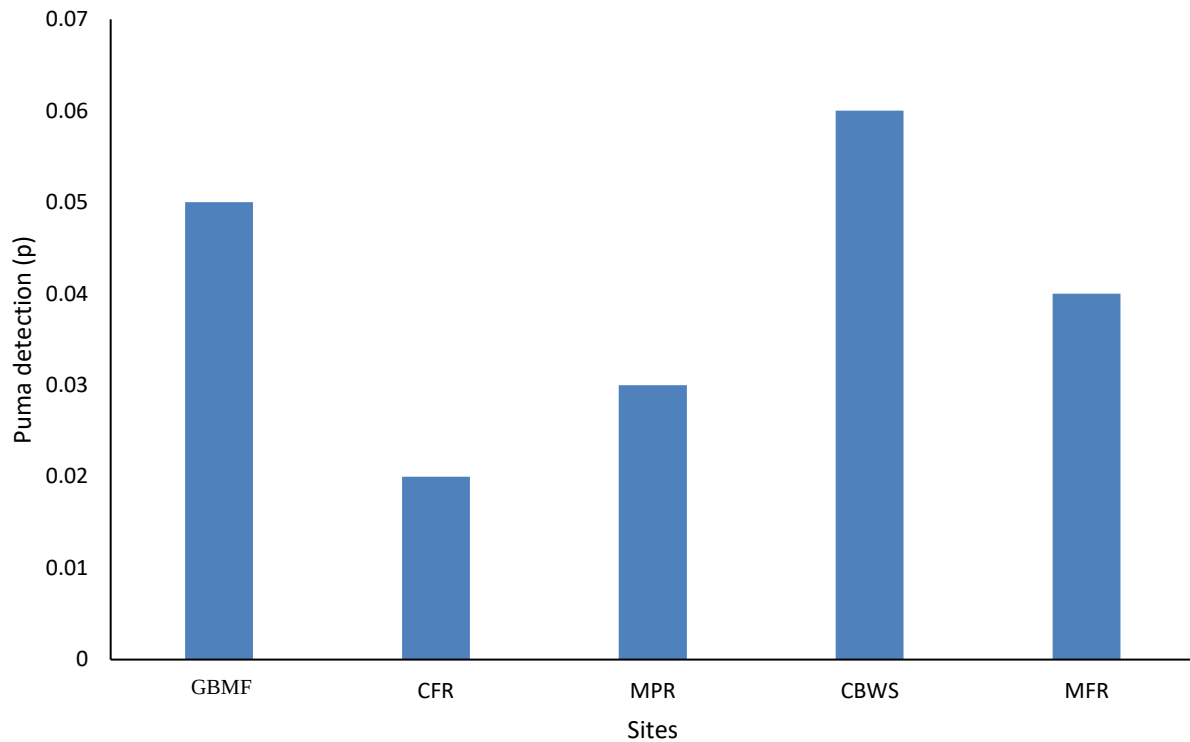


Figure 6. Averaged detection (p) estimates from multi-season fourth parameterization models with CIs across the Greater Belize Maya Forest (GBMF) 11 years, Chiquibul Forest Reserve (CFR) 5 years, Mountain Pine Ridge Forest Reserve (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR) 3 years, from camera trap data.

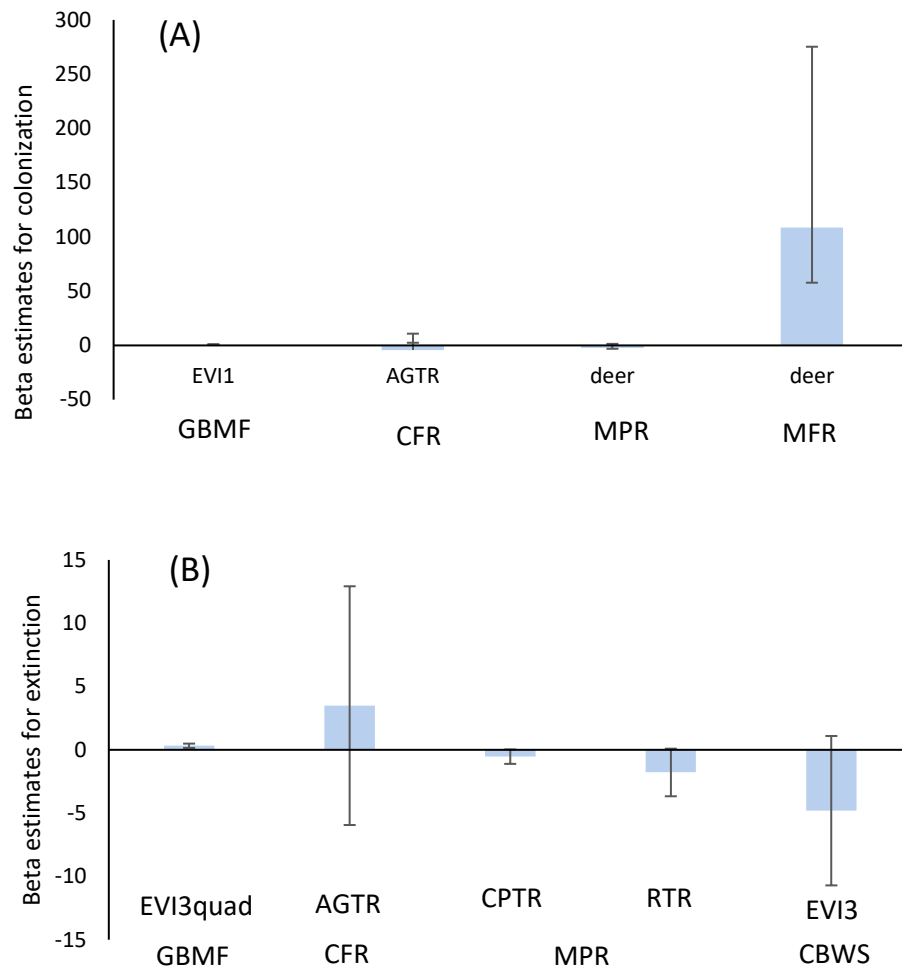


Figure 7. Magnitude of beta estimates of covariates on colonization (A) and extinction (B) from top multi-season first parameterization models. Estimates are from the Greater Belize Maya Forest (GBMF) 11 years, Chiquibul Forest Reserve (5 years), Mountain Pine Ridge Forest Reserve (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years, and Manatee Forest Reserve (MFR) 3 years, from camera trap data.

EVI1=Enhanced vegetation index within 100 m buffer, EVI3=750 m buffer, quad=quadratic formula, AGTR=agouti trap rates, deer=red-brocket and white-tailed deer trap rates, CPTR=collared peccary trap rates, RTR=rodents (agouti and paca) trap rates

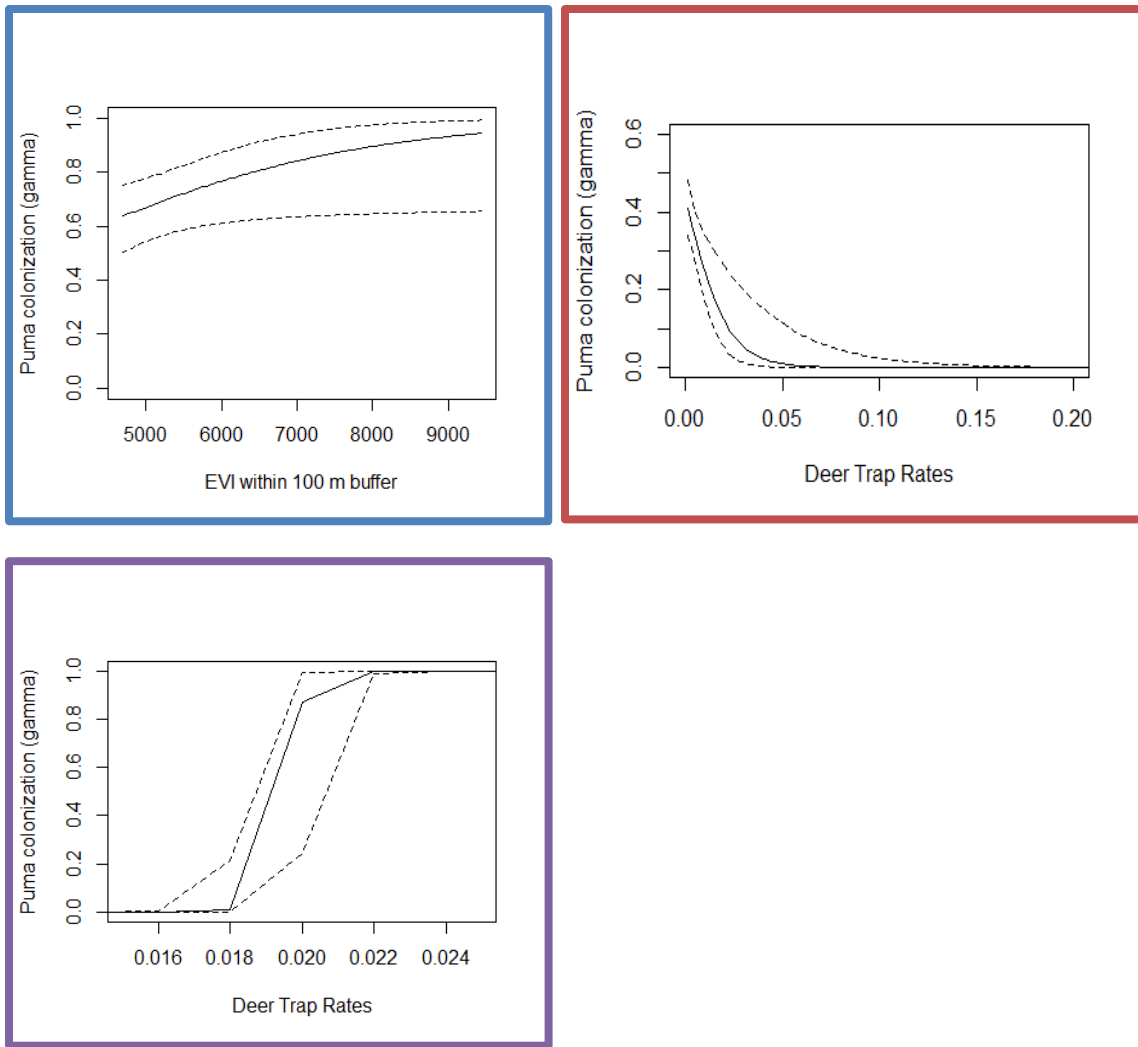


Figure 8. Puma colonization (gamma) estimates (y-axis) from selected multi-season, first-parameterization occupancy models implemented in RPresence for pumas (*Puma concolor*) plotted from top models with supported covariates (CIs did not cross zero) (x-axis) that influenced occupancy in the Greater Belize Maya Forest (blue) over 11 years, Mountain Pine Ridge Forest Reserve (red) over 18 years, and Manatee Forest Reserve (purple) over 3 years in Belize, Central America, from camera trap data.

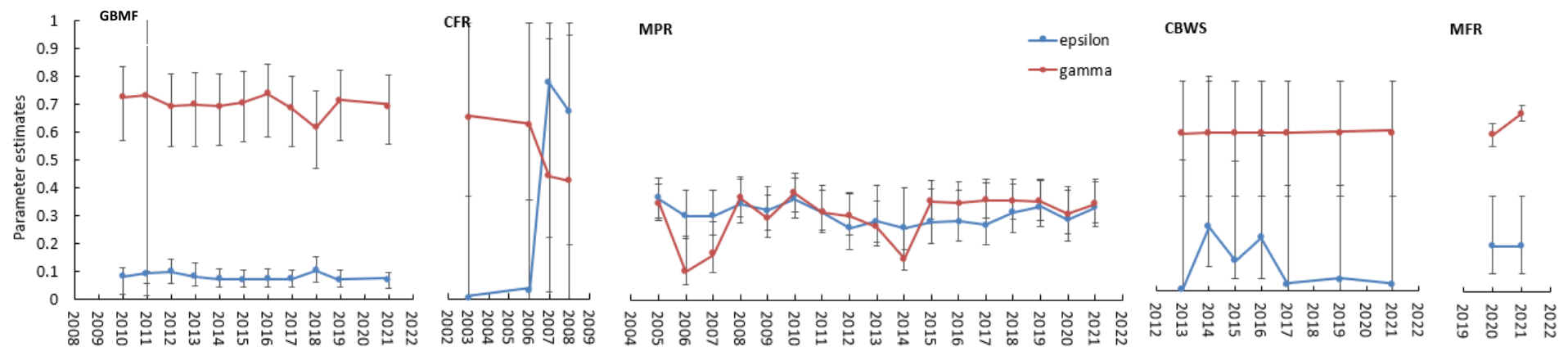


Figure 9. Estimates of (red) averaged yearly gamma (γ) (i.e. colonization) plus confidence intervals and (blue) yearly epsilon (ϵ) (i.e. extinction) estimates with CIs from selected multi-season fourth parameterization occupancy models implemented in RPresence for pumas (*Puma concolor*) over time (x-axis) for Greater Belize Maya Forest over 11 years, Chiquibul Forest Reserve over 5 years, Mountain Pine Ridge Forest Reserve over 18 years, Cockscomb Basin Wildlife Sanctuary over 8 years, and Manatee Forest Reserve over 3 years in Belize, Central America, from camera trap data.

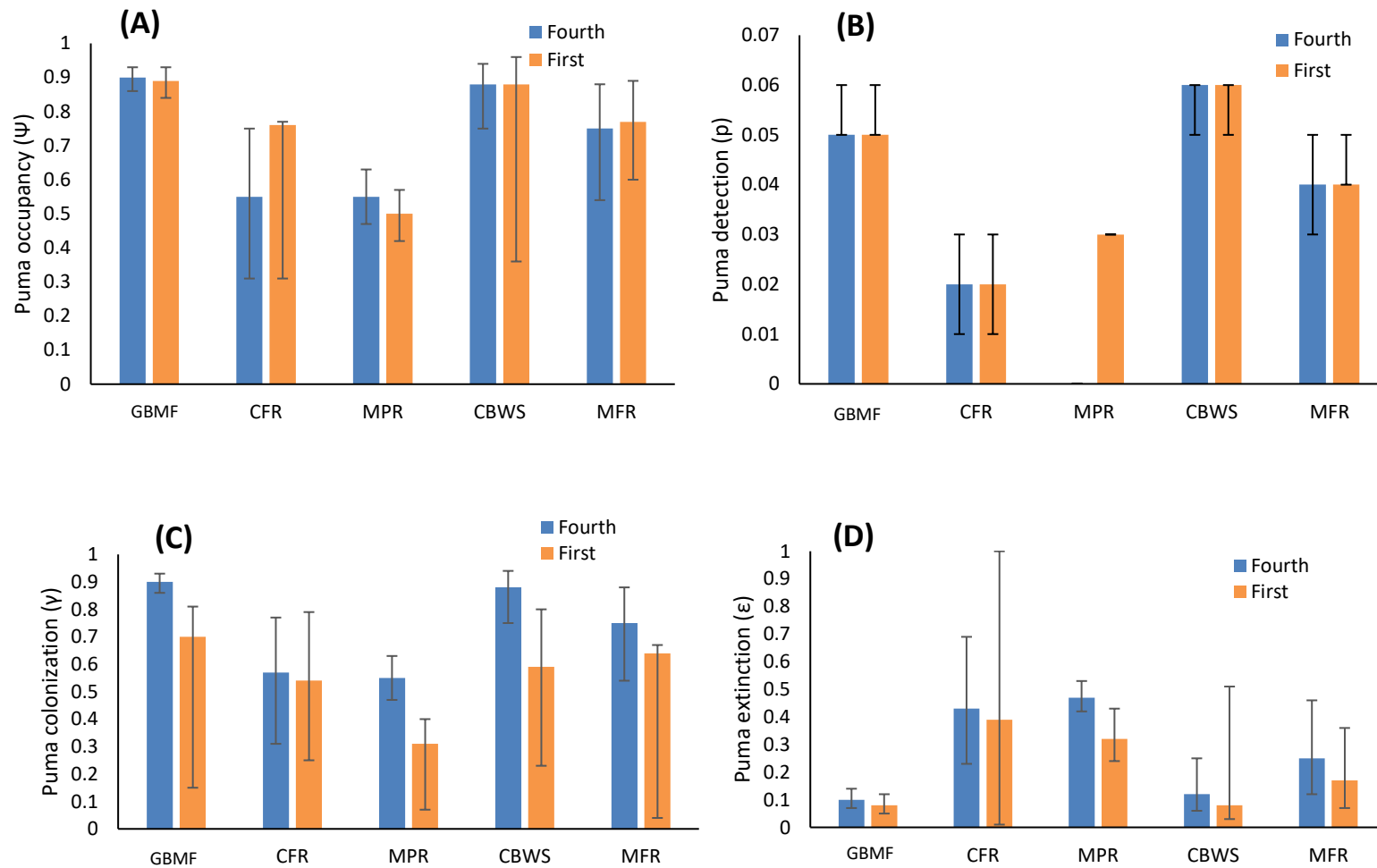


Figure 10. Comparison of parameters ψ (A), p (B), γ (C), and ϵ (D) from top models using both fourth and first parameterization multi-season occupancy modeling across the Greater Belize Maya Forest (GBMF) 11 years, Chiquibul Forest Reserve (CFR) 5 years, Mountain Pine Ridge Forest Reserve (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years, and Manatee Forest Reserve (MFR) 3 years in Belize, Central America, from camera trap data.

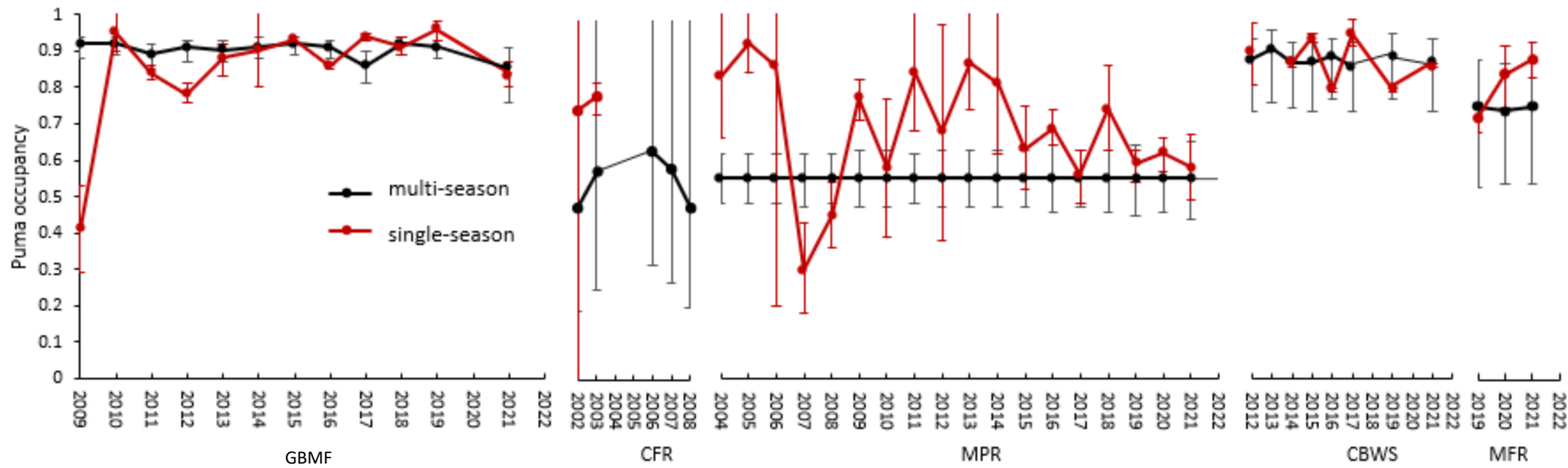


Figure 11. Comparison of single-season occupancy estimates (red) compared to multi-season occupancy estimates (black) for pumas run in Rpresence for Greater Belize Maya Forest (GBMF) 11 years, Chiquibul Forest Reserve (CFR) 5 years, Mountain Pine Ridge Forest Reserve (MPR) 18 years, Cockscomb Basin Wildlife Sanctuary (CBWS) 8 years, and Manatee Forest Reserve (MFR) 3 years in Belize Central America from camera trap data.

Table 1. All study sites including total years running, total functioning trap nights, and number of camera stations (Stations) at each site in Belize, Central America used in multi-season occupancy analyses.

Site	Years Running	Total Trap Nights	Stations
Greater Belize Maya Forest	2009-2019, 2021	72,585	20-147
<i>Yalbac</i>	2014-2019, 2021	10,036	9-35
<i>Gallon Jug</i>	2013-2019, 2021	21,226	29-42
<i>La Milpa</i>	2010-2019, 2021	17,497	20-27
<i>Hillbank</i>	2009-2019, 2021	23,826	20-43
Chiquibul Forest Reserve	2002-2008	3,540	10-30
Mountain Pine Ridge Forest Reserve	2004-2021	50,654	19-65
Cockscomb Basin Wildlife Sanctuary	2012-2017, 2019, 2021	14,400	20-22
Manatee Forest Reserve	2019-2021	8,460	20-37
Total	2002-2021	149,639	2,093

Table 2. Top, competing (within 2 delta AICs), chosen models*, number of parameters (npar), Akaike Information Criterion (AIC), difference in AIC between model and the top model (Delta AIC), model weights (weights), and Model likelihood (ML) from *a priori* (in italics) and **post hoc** (in bold), multi-season fourth parameterization occupancy models run in RPresence for pumas (*Puma concolor*), in the Greater Belize Maya Forest (GBMF) that consists of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug from 2009-2019, 2021, Mountain Pine Ridge Forest Reserve (MPR) from 2004-2021, Cockscomb Basin Wildlife Sanctuary (CBWS) 2012-2017, 2019, 2021, and Manatee Forest Reserve (MFR) 2019-2021 in Belize, Central America. Data come from camera trap surveys.

Fourth-parameterization:					
GBMF models	npar	AIC	DeltaAIC	weight	ML
$\psi \sim \text{EVI4quad } p \sim \text{EVI2quad}$	6	28091.18	0.00	0.34	1.00
$\psi \sim \text{EVI5quad } p \sim \text{EVI2quad}$	6	28091.78	0.60	0.25	0.74
$\psi \sim \text{EVI4quad } p \sim \text{EVI5quad}$	6	28092.82	1.64	0.15	0.44
CFR models	npar	AIC	DeltaAIC	weight	ML
$\psi \sim \text{disttwater } p \sim \text{CGTR} * \text{EVI5quad}$	8	684.41	0.00	0.36	1.00
$\psi \sim \text{disttwater} * \text{JTR } p \sim \text{CGTR} * \text{EVI5quad}$	10	684.73	0.32	0.31	0.85
$*\psi \sim \text{JTR } p \sim \text{CGTR}$	4	692.24	7.83	0.01	0.02
MPR models	npar	AIC	DeltaAIC	weight	ML
$*\psi \sim \text{cancovst } p \sim \text{cancovst}$	4	7961.39	0.00	1.00	1.00
CBWS models	npar	AIC	DeltaAIC	weight	ML
$*\psi \sim \text{disttosettle} + \text{ARMTR } p \sim \text{elevation}$	5	5284.58	0.00	0.49	1.00
$\psi \sim \text{disttosettle} * \text{ARMTR } p \sim \text{elevation}$	6	5285.81	1.23	0.27	0.54
MFR models	npar	AIC	DeltaAIC	weight	ML
$*\psi \sim \text{disttwater} * \text{JTR } p \sim \text{JTR}$	6	1459.52	0.00	0.57	1.00
$\psi \sim \text{disttwater} + \text{JTR } p \sim \text{JTR}$	5	1461.48	1.96	0.21	0.38
First-parameterization:					
GBMF models	npar	AIC	DeltaAIC	weight	ML
$\gamma \sim \text{EVI1 } \varepsilon \sim \text{EVI3quad}$	7	28077.72	0.000	0.236	1.000
$\gamma \sim \text{EVI2 } \varepsilon \sim \text{EVI3quad}$	7	28078.29	0.572	0.178	0.752
$\gamma \sim \text{EVI5 } \varepsilon \sim \text{EVI3quad}$	7	28078.63	0.915	0.150	0.633
$\gamma \sim \text{EVI4 } \varepsilon \sim \text{EVI3quad}$	7	28078.95	1.235	0.127	0.539
$\gamma \sim \text{EVI3 } \varepsilon \sim \text{EVI3quad}$	7	28079.10	1.381	0.118	0.501
$\gamma \sim 1 \varepsilon \sim \text{EVI3quad}$	6	28079.42	1.708	0.101	0.426
CFR models	npar	AIC	DeltaAIC	weight	ML
$\gamma \sim \text{AGTR } \varepsilon \sim \text{AGTR} * \text{EVI1quad}$	10	728.57	0.00	0.21	1.00
$\gamma \sim \text{AGTR } \varepsilon \sim \text{AGTR} + \text{EVI1quad}$	8	728.66	0.09	0.20	0.96
$*\gamma \sim \text{AGTR } \varepsilon \sim \text{AGTR}$	6	728.96	0.39	0.17	0.82
$\gamma \sim \text{AGTR } \varepsilon \sim 1$	5	729.64	1.07	0.12	0.59
MPR models	npar	AIC	DeltaAIC	weight	ML
$*\gamma \sim \text{deer } \varepsilon \sim \text{CPTR} + \text{rodents}$	7	7949.99	0.000	0.758	1.000
CBWS models	npar	AIC	DeltaAIC	weight	ML
$*\gamma \sim 1 \varepsilon \sim \text{EVI3quad}$	6	5314.08	0.00	0.11	1.00
$\gamma \sim 1 \varepsilon \sim \text{EVI2quad}$	6	5314.55	0.47	0.09	0.79
$\gamma \sim \text{HTR } \varepsilon \sim 1$	5	5315.03	0.95	0.07	0.62
$\gamma \sim \text{OTR } \varepsilon \sim 1$	5	5315.08	1.00	0.07	0.61
$\gamma \sim \text{small } \varepsilon \sim 1$	5	5315.25	1.16	0.06	0.56
$\gamma \sim 1 \varepsilon \sim \text{ARMTR}$	5	5315.43	1.34	0.06	0.51
$\gamma \sim \text{EVI1quad } \varepsilon \sim 1$	6	5315.94	1.86	0.04	0.39
MFR models	npar	AIC	DeltaAIC	weight	ML
$\gamma \sim \text{RBDTR } \varepsilon \sim \text{EVI3}$	6	1465.08	0.00	0.21	1.00
$\gamma \sim \text{RBDTR } \varepsilon \sim \text{EVI2}$	6	1464.55	0.47	0.17	0.79
$\gamma \sim \text{RBDTR } \varepsilon \sim \text{EVI5}$	6	1464.81	0.73	0.15	0.69
$\gamma \sim \text{RBDTR } \varepsilon \sim \text{EVI4}$	6	1465.05	0.98	0.13	0.61
$\gamma \sim \text{RBDTR } \varepsilon \sim \text{EVI2quad}$	7	1465.75	1.67	0.09	0.43

$\gamma \sim \text{RBDTR} \ \varepsilon \sim \text{EVI3quad}$	7	1465.99	1.91	0.08	0.38
$\gamma \sim \text{RBDTR} \ \varepsilon \sim \text{EVI4quad}$	7	1466.71	2.63	0.06	0.27
$\gamma \sim \text{RBDTR} \ \varepsilon \sim 1$	5	1467.27	3.19	0.04	0.20
$\gamma \sim \text{RBDTR} \ \varepsilon \sim \text{WTDTR}$	6	1469.34	5.26	0.02	0.07
$*\gamma \sim \text{deer} \ \varepsilon \sim 1$	5	1469.88	5.80	0.01	0.05

EVI1=enhanced vegetation index within a 100 m buffer, EVI2= enhanced vegetation index within a 250 m buffer, EVI3= enhanced vegetation index within a 500 m buffer, EVI4= enhanced vegetation index within a 750 m buffer, EVI5= enhanced vegetation index within a 1000 m buffer, quad=adding a quadratic equation onto the covariate, cancovst=canopy cover at station, disttosettle= distance to the nearest human settlement, ARMTR=nine-banded armadillo trap rates, disttowat=distance to the nearest water source, JTR=jaguar trap rates, deer=white-tailed and red brocket deer trap rates, CPTR=collared peccary trap rates, rodents=agouti and paca trap rates, HTR=human trap rates, WLPTR=white-lipped peccary trap rates

Table 3. Covariates that affected puma occupancy (Ψ), and detection (P), beta intercept (Int.), covariate beta estimate (Beta Est.), beta lower confidence limits (Beta Est. LCL, UCL), in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season fourth parameterization models, run in RPresence. Strong relationships for covariates (CIs do not overlap 0) are *italicized*. Data come from camera trap surveys.

Fourth-parameterization:				
Site	Years	Ψ	Int. Est. (LCL, UCL)	Beta Est. (LCL, UCL)
GBMF	2009-2019, 2021	EVI4quad	2.47 (2.16, 2.78)	-0.10 (-0.14, -0.06)
CFR	2002-2003, 2006-2008	JTR	0.15 (-0.63, 0.93)	0.59 (-0.37, 1.55)
MPR	2004-2021	cancovst	0.14 (-0.04, 0.32)	0.34 (0.14, 0.54)
CBWS	2012-2017, 2019, 2021	disttosettle+ARMTR	2.37 (1.63, 3.11)	-0.65 (-1.26, -0.04), 1.14 (-0.17, 2.45)
MFR	2019-2021	disttowat*JTR	1.47 (0.65, 2.29)	-0.39 (-1.27,0490), 1.01 (-0.26,2.29), 1.20 (-0.17,2.57)
Site	Years	P	Int. (LCL, UCL)	Beta Est. (LCL, UCL)
GBMF	2009-2019, 2021	EVI2quad	-2.80 (-2.84, -2.76)	-0.03 (-0.04, -0.02)
CFR	2002-2003, 2006-2008	CGTR	-3.86 (-4.19, -3.53)	0.21 (0.07, 0.35)
MPR	2004-2021	cancovst	-3.53 (-3.63, -3.43)	0.22 (0.14, 0.30)
CBWS	2012-2017, 2019, 2021	Elevation	-2.80 (-2.88, -2.72)	0.23 (0.15, 0.31)
MFR	2019-2021	JTR	-3.19 (-4.95, -1.43)	0.25 (0.13, 0.37)
First-parameterization:				
Site	Years	γ	Int. Est. (LCL, UCL)	Beta Est. (LCL, UCL)
GBMF	2009-2019, 2021	EVI1	0.94 (0.34, 1.53)	0.39 (0.01, 0.78)
CFR	2002-2003, 2006-2008	AGTR	-1.32 (-6.96, 4.32)	-4.23 (-15.05, 6.59)
MPR	2004-2021	deer	-1.04 (-0.61, -1.47)	-2.26 (-3.67, -0.85)
CBWS	2012-2017, 2019, 2021	NA	NA	NA
MFR	2019-2021	deer	35.86 (23.45, 48.27)	135.90 (89.04, 182.76)
Site	Years	ϵ	Int. (LCL, UCL)	Beta Est. (LCL, UCL)
GBMF	2009-2019, 2021	EVI3quad	-2.90 (-3.30, -2.50)	0.32 (0.15, 0.49)
CFR	2002-2003, 2006-2008	AGTR	0.63 (-3.98, 5.2)	3.49 (-5.94, 12.92)
MPR	2004-2021	CPTR+rodents	-1.01 (-1.50, -0.52)	-0.54 (-1.11, 0.03), -1.78 (-3.67, 0.09)
CBWS	2012-2017, 2019, 2021	EVI3quad	-1.79 (-2.83, -0.75)	-4.81 (-10.71, 1.09)
MFR	2019-2021	NA	NA	NA

EVI1=enhanced vegetation index within a 100 m buffer, EVI2= enhanced vegetation index within a 250 m buffer, EVI3= enhanced vegetation index within a 500 m buffer, EVI4= enhanced vegetation index within a 750 m buffer, quad=adding a quadratic term on the covariate, cancovst=canopy cover at station, disttosettle= distance to the nearest human settlement, ARMTR=nine-banded armadillo trap rates, disttowat=distance to the nearest water source, JTR=jaguar trap rates, deer=white-tailed and red brocket deer trap rates, CPTR=collared peccary trap rates, rodents=agouti and paca trap rates, WLPTR=white-lipped peccary trap rates

Table 4. Minimum and maximum puma occupancy (Ψ) and p estimates with lower and upper confidence limits (LCL, UCL) and derived colonization (γ) and extinction (ε) estimates with lower and upper confidence limits (LCL, UCL), in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season fourth parameterization models, run in RPresence. Data come from camera trap surveys.

Fourth parameterization				
Site	Min Ψ (LCL, UCL)	Max Ψ (LCL, UCL)	Min p (LCL, UCL)	Max p (LCL, UCL)
GBMF	0.34 (0.14, 0.62)	0.93 (0.90, 0.95)	0.03 (0.03, 0.04)	0.06 (0.06, 0.06)
CFR	0.43 (0.26, 0.62)	0.87 (0.20, 0.99)	0.02 (0.01, 0.03)	0.07 (0.03, 0.15)
MPR	0.55 (0.28, 0.79)	0.55 (0.46, 0.64)	0.03 (0.02, 0.03)	0.06 (0.05, 0.08)
CBWS	0.66 (0.43, 0.83)	1.00 (0.60, 1.00)	0.04 (0.03, 0.05)	0.09 (0.08, 0.11)
MFR	0.07 (0.01, 0.45)	1.00 (0.32, 1.00)	0.03 (0.03, 0.04)	0.10 (0.06, 0.15)
Site	Min γ (LCL, UCL)	Max γ (LCL, UCL)	Min ε (LCL, UCL)	Max ε (LCL, UCL)
GBMF	0.34 (0.14, 0.62)	0.93 (0.90, 0.95)	0.07 (0.05, 0.10)	0.66 (0.38, 0.86)
CFR	0.43 (0.26, 0.62)	0.87 (0.20, 0.99)	0.13 (0.01, 0.80)	0.57 (0.38, 0.74)
MPR	0.55 (0.28, 0.79)	0.55 (0.46, 0.64)	0.20 (0.11, 0.33)	0.55 (0.48, 0.62)
CBWS	0.66 (0.43, 0.83)	1.00 (0.60, 1.00)	0.00 (0.00, 0.40)	0.34 (0.17, 0.57)
MFR	0.09 (0.10, 0.48)	1.00 (0.32, 1.00)	0.00 (0.00, 0.68)	0.91 (0.52, 0.99)
First parameterization				
Site	Ψ (LCL, UCL)	Ψ (LCL, UCL)	p (LCL, UCL)	p (LCL, UCL)
GBMF	0.16 (0.04, 0.45)	0.95 (0.92, 0.96)	0.05 (0.05, 0.06)	0.05 (0.05, 0.06)
CFR	0.76 (0.50, 0.91)	0.76 (0.50, 0.91)	0.02 (0.02, 0.03)	0.02 (0.02, 0.03)
MPR	0.22 (0.14, 0.34)	0.88 (0.76, 0.94)	0.03 (0.03, 0.03)	0.03 (0.03, 0.03)
CBWS	0.77 (0.60, 0.88)	0.99 (0.91, 1.00)	0.06 (0.05, 0.06)	0.06 (0.05, 0.06)
MFR	0.48 (0.28, 0.69)	0.90 (0.80, 0.95)	0.04 (0.04, 0.05)	0.04 (0.04, 0.05)
Site	γ (LCL, UCL)	γ (LCL, UCL)	ε (LCL, UCL)	ε (LCL, UCL)
GBMF	0.15 (0.02, 0.67)	0.95 (0.66, 0.99)	0.05 (0.04, 0.08)	0.94 (0.61, 0.99)
CFR	0.00 (0.00, 1.00)	0.75 (0.00, 0.93)	0.20 (0.00, 0.60)	1.00 (0.00, 1.00)
MPR	0.00 (0.00, 0.00)	0.42 (0.35, 0.50)	0.00 (0.00, 0.00)	0.40 (0.33, 0.47)
CBWS	0.59 (0.33, 0.81)	0.59 (0.33, 0.81)	0.00 (0.00, 0.00)	0.18 (0.08, 0.35)
MFR	0.00 (0.00, 0.00)	1.00 (1.00, 1.00)	0.17 (0.07, 0.36)	0.17 (0.07, 0.36)

Table 5. Average puma occupancy estimates (Ψ) with lower and upper confidence limits (LCL, UCL) in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season fourth parameterization models, run in RPresence. Data come from camera trap surveys.

<i>Fourth parameterization</i>					<i>First parameterization</i>				
Site	Ψ	p	γ	ϵ	Site	Ψ	p	γ	ϵ
GBMF	0.90	0.05	0.90	0.10	GBMF	0.89	0.05	0.70	0.08
CFR	0.55	0.02	0.57	0.43	CFR	0.76	0.02	0.54	0.39
MPR	0.55	0.03	0.55	0.47	MPR	0.50	0.03	0.31	0.32
CBWS	0.88	0.06	0.88	0.12	CBWS	0.88	0.06	0.59	0.08
MFR	0.75	0.04	0.75	0.25	MFR	0.77	0.04	0.64	0.17

Supplemental Materials

S1. Pearson's correlation matrices for A) Cockscomb Basin Wildlife Sanctuary B) Manatee Forest Reserve C) Mountain Pine Ridge Forest Reserve D) Greater Belize Maya Forest, used to determine correlated covariates ($|r|>0.7$) that could not be use in the same occupancy models. Pink highlighted cells indicate correlated variables.

	small	birds	rodents	ungulates	CPTR	GCTR	CGTR	RBDTR	AGTR	PATR	ARMTR	EVIS	EV4	EV3	EV2	EV1	elevation	humans	ocelots	jag	DTW	DTR	DTS	WLPTR
small	1																							
birds	0.8523	1																						
rodents	0.18008	0.08554	1																					
ungulates	0.12089	0.1611	0.31438	1																				
CPTR	0.16662	0.20842	0.12763	0.31317	1																			
GCTR	0.89408	0.9471	0.11278	0.23033	0.26373	1																		
CGTR	0.1994	0.18138	-0.04681	0.02207	-0.05252	-0.03609	1																	
RBDTR	0.15268	0.17613	0.10004	0.34468	-0.09202	0.12609	0.14913	1																
AGTR	0.25697	0.07719	0.34097	0.00509	0.06215	0.07256	-0.01658	0.02792	1															
PATR	0.10266	0.05461	0.04567	0.33261	0.11426	0.09485	-0.03767	0.09674	0.01681	1														
ARMTR	0.24656	0.07697	0.14617	0.134	0.04418	0.07201	0.12569	-0.0067	0.01636	0.04249	1													
EVIS	0.26768	0.27625	0.04664	0.08299	0.17251	0.32459	0.02094	0.01727	0.11327	0.01363	-0.02264	1												
EV4	0.26911	0.27549	0.05022	0.09373	0.17193	0.32356	0.02125	0.01814	0.11482	0.0137	-0.01997	0.96509	1											
EV3	0.26758	0.27724	0.03865	0.09764	0.18554	0.32644	0.01495	0.01801	0.1232	-0.0015	-0.0227	0.97445	0.98786	1										
EV2	0.2602	0.27512	0.03797	0.12467	0.19378	0.3266	-0.00023	0.0299	0.12404	-0.00252	-0.0353	0.92242	0.93804	0.97083	1									
EV1	0.2468	0.2563	0.04008	0.14242	0.18023	0.30761	-0.00528	0.03122	0.12965	0.00091	0.03546	0.87889	0.89102	0.92931	0.96285	1								
elevation	-0.09581	-0.08407	-0.08195	-0.00102	-0.00104	-0.05264	0.05211	-0.07735	0.0176	-0.09324	-0.04838	-0.0576	-0.05018	-0.05122	-0.06237	-0.07938	1							
humans	-0.03846	0.01467	0.01435	-0.08018	0.08462	-0.04042	0.20005	-0.1306	-0.04888	0.00165	-0.04275	0.20328	0.18571	0.16478	0.15724	0.15211	-0.15079	1						
ocelots	0.1035	0.09343	0.04133	-0.01352	-0.02082	0.09743	-0.01107	0.14087	0.04129	0.02968	-0.12392	-0.02954	-0.04197	-0.06319	-0.05893	-0.04072	-0.26074	0.0136	1					
jag	-0.10152	-0.09175	-0.0293	-0.2306	-0.15384	-0.0942	-0.13644	-0.11686	-0.09239	0.00079	-0.15249	-0.27886	-0.27763	-0.26661	-0.23205	-0.21133	-0.12425	-0.05283	0.52214	1				
disttowat	0.10737	0.12223	0.16995	-0.23432	0.07325	0.12091	0.02198	-0.12011	0.03322	-0.16927	0.04359	-0.03378	-0.04277	-0.05457	-0.05331	-0.06238	0.24260	0.06027	-0.07518	0.10271	1			
disttoroac	0.21135	0.20087	0.08867	0.11626	0.17119	0.17429	0.21164	-0.01429	0.17922	0.03232	0.02658	0.18036	0.17961	0.16744	0.11921	0.08398	0.30264	-0.12538	-0.17403	-0.26558	0.00805	1		
disttosest	0.0772	0.29702	0.06502	0.05547	0.21445	0.25962	0.24444	0.01003	0.13236	0.02338	0.04459	0.1959	0.18969	0.17203	0.12833	0.09847	0.03195	-0.05088	0.00715	-0.20327	0.05814	0.86425	1	
WLPTR	0.04396	0.0719	0.28951	0.0286	0.19366	0.14141	0.02316	0.01529	-0.01723	0.31388	0.21205	0.06428	0.06487	0.06669	0.09082	0.11113	0.04846	-0.05561	-0.06959	-0.18372	-0.21948	0.10299	0.01670	1

	small	birds	rodents	deer	ungulates	CHCHTR	CPTR	GCTR	CGTR	WTDTR	RBDTR	AGTR	PATR	ARMTR	EVIS	EV4	EV3	EV2	EV1	elevation	humans	ocelots	jag	DTW	DTR	DTS
small	1																									
birds	0.719	1																								
rodents	0.3638	-0.08	1																							
deer	0.0078	0.0977	0.1286	1																						
ungulate	0.0626	0.0223	0.1232	0.3619	1																					
CHCHTR	0.249	0.0748	0.2028	-0.003	0.5271	1																				
CPTR	0.0646	-0.005	0.0934	0.0095	0.9603	0.564	1																			
GCTR	0.703	0.5983	-0.089	0.0979	-0.01	0.0202	-0.039	1																		
CGTR	0.0294	0.0636	-0.049	0.0787	0.2399	0.2098	0.2514	0.0066	1																	
WTDTR	-0.075	-0.107	-0.020	0.4721	0.0803	-0.021	-0.046	-0.105	-0.05	1																
RBDTR	0.0377	0.507	0.549	0.5413	0.3723	0.0048	0.118	0.502	0.0381	0.1467	1															
AGTR	0.5944	-0.114	0.5867	-0.086	0.0251	0.2299	0.0524	-0.125	-0.041	0.0264	-0.107	1														
PATR	-5E-04	-0.011	0.0608	0.2274	0.1343	0.0741	0.0759	-0.014	-0.029	-0.055	0.2763	-0.03	1													
ARMTR	0.1521	0.0024	0.1391	-0.18	0.1605	-0.005	0.1853	0.0025	0.005	-0.051	-0.047	0.019	0.1631	1												
EVIS	-0.075	0.0197	-0.13	0.1851	0.149	0.2302	0.1042	0.0088	0.0189	0.0399	0.1824	-0.077	-0.102	-0.22	1											
EV4	-0.089	-0.008	-0.123	0.174	0.1502	0.2065	0.1087	-0.019	0.0157	0.0437	0.1785	-0.066	-0.103	-0.22	0.9972	1										
EV3	-0.052	-0.016	-0.115	0.1854	0.1495	0.153	0.1706	-0.020	0.0069	0.0356	0.1719	-0.061	-0.026	-0.209	0.9543	0.9319	1									
EV2	-0.085	-0.014	-0.1	0.1635	0.1546	0.1813	0.1148	-0.023	-0.01	0.0414	0.1744	-0.056	-0.082	-0.205	0.9847	0.9871	0.9343	1								
EV1	-0.068	-7E-04	-0.083	0.0948	0.1491	0.1826	0.1311	-0.01	-0.009	-0.125	0.1543	-0.047	-0.067	-0.201	0.9553	0.9573	0.9658	0.9743	1							
elevation	-0.115	-0.098	-0.117	0.042	0.095	0.2303	0.0891	-0.108	-0.081	0.0832	0.0153	0.0124	-0.155	-0.264	0.8957	0.8762	0.8632	0.8535	0.8282	1						
humans	-0.125	-0.178	-0.076	-0.073	-0.028	-0.025	-0.177	-0.032	-0.03	-0.188	0.0307	-0.082	-0.032	-0.249	-0.232	-0.244	-0.259	-0.247	-0.210	-0.096	1					
ocelots	0.0322	-0.141	0.1236	0.3091	0.2865	0.1432	0.2143	-0.148	-0.051	0.5397	-0.1402	0.2006	-0.002	0.0366	0.2271	0.2191	0.213	0.222	0.1432	0.1182	-0.063	1				
jag	0.3025	0.3888	-0.082	-0.011	0.2377	-0.002	0.2573	0.391	-0.031	-0.063	0.0118	0.0137	-0.113	-0.076	0.0732	0.0868	0.0715	0.0759	0.0876	-0.059	0.0832	0.0237	1			
disttowat	0.0672	-0.275	0.0508	0.0512	0.0024	-0.042	-0.002	-0.215	0.0262	0.3908	-0.032	0.2732	-0.144	0.2658	-0.098	-0.09	-0.079	-0.068	-0.14	0.0062	-0.096	0.2094	-0.142	1		
disttoroac	0.0658	-0.075	0.1413	0.0432	-0.005	-0.038	-0.076	-0.074	0.0049	0.0869	0.0182	0.117	0.0955	0.2604	-0.057	-0.089	-0.046	-0.015	-0.018	-0.211	-0.052	0.0742	-0.087	0.383	1	
disttosest	-0.11	-0.14	-0.03	0.0071	0.1494	0.0705	0.1576	-0.144	0.0168	0.0738	-0.023	0.0519	-0.152	-0.203	0.6301	0.6554	0.6572	0.6534	0.6412	0.6091	-0.186	0.0582	-0.014	0.1183	-0.14	1

	EVIS	EV4	EV3	EV2	EV1	DTS	DTR	DTW	elevation	roadwidth	humans	ocelots	birds	small	WTDTR	RBDTR	AGTR	ARMTR	PATR	OTTR	CGTR	GCTR	CHCHTR	WLTPTR	CPTR	HTR	JTR	OTR
EVIS	1																											
EV4	0.9987	1																										
EV3	0.9939	0.9976	1																									
EV2	0.994	0.998	0.9954	1																								
EV1	0.9893	0.9795	0.9827	0.9904	1																							
elevation	0.006	0.0067	0.0067	0.0052	0.0035	1																						
roadwidth	0.2428	0.2386	0.2326	0.2327	0.2304	0.0076	1																					
humans	-0.0213	-0.0212	-0.024	-0.032	-0.0453	-0.0043	-0.056	1																				
ocelots	-0.0425	-0.0408	-0.0394	-0.0393	-0.0503	0.118	0.0888	0.01	1																			
birds	-0.2208	-0.2191	-0.2207	-0.221	-0.218	-0.0748	-0.1059	0.0414	0.1018	1																		
small	0.2467	0.2557	0.2664	0.2783	0.2859	0.024	0.174	-0.1825	-0.1938	-0.1874	1																	
WTDTR	0.0174	0.0191	0.0241	0.0234	0.024	-																						

S2. Landscape variables extracted from geographic information system (GIS) layers obtained from the Biodiversity and Environmental Resource Data System of Belize (accessed)) site in Belize, Central America and from Moderate Resolution Imaging Spectroradiometer (MODIS). Macrohabitat variables were measured manually in the field or extracted from GIS in various radii surrounding camera traps. Trap rates (TR) come from photo data as the number of independent photo events per 100 trap nights. Covariates listed were used in *a priori* and *post hoc* models on both parameters: γ (local colonization) and ε (local extinction) in multi-season, first and forth parameterization models.

Landscape variables - macrohabitat	<i>A priori</i>	Justification
Enhanced vegetation index at 100m, 250m, 500m, 750m, 1,000m buffers (EVI1, EVI2, EVI3, EVI4, EVI5)	$\gamma +, \varepsilon -$	More vegetation index (i.e. canopy and some ground vegetation) more prey species, better for ambush hunting strategy, caching, avoiding other predators, and more likely to be increase site usage (Ironsides et al. 2017)
Enhanced vegetation index at 100m, 250m, 500m, 750m, 1,000m buffers (EVI1quad, EVI2quad, EVI3quad, EVI4quad, EVI5quad) (quadratic)	$\gamma +, \varepsilon -$ then $\gamma -, \varepsilon +$	Same as above but if EVI gets too dense, it gets harder to see prey and move (Ironsides et al. 2017)
Biotic variables		
White-tail deer trap rates (WTDTR)	$\gamma +, \varepsilon -$	Pumas are deer specialists so they will choose areas with more WTDTR (Novak et al. 2005)
Red brocket deer trap rates (RBDTR)	$\gamma +, \varepsilon -$	Same as above but more so because the smaller deer species will be in a better weight range for the puma (Novak et al. 2005)
Agouti trap rates (AGTR)	$\gamma +, \varepsilon -$	As a common prey species, pumas will choose areas with higher trap rates and will follow signs (Novak et al. 2005)
Paca trap rates (PATR)	$\gamma +, \varepsilon -$	same as above
Armadillo trap rates (ARMTR)	$\gamma +, \varepsilon -$	same as above
Ocellated turkey trap rates (OTTR)	$\gamma +, \varepsilon -$	same as above
Great curassow trap rates (GCTR)	$\gamma +, \varepsilon -$	same as above
Crested guan trap rates (CGTR)	$\gamma +, \varepsilon -$	same as above
Chachalaca trap rates (CHCHTR)	$\gamma +, \varepsilon -$	same as above
White-lipped peccary trap rates (WLPTR)	$\gamma +, \varepsilon -$	same as above
Collared peccary trap rates (CPTR)	$\gamma +, \varepsilon -$	same as above
Deer trap rates (DTR)	$\gamma +, \varepsilon -$	same as above
Ungulates trap rates (UTR)	$\gamma +, \varepsilon -$	same as above
Rodent (Agouti and Paca) trap rates (RTR)	$\gamma +, \varepsilon -$	same as above
Ground Bird trap rates (BTR)	$\gamma +, \varepsilon -$	same as above
Small prey (0-5kg) trap rates (STR)	$\gamma +, \varepsilon -$	same as above
Ocelot trap rates (OTR)	$\gamma +, \varepsilon -$	As the dominant carnivore, pumas will key in on ocelot sign (scent, markings, sight) as an indicator of good habitat and resources (Donadio & Buskirk 2006)

Jaguar trap rates (JTR)	$\gamma -, \varepsilon +$	As the subordinate carnivore, pumas will try to avoid general areas with higher jaguar trap rates (Donadio & Buskirk 2006)
Human trap rates (HTR)	$\gamma -, \varepsilon +$	Perceived risk is higher around humans due to scent, sound, vehicles causing avoidance of area (Gray et al. 2016).

S3. Average puma occupancy estimates (Ψ) with lower and upper confidence limits (LCL, UCL) in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season fourth parameterization models, run in RPresence. Data come from camera trap surveys.

Year	GBMF Ψ	CFR Ψ	MPR Ψ	CBWS Ψ	MFR Ψ
2002	-	0.48 (0.29, 0.67)	-	-	-
2003	-	0.58 (0.33, 0.78)	-	-	-
2004	-	-	0.55 (0.48, 0.62)	-	-
2005	-	-	0.55 (0.48, 0.62)	-	-
2006	-	0.64 (0.32, 0.85)	0.55 (0.48, 0.62)	-	-
2007	-	0.59 (0.32, 0.79)	0.55 (0.47, 0.62)	-	-
2008	-	0.48 (0.28, 0.66)	0.55 (0.48, 0.62)	-	-
2009	0.92 (0.88, 0.94)	-	0.55 (0.47, 0.63)	-	-
2010	0.92 (0.89, 0.94)	-	0.55 (0.47, 0.63)	-	-
2011	0.89 (0.85, 0.92)	-	0.55 (0.48, 0.62)	-	-
2012	0.91 (0.87, 0.93)	-	0.55 (0.47, 0.63)	0.88 (0.74, 0.94)	-
2013	0.90 (0.87, 0.93)	-	0.55 (0.47, 0.63)	0.91 (0.76, 0.96)	-
2014	0.91 (0.88, 0.94)	-	0.55 (0.47, 0.63)	0.87 (0.75, 0.93)	-
2015	0.92 (0.89, 0.94)	-	0.55 (0.47, 0.63)	0.87 (0.74, 0.93)	-
2016	0.91 (0.88, 0.93)	-	0.55 (0.46, 0.64)	0.89 (0.77, 0.94)	-
2017	0.86 (0.81, 0.90)	-	0.55 (0.47, 0.63)	0.86 (0.74, 0.93)	-
2018	0.92 (0.89, 0.94)	-	0.55 (0.46, 0.63)	-	-
2019	0.91 (0.88, 0.93)	-	0.55 (0.45, 0.64)	0.89 (0.77, 0.95)	0.75 (0.53, 0.88)
2020	-	-	0.55 (0.46, 0.63)	-	0.74 (0.54, 0.87)
2021	0.85 (0.76, 0.91)	-	0.55 (0.44, 0.65)	0.87 (0.74, 0.94)	0.75 (0.54, 0.88)

S4. Average puma colonization estimates (γ) with lower and upper confidence limits (LCL, UCL) in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season fourth parameterization models, run in RPresence. Data come from camera trap surveys.

Year	GBMF γ	CFR γ	MPR γ	CBWS γ	MFR γ
2002	-	-	-	-	-
2003	-	0.66 (0.37, 0.86)	-	-	-
2004	-	-	-	-	-
2005	-	-	0.36 (0.30, 0.43)	-	-
2006	-	0.63 (0.36, 0.84)	0.10 (0.05, 0.24)	-	-
2007	-	0.44 (0.22, 0.72)	0.17 (0.10, 0.29)	-	-
2008	-	0.43 (0.19, 0.76)	0.38 (0.31, 0.46)	-	-
2009	-	-	0.31 (0.23, 0.39)	-	-
2010	0.72 (0.57, 0.84)	-	0.40 (0.33, 0.47)	-	-
2011	0.73 (0.06, 0.06)	-	0.33 (0.26, 0.41)	-	-
2012	0.69 (0.55, 0.81)	-	0.31 (0.24, 0.40)	-	-
2013	0.70 (0.55, 0.82)	-	0.27 (0.20, 0.37)	0.60 (0.36, 0.80)	-
2014	0.70 (0.56, 0.81)	-	0.15 (0.11, 0.26)	0.60 (0.36, 0.80)	-
2015	0.71 (0.57, 0.82)	-	0.37 (0.30, 0.45)	0.60 (0.36, 0.80)	-
2016	0.74 (0.58, 0.84)	-	0.36 (0.29, 0.44)	0.60 (0.36, 0.80)	-
2017	0.69 (0.55, 0.80)	-	0.37 (0.30, 0.45)	0.60 (0.36, 0.80)	-
2018	0.62 (0.47, 0.75)	-	0.37 (0.30, 0.45)	-	-
2019	0.71 (0.57, 0.82)	-	0.37 (0.30, 0.45)	0.60 (0.36, 0.80)	-
2020	-	-	0.32 (0.25, 0.41)	0.60 (0.36, 0.80)	0.59 (0.55, 0.64)
2021	0.69 (0.56, 0.80)	-	0.36 (0.29, 0.44)	0.60 (0.36, 0.80)	0.68 (0.65, 0.71)

S5. Average puma extinction estimates (ϵ) with lower and upper confidence limits (LCL, UCL) in the Greater Belize Maya Forest (GBMF) combined consisting of Yalbac, Rio Bravo La Milpa, Rio Bravo Hill Bank, and Gallon Jug in Belize, Central America, Mountain Pine Ridge Forest Reserve (MPR), Cockscomb Basin Wildlife Sanctuary (CBWS), and Manatee Forest Reserve (MFR). Estimates obtained from top/chosen multi-season, fourth parameterization models, run in RPresence. Data come from camera trap surveys.

Year	GBMF ϵ	CFR ϵ	MPR ϵ	CBWS ϵ	MFR ϵ
2002	-	-	-	-	-
2003	-	0.00 (0.00, 1.00)	-	-	-
2004	-	-	-	-	-
2005	-	-	0.38 (0.31, 0.45)	-	-
2006	-	0.03 (0.00, 1.00)	0.31 (0.23, 0.41)	-	-
2007	-	0.78 (0.00, 1.00)	0.31 (0.24, 0.41)	-	-
2008	-	0.68 (0.00, 1.00)	0.36 (0.29, 0.45)	-	-
2009	-	-	0.33 (0.26, 0.42)	-	-
2010	0.08 (0.02, 0.05)	-	0.38 (0.31, 0.45)	-	-
2011	0.09 (0.01, 0.10)	-	0.33 (0.25, 0.43)	-	-
2012	0.10 (0.06, 0.14)	-	0.27 (0.19, 0.40)	-	-
2013	0.08 (0.05, 0.13)	-	0.30 (0.21, 0.43)	0.00 (0.00, 0.50)	-
2014	0.07 (0.05, 0.11)	-	0.27 (0.19, 0.42)	0.24 (0.09, 0.82)	-
2015	0.07 (0.04, 0.11)	-	0.29 (0.21, 0.41)	0.11 (0.05, 0.50)	-
2016	0.07 (0.04, 0.11)	-	0.30 (0.22, 0.41)	0.20 (0.05, 0.59)	-
2017	0.07 (0.05, 0.11)	-	0.28 (0.20, 0.44)	0.02 (0.00, 0.40)	-
2018	0.10 (0.06, 0.15)	-	0.32 (0.25, 0.43)	-	-
2019	0.07 (0.04, 0.11)	-	0.35 (0.27, 0.45)	0.04 (0.00, 0.40)	-
2020	-	-	0.30 (0.22, 0.42)	-	0.17 (0.07, 0.36)
2021	0.07 (0.04, 0.10)	-	0.35 (0.27, 0.45)	0.02 (0.00, 0.36)	0.17 (0.07, 0.36)