

**CORRELATES OF A RAINFOREST MAMMALIAN CARNIVORE COMMUNITY IN THE
CHIQUIBUL FOREST RESERVE**

**A Dissertation Presented for the
Doctor of Philosophy
Degree
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DEDICATION

To the green fire. Always.

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ABSTRACT

Naturally rare and cryptic, Neotropical mammalian carnivores are difficult to study, leading to gaps in our knowledge of their ecology. Although technological advances have enhanced our knowledge of large carnivore ecology in the tropics (i.e., jaguar [*Panthera onca*] and puma [*Puma concolor*]), we have a limited understanding of factors affecting their coexistence with each other and other carnivores, particularly in areas subject to resource extraction (i.e., selective logging). My goal was to determine the factors affecting individual species site-use and carnivore coexistence in a managed forest reserve in Belize, Central America. From January–August 2016, I sampled the carnivore community in the Chiquibul Forest Reserve (CFR) via a network of trail cameras on a 2.25 x 2.25 km grid, and characterized the surrounding sites at both site-specific (e.g., vegetation structure, prey availability and cover) and landscape (e.g., distance to water sources, distance to forest reserve boundaries) levels. I used information-theoretic models in an occupancy-modeling framework to understand the 1) seasonal effects of factors on carnivore distribution throughout the CFR, 2) importance of pathway (i.e., trail, road, logging tract) characteristics in determining carnivore site-use intensity in the CFR, and 3) coexistence among carnivores. The importance of site-specific categories in determining carnivore distributions changed between seasons for all species except jaguar. Top models for carnivores at both site-specific and landscape levels confirmed that pathway characteristics impact carnivore site-use intensity, but not site-use. Except for ocelot and grey fox, all analyses provide evidence that carnivores use sites independently from other species. Variables generally failed to predict carnivore site-use, but percent vertical visual obstruction was an important predictor of species site-use intensity. The non-homogeneous, but well-structured, vegetation mosaic created by both logging activities and natural (e.g., hurricanes) disturbance appears to provide resources that facilitate carnivore presence in the CFR. However, increasing protection around key features (i.e., riparian areas) could help mitigate added pressure on carnivores from human disturbance during limiting periods. Carnivores are generally tolerant of pathways and may concentrate their activities on structures left fallow after logging.

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INTRODUCTION

Naturally rare and cryptic, Neotropical mammalian carnivores are difficult to study, leading to gaps in our knowledge of their ecology. Despite efforts to study large, charismatic carnivores such as the jaguar (*Panthera onca*), direct investigations of their relationships with humans, structural habitat components (e.g., vegetation, water sources), and other carnivores are lacking. Without a working knowledge of these relationships, particularly as it relates to areas subject to multiple-use management regimes, we cannot preempt or mitigate changes to tropical wildlife communities and ecosystems.

Until recently, few have established meaningful relationships between Neotropical carnivore populations and factors affecting their distribution at different spatial scales (Davis et al. 2011, Porfirio et al. 2016, Nagy-Reis et al. 2017, Nagy-Reis et al. 2018, Santos et al. 2019). Long-term monitoring efforts emphasize the distribution (hypothetical or realized), survival, and abundance or density of a few charismatic species, such as jaguar (Sanderson et al. 2002, Harmsen et al. 2017), puma (*Puma concolor*; Kelly et al. 2008, Wultsch et al. 2014), and ocelot (*Leopardus pardalis*; Wultsch et al. 2014, Satter et al. 2018), without directly examining factors affecting observed numbers or population changes (e.g., prey availability, vegetation structure, etc.). How such factors affect carnivore populations (for example, in areas where selective logging occurs) has important implications for managing these species, as these practices change forest structure and composition which directly affects resources available for and used by carnivores.

Active logging creates a dense understory in rainforest systems because of a rapid increase in stem density with additional sunlight as the forest regenerates and re-establishes tree species (Johns 1985). Without logging, closed-canopy forests that restrict understory vegetation growth characterize these rainforests (Kricher 1999, Bridgewater 2012). Some suggest that in areas where resource extraction (e.g., selective logging) occurs, the necessary establishment of infrastructure (e.g., construction of roads and skidder tracks) that provides access to these areas has negative effects on wildlife, including carnivores. For example, in the Pacific Northwest, Bull et al. (2001) noted an increase in human use of post-harvest roads built in previously inaccessible areas to facilitate timber extraction negatively affected the distribution of certain carnivore species (e.g., wolverines [*Gulo gulo*] and fishers [*Martes pennanti*]). Humans trap wolverines, and fishers are habitat specialists associated with closed-canopy late-successional forests. Such characteristics make these two species particularly sensitive to forest fragmentation and disturbance generated by roads and trails. The behavior and habits of these two mustelids may be similar to their Central American counterpart, the tayra (*Eira barbara*), of which little is known. Kerley et al. (2002) found similarly negative effects of roads and human disturbance on the survivorship and foraging efficiency of Amur tigers (*Panthera tigris altaica*), suggesting that even in areas that are supposed to be protected

from humans, the presence of roads will facilitate a decline in large carnivore populations. Furthermore, roads and trails may increase poaching of flora and fauna in previously inaccessible areas (Kerley et al. 2002) and be the root of observed reduction in wildlife diversity in some harvested forests (Laurance et al. 2006). However, roads and trails associated with logging activities may have long-term positive effects on carnivores by facilitating movement across the landscape, reducing energy costs associated with wide-ranging habits, and providing greater access to resources that might not otherwise be readily available (Mohamed et al. 2013, Roopsind et al. 2017, Tobler et al. 2018). The diverse vegetation structure created by these practices may generate favorable conditions for some prey species, such as red brocket deer (*Mazama temama*; Tobler et al. 2018), and increased prey species abundance (Harris and McElveen 1981, Pardini 2004, Stephen and Sanchez 2014), richness, and diversity (Leopold 1933, Bridgewater 2012, Roopsind et al. 2017, Tobler et al. 2018). The greater mammalian species diversity seen in the actively logged Chiquibul Forest Reserve relative to 3 other sites in the Maya Mountain Massif (Bridgewater 2012) attests to the potentially positive influence of forest management practices on wildlife communities.

A variety of studies document the importance of prey in regulating carnivore populations, with the classic example being the snowshoe hare (*Lepus americanus*)-lynx (*Lynx canadensis*) paradigm (Elton and Nicholson 1942, Krebs et al. 2001) in which the rise and fall in predator numbers mirrors that of its prey, but with a time-lag. In Belize, Weckel et al. (2006) were the first to examine the distribution of jaguars and their prey through space and time. Subsequent studies in Belize and elsewhere have repeated or expanded upon their methods to include the spatial and temporal overlap of jaguars and pumas, and these two felids with their prey across different environmental gradients and human-altered landscapes (Foster et al. 2009, Foster et al. 2010, Harmsen et al. 2011, Foster et al. 2013). Others have similarly examined the relationship between ocelots and margay (*Leopardus wiedii*) and the availability of their prey (Irineo and Santos-Moreno 2014, Nagy-Reis et al. 2017, Santos et al. 2019), but studies investigating the importance of prey in different seasons relative to other factors are lacking (Farrell et al. 2000, Santos et al. 2019).

Human expansion has generated a variety of effects on carnivores, with habitat fragmentation, loss, and degradation from anthropogenic activities increasing conflict and competition for land and prey resources (Barnes et al. 1991, Newmark et al. 1994, Foster et al. 2009). Carnivores may be particularly vulnerable to these effects as a result of biological characteristics, such as large body sizes (relating directly to area requirements and wide-ranging habits), delayed sexual maturity, and occurrence at low densities (Noss et al. 1996; Sargeant et al. 1998, Crooks 2002, Cardillo et al. 2005). Some suggest that if carnivores, such as the jaguar, are to persist, large swaths of land protected from development are necessary (Sanderson et al. 2002). Yet, studies that examine the long-term persistence of carnivores provide weak evidence regarding the negative effects of human practices, as many are

literature reviews, analyses of pooled data from a variety of publications, or theoretical models that lack quantitative verification. For example, Grant et al. (1992), Woodroffe and Ginsberg (1998), and Cardillo et al. (2005) each conducted analyses using unstandardized data derived from a variety of publications to make broad-scale inferences on carnivore home-ranges, probability of species extinction based on population density and reserve size, and extinction risk based on body-mass interactions with predictor variables (e.g., gestation length, population density, geographic range size, etc.), respectively. Similarly, Rabinowitz and Zeller (2010) present a geographic information system (GIS) model for the best locations to preserve contiguous tracts of forest for jaguar conservation, yet they recognize that their models require rigorous field assessment and quantitative verification. Preserving contiguous forest may not benefit several members of the carnivore community, including grey fox (*Urocyon cinereoargenteus*) that require varied vegetation structure (Cypher 2003), and tayra that have apparently adapted well to human-altered landscapes (Cove et al. 2014). Indeed, several carnivore species, including jaguars, apparently take advantage of changes brought on by agricultural practices and selective logging (Cove et al. 2014, Paviolo et al. 2018, Tobler et al. 2018), yet we lack an understanding of how species interact in the tropics under these conditions.

Studies typically focus on large tropical felids and other easily captured species when examining interactions of >1 species (Weckel et al. 2006, Harmsen et al. 2009, Davis et al. 2011, Ramesh et al. 2012, Foster et al. 2013). Until recent developments in computer software programs, we investigated species individually, rather than directly evaluating their interactions with one another and relationships with the environment (Mackenzie et al. 2004, Rota et al. 2016, Nagy-Reis et al. 2017). Both competition and predation risk can change how a species uses an area (Richmond et al. 2010, Waddle et al. 2010, Krohner and Ausband 2018, Ladle et al. 2018, Murphy et al. 2018). Ignoring interspecific associations may lead to incorrect inference regarding species' habitat associations and distributions (Richmond et al. 2010, Rota et al. 2016, Nagy-Reis et al. 2017, Murphy et al. 2018) and the application of detrimental management regimes.

Carnivore conservation requires a sound understanding of carnivore ecology at multiple spatial and temporal scales. Therefore, my goal is to understand mammalian carnivore community ecology in a tropical broad-leaf rainforest. My 3 specific objectives are:

Objective 1: Examine the seasonal importance of factors affecting rainforest carnivore distribution.

- Determine how prey availability and cover, vegetation structure, environmental characteristics (e.g., slope, aspect, site harvest-history), and landscape-level (i.e., distance to water and forest reserve boundary) factors affect jaguar, puma, ocelot, grey fox, and tayra during the dry and rainy seasons.

- Establish the seasonal importance of prey availability and cover, vegetation structure, and environmental characteristics on carnivore distributions.

Objective 2: Examine the effects of roads and logging tracts on rainforest carnivores.

- Determine how road and logging tract structure, human disturbance, vegetation structure, and landscape-level (i.e., distance to CFR boundary, distance to human settlement, and road and logging tract density) characteristics of roads and logging tracts affect jaguar, puma, ocelot, grey fox, and tayra site-use intensity and site-use.

Objective 3: Examine correlates of rainforest carnivore community structure and dynamics.

- Establish if carnivore species occur independently of other carnivores.
- Understand how vegetation structure and forest infrastructure (i.e., pathway density) affects carnivore independence, co-occurrence, and site-use intensity.

STUDY AREA

Approximately one-third of Belize is under some sort of protection (Fig. 1), with the vast majority of the country still forested. However, these areas are susceptible to illegal resource extraction, agricultural incursion, and human settlements due to a lack of resources for law enforcement (Bridgewater 2012). Such practices have led to significant forest losses, at a rate of 2% of forest cover per year (Bridgewater 2012).

The CFR (59,822 ha; Fig. 1) is located in the Maya Mountain Massif, adjacent to the Caracol Archaeological Reserve (CAR; 10,339 ha; Arevalo 2011). The Chiquibul National Park (CNP; 106,838 ha) surrounds both reserves. Together they represent the largest protected area in Belize (Association of Protected Areas Management Organizations 2011; Arevalo 2011). The CFR has a subtropical climate with two distinct seasons: dry (February–June) and rainy (July–January), the latter coinciding with the hurricane season (Salas and Meerman 2008). A mosaic of deciduous and evergreen tropical broadleaf rainforest is the dominant ecosystem, but a small pocket of submontane pine forest exists at the reserve’s center (Meerman and Sabido 2001). The CFR is subject to selective logging practices from March–May each year by Bull Ridge Limited, the single logging concession in the reserve. The non-governmental organization Friends for Conservation and Development (FCD) and the Belize Forest Department oversees all research and management activities in the CFR.

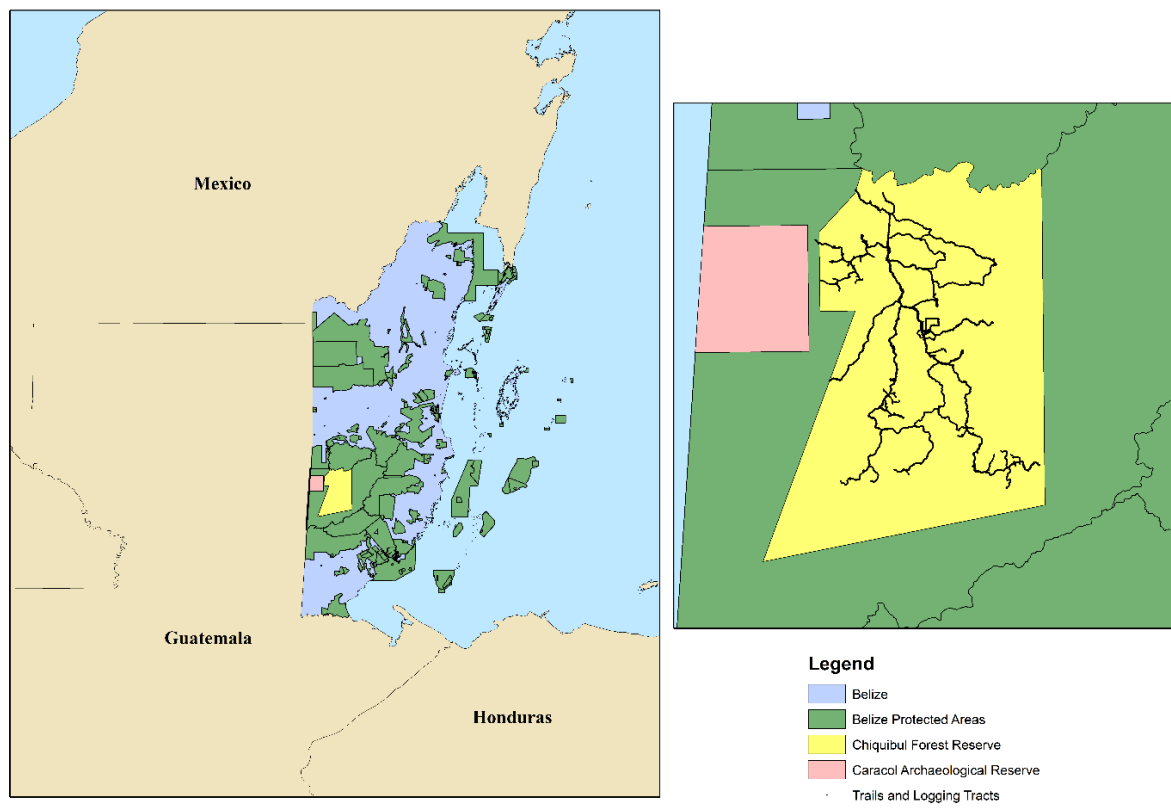


Figure 1. Belize, Central America, and a map of the Chiquibul Forest Reserve and surrounding areas, 2016.

DEFINING A “CARNIVORE”

A “carnivore” is a flesh-eating animal, or an animal whose diet is primarily composed of meat. However, although the majority of animals that belong to Order Carnivora do eat meat, meat is not always the most important food item to their diet. For example, the omnivorous habits of coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and black bears (*Ursus americanus*) – all belonging to Order Carnivora – is well documented (Bekoff and Gese 2003, Gehrt and Clark 2003, Pelton 2003). Similarly, in the tropics, the coati (*Nasua narica*) belongs to the raccoon family (Procyonidae) and Order Carnivora, with fruit and invertebrates composing an important part of its diet. Additionally, while the common opossum (*Didelphis marsupialis*) is not in Order Carnivora, it is a known scavenger and predator. Such taxonomic inconsistencies lead me to define a “carnivore” in the CFR as anything that makes meat a part of its diet. Therefore, a carnivore in the CFR 1) does not necessarily belong to Order Carnivora, and 2) may be an obligate carnivore, or omnivorous with carnivorous tendencies (Table 1). Figures 2 and 3 display the 5 most commonly captured carnivores in the CFR.

Table 1. Large and meso-carnivore species, Chiquibul Forest Reserve, Belize, Central America, 2016.

Group	Order	Common Name	Scientific Name	Obligate Carnivore
Large carnivore	Carnivora	Coyote	<i>Canis latrans</i>	No
	Carnivora	Jaguar	<i>Panthera onca</i>	Yes
	Carnivora	Puma	<i>Puma concolor</i>	Yes
Mesocarnivore	Carnivora	Striped hog-nosed skunk	<i>Conepatus semistriatus</i>	No
	Carnivora	Tayra	<i>Eira barbara</i>	No
	Carnivora	Grison	<i>Galictis vittata</i>	No
	Carnivora	Ocelot	<i>Leopardus pardalis</i>	Yes
	Carnivora	Margay	<i>Leopardus wiedii</i>	Yes
	Carnivora	Long-tailed weasel	<i>Mustela frenata</i>	Yes
	Carnivora	White-nosed coati	<i>Nasua narica</i>	No
	Carnivora	Raccoon	<i>Procyon lotor</i>	No
	Carnivora	Jaguarundi	<i>Puma yagouaroundi</i>	Yes
	Carnivora	Southern spotted skunk	<i>Spilogale augustifrons</i>	No
	Carnivora	Grey fox	<i>Urocyon cinereoargenteus</i>	No
	Didelphimorphia	Common opossum*	<i>Didelphis marsupialis</i>	No

* Not in Order Carnivora, however, has carnivorous tendencies.



Figure 2. From left to right: grey fox (*Urocyon cinereoargenteus*), tayra (*Eira barbara*), and ocelot (*Leopardus pardalis*), the 3 mesocarnivores most commonly captured on camera in the Chiquibul Forest Reserve, 2016. © L. N. Watine, The University of Tennessee



Figure 3. From left to right: jaguar (*Panthera onca*) and puma (*Puma concolor*), the 2 large carnivores most commonly captured on camera in the Chiquibul Forest Reserve, 2016. © L. N. Watine, The University of Tennessee

CAMERA SURVEYS

Wildlife monitoring efforts and ecological investigations traditionally entailed physically capturing and marking (e.g., radio-collars, tags, etc.) individuals from representative populations (Dillon and Kelly 2008). However, not only are such practices expensive (Hebblewhite and Haydon 2010), dangerous for researchers and animals, and time-intensive (e.g., it is difficult to sample species that naturally occur at low densities), they may provide poor-quality data in tropical rainforest systems where tree density, terrain, and access impedes capture and accurate location of individuals via radio-telemetry (Rabinowitz 1986, Sunquist et al. 1989, Caso 1994, Azevedo and Murray 2007, Dillon and Kelly 2008) or GPS (global-positioning satellite) technology (Cavalcanti and Gese 2009, Hebblewhite and Haydon 2010, Tomkiewicz et al. 2010, Boris Arevalo, personal communication).

Studies on wildlife demographics (Karanth 1995, Jenelle et al. 2002, Kelly 2003, Sollmann et al. 2013, Rich et al. 2014) and habits (Savidge and Seibert 1988, Weckel et al. 2006, Gerber et al. 2012, Garrote et al. 2012, Robinson et al. 2015) have used remote cameras with varying success. This technology is particularly useful for carnivores with distinct markings that can identify individuals in a population (e.g., rosettes on jaguar; Kelly 2003, Silver 2004, Kelly et al. 2013). Kelly (2003) successfully used remote cameras in the CFR to identify and monitor the jaguar population. However, all research efforts ceased in 2010 because of camera theft by illegal immigrants.

Remote camera technology continues to improve, including features such as infrared and “no-glow” capabilities, video with audio recording, and the potential to store thousands of photos, making them an invaluable tool when conducting research in remote regions. Appropriate study and sampling designs allow wildlife researchers to obtain similar information as radio-telemetry or GPS technologies with this non-invasive and relatively inexpensive tool (Silver et al. 2004, Rowcliffe et al. 2008, O’Brien and Kinnaird 2011). Furthermore, when used in conjunction with data on different ecological components (e.g., vegetation structure, prey availability), we can begin to understand the carnivore distributions, and their use of resources on the landscape.

OCCUPANCY ESTIMATION AND MODELING

Following Kelly (2003), Silver (2004), and others that have successfully used remote cameras to study carnivores, I established double-camera sites throughout the CFR (Figure 5; Chapters 1-3). From January–August 2016, I obtained 84,008 images across 51 sites. Of those images, 74%

(i.e., 61,795) were identifiable species, with the remaining images representing vegetation movement, rain and wind events, and vehicular traffic.

Unlike Kelly (2003), who sought to establish and monitor changes to the CFR's jaguar population, I used an occupancy modeling framework to examine interspecific carnivore relationships and factors affecting their coexistence, in addition to individual species relationships with characteristics of the CFR. When used in a mark-recapture framework, camera traps may over or under-estimate true population density. This is often a product of the spatial and temporal extent of the study, camera placement, and limited replications, particularly when compared to studies that use radio telemetry and GPS telemetry data to answer questions related to density (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008, Foster and Harmsen 2012, Sollmann et al. 2013). Although information regarding population structure is useful, this metric is only pertinent to a specific area, and is uninformative for managers who wish to understand broader patterns in species' relationships (e.g., habitat use, interspecific associations, etc.). Occupancy estimation can provide a better understanding of how different factors affect a species in a similar ecosystem under the same management regime and provide a good framework for broad-scale monitoring programs.

According to MacKenzie et al. (2017), until the late 1990's–early 2000's, we knew more about estimating abundance, survival, and birth and death rates via capture-recapture data than we did about one of the most basic questions in wildlife science: is a species present? Using the concept of island biogeography as its base, methods were developed to understand patch-occupancy dynamics, where a study area was designated as a “patch” viewed similar to an island, and scientists sought to determine the proportion of patches occupied by a species. In these studies, multiple patches were surveyed to determine if a species was present, which became known as “patch-occupancy dynamics.” However, those using these methods soon realized that it was unreasonable to always expect to observe a species in a patch, even if it was really present, and incorporated a parameter to account for the imperfect detection of the species that would enhance our ability to estimate the probability that a species occupies a patch. An example of the importance of incorporating this detection parameter into estimating if a species is present is highlighted in Table 2, which displays both naïve and true occupancy probability estimates for 5 commonly captured carnivore species in the CFR and different p and ψ untransformed estimates across all seasons, within specific seasons, and on trails and logging tracts. The true occupancy estimate is derived by incorporating species detections, whereas the naïve occupancy estimate does not incorporate this parameter, and thus grossly underestimates the probability that a species uses a site. Taken together, p and ψ provide information on the drivers of species distributions in an area or use of a specific site (MacKenzie et al. 2006, MacKenzie et al. 2017).

As these methods evolved, there was a shift from viewing occupancy as the proportion of patches occupied, to the probability a species occurs in a study area, to an estimate of site-

use by a species. The latter perspective is typically used in a single contiguous area in which a species is known to occur, and scientists want to understand how different variables are correlated with a species site-use and detectability. As both our understanding of the different conditions that occupancy estimation can be applied to (e.g., habitat modeling [Tyre et al. 2003, Gu and Swihart 2004] and metapopulation incidence functions [Moilanen 2002]) progressed alongside technological advancements, methods were developed that allowed scientists to apply different environmental covariates to the detection (p) and site-use (ψ) parameters.

Table 2. Probability estimates for 5 carnivore species' naïve occupancy, true occupancy, and when detection and occupancy are constant, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Sites Detected	Total Sites	Naïve Ψ^a	True Ψ^b	p^c	Ψ^d
Jaguar	Both	47	51	0.16	0.92	0.16	1.00
	Dry	36	51	0.14	0.71	0.17	0.79
	Rainy	32	51	0.17	0.63	0.22	0.76
Puma	Both	47	51	0.21	0.9	0.21	1.00
	Dry	44	51	0.23	0.86	0.25	0.89
	Rainy	30	51	0.17	0.59	0.25	0.68
Ocelot	Both	43	51	0.22	0.84	0.22	1.00
	Dry	42	51	0.24	0.82	0.29	0.84
	Rainy	35	51	0.19	0.69	0.19	1.00
Grey fox	Both	31	51	0.12	0.61	0.2	0.61
	Dry	22	51	0.11	0.43	0.26	0.44
	Rainy	22	51	0.13	0.43	0.26	0.49
Tayra	Both	29	51	0.06	0.57	0.09	0.66
	Dry	23	51	0.06	0.45	0.1	0.64
	Rainy	14	51	0.05	0.27	0.1	0.51

^aThe proportion of sites occupied, without accounting for non-detection. ^bThe proportion of sites where carnivores were detected ≥ 1 time. ^cProbability we will detect the species when detection is constant (i.e., without accounting for the effects of variables), given that the species is present. ^dProbability that the species occurs at the site when site-use is constant (i.e., without accounting for the effects of variables).

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CHAPTER I
SEASONAL IMPORTANCE OF FACTORS AFFECTING RAINFOREST CARNIVORE
DISTRIBUTIONS

ABSTRACT

Beyond the suggestion that water and food resources affect Neotropical wildlife species, we have a limited understanding of the effects of seasons on carnivore distributions. Without a solid understanding of the ecology of the system under study that includes the effects of seasons on observed patterns, we cannot create informative models that allow us to interpret the effects of spatial characteristics on carnivore distributions. Therefore, my goal was to evaluate several spatial characteristics important to predicting the distributions of 5 commonly captured Neotropical carnivores. Using trail cameras and sampling vegetation during both the dry and rainy seasons, I investigated the effects of prey availability and cover, vegetation structure, permanent site characteristics (e.g., site harvest-history, slope, aspect), and landscape-level characteristics' (e.g., distance to water sources and) on jaguar, puma, ocelot, grey fox, and tayra in the Chiquibul Forest Reserve in Belize, Central America. The importance of site-specific categories in determining carnivore distributions changed between seasons for all species except jaguars. Both prey and vegetation appeared in supported models more frequently than permanent site characteristics. Distance to water sources varied in its effects on jaguar, ocelot, grey fox, and tayra site-use during the dry season, and predicted how puma site-use intensity. Landscape-level variables during the rainy season had meaningful effects on puma and grey fox site-use alone, suggesting site-use is constant for other species during this period at larger spatial scales. Variables supported in both site-use intensity and site-use processes for a species (i.e., puma and grey fox) sometimes had opposing effects, emphasizing the importance of having a working knowledge of species and systems to interpret effects on parameters. Reducing palm density and canopy cover may increase puma and tayra site-use intensity, which would decrease overall vegetation density and potentially increase ocelot site-use intensity during the dry season. Pumas typically used sites interior to the forest reserve where logging activities were infrequent, suggesting that pumas may be more sensitive than other species to changes beyond the effects of seasons. Increasing protection around key features (i.e., riparian areas) could help mitigate added pressure on carnivores from human disturbance during limiting periods.

KEY WORDS: Prey, seasonal effects, spatial scale, vegetation structure, water.

INTRODUCTION

Investigations of the effects of seasons on carnivores typically describe differences in diet between several important species (Farrell et al. 2000, Bianchi et al. 2014), activity patterns

(Perez-Irineo and Santos-Moreno 2014), or the importance of a few categories (e.g., prey or vegetation type; Dell'Arte et al. 2007, Burton et al. 2012, Cove et al. 2014, Irineo and Santos-Moreno 2014, Kalle et al. 2014) on species distributions or abundance. In the tropics, this latter suite of studies usually focuses on the dry season, which is the resource-limiting season (i.e., water is scarce). Additionally, the dry season provides greater access to humans who study these systems than the rainy season, leading to temporal bias on the effects of different factors on carnivore distributions. Large carnivores (e.g., jaguar [*Panthera onca*] and puma [*Puma concolor*]) dominate these studies due to the relative ease with which they and their prey are captured with trail cameras (Cavalcanti and Gese 2010, Harmsen et al. 2011, Morrison et al. 2014, Paviolo et al. 2018, Guerisoli et al. 2019), compared with more cryptic mesocarnivores. With a few exceptions (Farrell et al. 2000, Santos et al. 2019), studies also rarely document the seasonal importance of prey availability. Because of the bias towards sampling large carnivores and the few studies quantifying seasonal importance of resources, there is a knowledge deficit regarding the seasonal effects of factors on Neotropical rainforest carnivore distributions.

When water becomes scarce, both predatory and prey species seek out permanent water sources in the form of rivers and streams, with prey also using juicy fruits for water (Paredes et al. 2017, Montalvo et al. 2018). Masting trees such as sapodilla (*Manilkara* spp.) and figs (*Ficus* spp.) provide many avian and mammalian prey species with predictable food sources during the dry season (Janzen 1973, Herre 1996, Bridgewater 2012), creating conditions that likely facilitate constant prey populations. However, with greater water availability during the rainy season, prey may occur more evenly across the landscape (Emmons 1987), which could require some predators (e.g., jaguars) to search more intensively for prey than during the dry season (Montalvo et al. 2018). Furthermore, in areas subject to logging activities, canopy gaps stimulate understory plant growth (Denslow et al. 1998) that decreases visibility for both predators and prey, creating conditions unsuitable for prey aggregation (Emmons 1987), and thus limiting prey availability for carnivores.

Although protected areas provide opportunities to study carnivores in relatively natural environments, exposure to varying scales of disturbance (Michalski and Peres 2005, Paviolo et al. 2009) is common, as most species disperse to and settle in unprotected areas that are more common on the landscape (Woodroffe and Ginsberg 1998, Athreya et al. 2013). Certain levels of human disturbance can be beneficial for tropical wildlife, as pathways built for recreation and resource extraction can facilitate species access to resources and ease of movement across the landscape (Montalvo et al. 2018, Tobler et al. 2018). As Montalvo et al. (2018) demonstrated, both predators and prey benefited from the presence of pathways that facilitated access to watering holes during the dry season. However, these same structures can negatively affect how wildlife use the landscape, particularly in areas where resource extraction generates favorable conditions for poaching and human encroachment (Laurance et al. 2006,

Mayor et al. 2015). Species that are sensitive to humans may require a refuge to retreat to during stressful periods (e.g., the dry season) so that they are not expending energy to avoid humans while also finding resources.

Until recently, time, money, technological constraints, and access to remote areas limited our understanding of tropical carnivore ecology (Rabinowitz 1986, Dillon and Kelly 2008, Hebblewhite and Haydon 2010, Tomkiewicz et al. 2010). The advent of camera traps has allowed more spatial and temporal replication and the ability to capture ≥ 1 species, with minimal start-up costs (O'Brien and Kinnaird 2011, Neigy-Reis et al. 2017, Montalvo et al. 2018, Santos et al. 2019). Additionally, greater computing power and new statistical methodologies facilitate multi-species analyses. Occupancy modeling is a powerful tool that directly models both detection (p) and site-use (ψ) processes simultaneously to allow us to explore drivers of species distributions (MacKenzie et al. 2017). This analysis framework enhances inference on species' distributions by applying covariates to p and ψ parameters. Where p used to be a nuisance parameter, occupancy analyses now use this parameter to improve predictions and as a variable of interest in its own right (MacKenzie et al. 2006, MacKenzie et al. 2017, Ladle et al. 2018). As more studies apply occupancy modeling to camera trap data on continuous landscapes instead of patches, there is a shift in the interpretation of p towards viewing it as an index of site-use intensity (Ladle et al. 2018). Correctly interpreting p in this context requires a baseline-knowledge of the species under study, as a negative beta value for this parameter could have several meanings, particularly at different spatial scales. For example, a traditional interpretation of negative beta-value for p affected by covariates would indicate the species is avoiding certain characteristics. However, when taken together with ψ , negative p might suggest that the conditions at the site provide ideal cover and other resources that facilitate the species' ability to remain at the site. This has important implications for seasonal differences in species resource-use: if we manage resources based on rainy-season conditions and do not account for the dry season, we might negatively affect wildlife populations over time (Van Horne 1983).

Therefore, my goal was to understand the factors important in determining the distribution of 5 commonly captured carnivores in the Chiquibul Forest Reserve during both the dry and rainy season. I investigated the effects of both site-specific and landscape-level factors on jaguar, puma, ocelot (*Leopardus pardalis*), grey fox (*Urocyon cinereoargenteus*), and tayra (*Eira barbara*). I hypothesized that the importance of site-specific categories (i.e., prey availability and cover, vegetation structure, and permanent site-characteristics) would change between seasons for each species, with vegetation structure playing a more important role during the dry-season. Because the harvest-status of each site could act as an indicator of human disturbance, I predicted it would also play a role in species site-use intensity between

seasons. Finally, I hypothesized that distance to water sources would affect carnivores during the dry season, but site-use would be constant during the rainy season.

METHODS

I examined factors affecting jaguar, puma, ocelot, grey fox, and tayra during the dry and rainy seasons in the Chiquibul Forest Reserve (CFR) from January–August 2016 by conducting camera surveys and assessing characteristics (i.e., site-specific and landscape-level). The survey period covered 12 weeks of the dry season and 7 weeks of the rainy season.

Study Area

The Chiquibul Forest Reserve (CFR; 59,822 ha) is in the Maya Mountain Massif, adjacent to the Caracol Archaeological Reserve (CAR; 10,339 ha) in Belize. The Chiquibul National Park (CNP; 106,838 ha) surrounds both reserves, and represents the largest protected area in Belize (Association of Protected Areas Management Organizations 2011; Arevalo 2011). The CFR has a subtropical climate with two distinct seasons: dry (February–May) and rainy (June–January), the latter coinciding with the hurricane season (Salas and Meerman 2008). Tropical broadleaf semi-deciduous rainforest is the dominant ecosystem, but a small pocket of submontane pine forest exists at the reserve's center (Meerman and Sabido 2001). Multiple-use activities such as recreation, gold-mining, research, and logging which have created a network of dirt roads and hiking trails throughout the reserve in various states of use and neglect. Currently, the CFR is subject to selective logging practices from March–May each year by Bull Ridge Limited, the single logging concession in the reserve. The logging concession organized the CFR into 500 ha blocks, and the Belize Forest Department allows Bull Ridge to conduct logging operations in up to 2 of these blocks (i.e., 1000 ha) each year. The non-governmental organization Friends for Conservation and Development (FCD) and the Belize Forest Department oversees all research and management activities in the CFR.

Camera Surveys

To understand factors affecting seasonal distributions of carnivores in the CFR, I established a systematic grid (N = 51; Fig. 4) of Moultrie M-880 Mini Game Camera trail cameras (Moultrie Feeders, EBSCO Industries, Inc., Alabaster, AL) with infrared (IR) abilities every 2.25 x 2.25-km. Each camera received a blank SanDisk Ultra 16GB SD card, allowing for the collection of up to 9,999 photos. I recorded each site's UTM coordinates with a handheld GPS unit under the North American Datum of 1927 (NAD27).

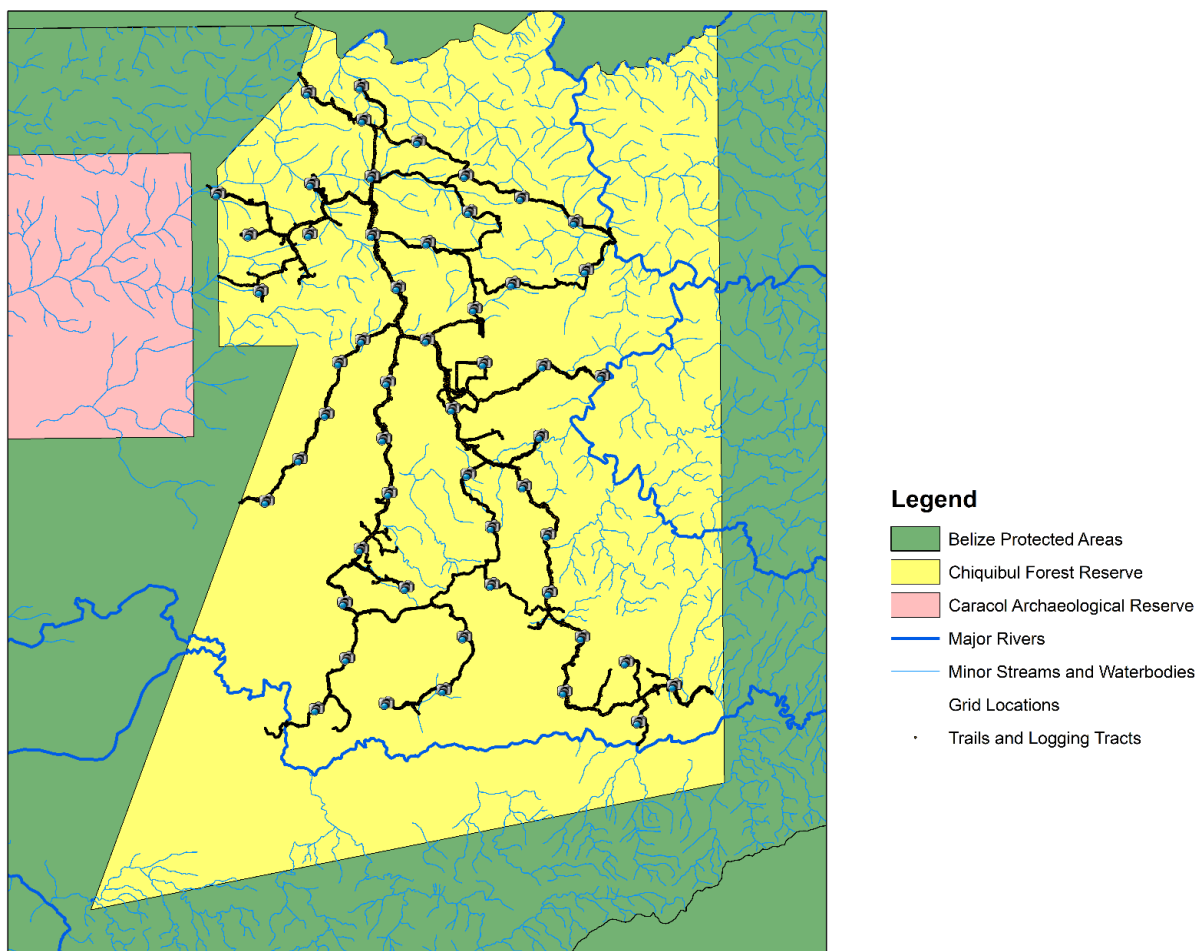


Figure 4. A map of the Chiquibul Forest Reserve camera locations, trails and logging tracts, water sources, and surrounding areas, Belize, Central America, 2016.

My systematic sampling regime established camera sites along logging tracts, trails (human and animal; Kelly 2003), streams, and interior forest (e.g., not bisected by roads/trails/natural movement pathways; >30-m from any human-built pathway). Following protocols established by researchers studying carnivores in Belize (Silver et al. 2004, Kelly et al. 2013), each site received 2 cameras, placed on opposing trees, to reduce the chances of data loss from camera malfunctions, animals moving too close to cameras, or too quickly past a single camera. I set cameras >3 m from site-center to maximize my chances of capturing animals, with cameras placed on trees or other suitable objects (e.g., wooden stake) >5 cm dbh. Trail cameras are sensitive enough that they can be accidentally triggered by waving vegetation, sunlight, and rain; therefore, I cleared vegetation between and within 1 m of the cameras, faced cameras in directions other than east or west whenever possible, and offset cameras by 0.3 m so that they were not directly opposite of one another to prevent camera IR or flash from triggering the opposite camera (Silver et al. 2004). I recorded the height, direction faced, and distance between cameras, and held a card to each camera with the site number, date, and time to document site set-up, and site-check/reset.

I set all cameras to take 3 photos/event with a 5-second delay between picture events once triggered. This setting facilitated my ability to capture potentially cryptic species (e.g., tayra) that may remain in range after the initial capture but initially moved too fast for cameras to accurately capture. I re-visited sites every 2–3 weeks to avoid data loss. The function “Motion Freeze” was set to “On” to maximize image clarity, and all photos were imprinted with the camera’s name, date, time, temperature (Celsius), and moon phase.

Site-Specific Characteristics

Prey Availability and Cover

I assessed prey availability at each site by dividing the number of prey capture-events by the total number of wildlife capture-events for the site. Although I counted the number of individuals captured during each event, I did not factor the number of individuals into prey-availability metrics. I determined all prey (AllPrey [i.e., mammal and avian combined]), mammalian prey (MPrey), and avian prey (BPrey) available at sites for large carnivores and mesocarnivores, respectively (Table 3). I did not examine the relationships between carnivores and individual prey items (e.g., puma and red brocket deer [*Mazama americana*], ocelot and dove spp. etc.) because others have established that these species-specific relationships exist, but have not looked at the entire prey-base available. I counted all logs (e.g., coarse woody debris ≥ 10 cm at midpoint) and stumps (<1.37 m tall and ≥ 10 cm diameter) within the 0.1 ha plot (Fig. 5) to obtain density (#/ha) of each at the site as an index of prey cover.

Permanent Characteristics

In the middle of a 0.1 ha plot centered on the camera sites (Fig. 5), I recorded the following permanent characteristics: slope (%) and aspect (direction) with a SUUNTO clinometer, and elevation (m) with a handheld GPS unit. The harvest-history of the site was documented, with

each site assigned one of the following histories: none (i.e., it has not been harvested by a logging concession in the last 15 years, but might be in the future), protection (i.e., the logging concession is not allowed to conduct timber harvest in that area), and harvested (i.e., the site was part of logging operations in the last 15 years).

Vegetation Structure

To characterize vegetation structure at each site, I recorded site-specific vegetation characteristics in a 0.1-ha circular plot centered on the camera site (Fig. 5). I measured vertical visual obstruction with a 2-m cover pole (Griffith and Youtie 1988) in the surrounding forest and through site-center. To obtain metrics describing vertical visual obstruction in the surrounding forest, I set the cover pole at plot center (i.e., between the two cameras), and viewed it from 5.6-m away at a height of 1 m at 5 points along 2 parallel 35.6-m transects (N = 10 points). These 2 transects were oriented parallel to each other and the camera sets. I used these measurements to derive total variance in vertical forest cover (VarForVVO) and to estimate total percent forest cover (%ForVVO) at each site. On a third transect through site center, I viewed the cover pole from a height of 1-m from both ends (i.e., 17.8-m from site center) of the transect and used these measurements to estimate percent vertical visual obstruction through site center (%SCVVO).

Along the 3 parallel transects used to obtain vertical visual obstruction metrics, I used the line-intercept method (Hays et al. 1981) to quantify horizontal visual obstruction (%HVO). To obtain %HVO, I held a 50 m tape 1 m above the ground and measured the horizontal spread (cm) of vegetation (e.g., herbaceous, palm, shrub) 0.5-1.0-m tall that hit the line. I assessed total canopy cover (%CCAll), hardwood canopy cover (%CCHW), and palm canopy cover (%CCPalm) along these same three transects with a yes/no densitometer every 2 m, viewed from a height of 1 m. Finally, along the transect through site center, I obtained tree species richness (i.e., total [TreeRich], hardwood [HWRich], and palm [PalmRich]) at the site by counting the number of different species of trees and assigning them to their respective categories.

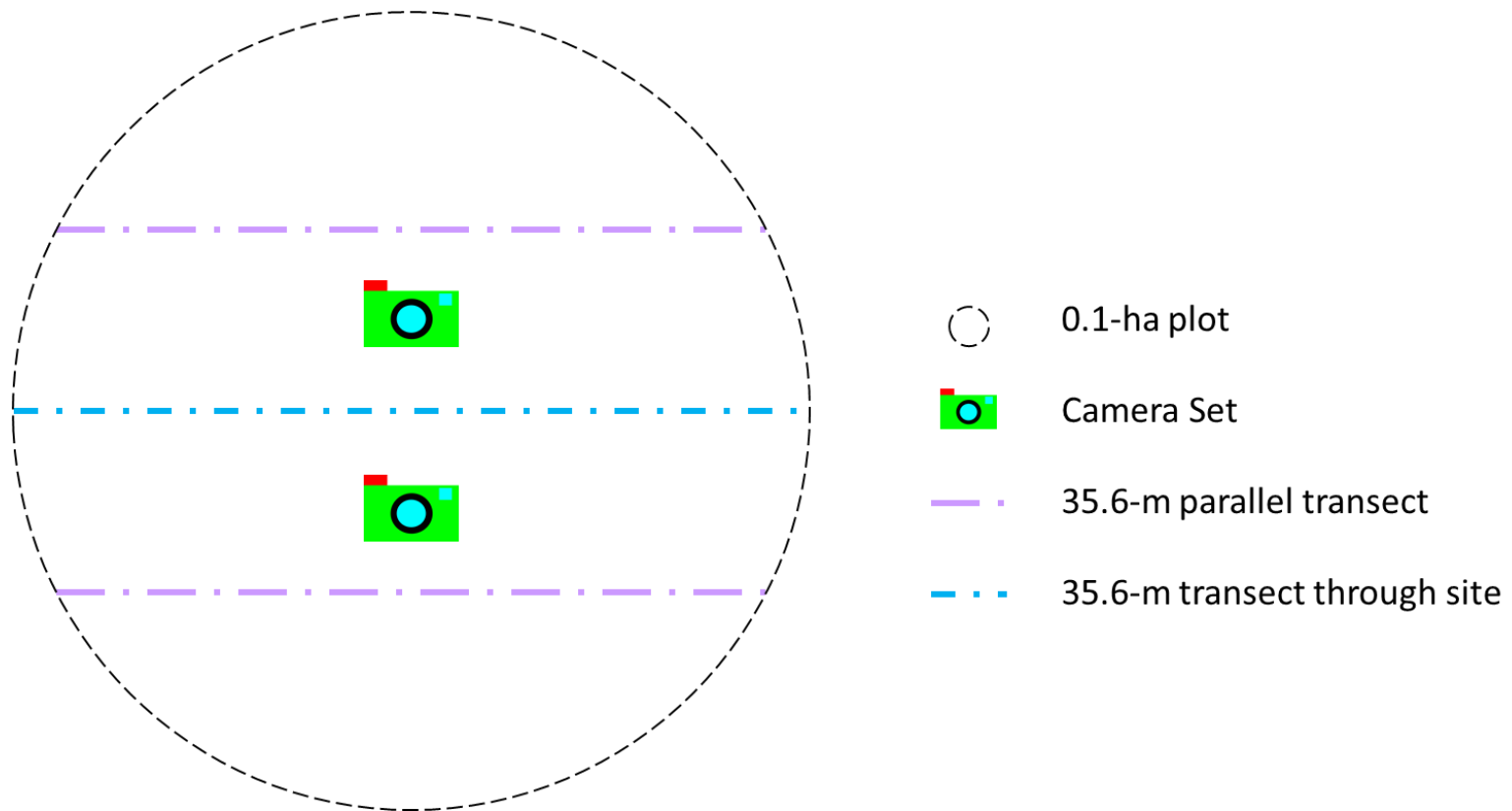


Figure 5. Camera site vegetation plots, Chiquibul Forest Reserve, Belize, Central America, 2016.

Table 3. Captured prey items, Chiquibul Forest Reserve, Belize, Central America, 2016.

Category	Common Name	Scientific Name	Prey Group ^a
Mammals	Paca	<i>Agouti paca</i>	B
	Agouti	<i>Dasyprocta punctata</i>	B
	Nine-banded armadillo	<i>Dasypus novemcinctus</i>	LC
	Common opossum	<i>Didelphis marsupialis</i>	B
	Red brocket deer	<i>Mazama americana</i>	LC
	White-tailed deer	<i>Odocoileus virginianus</i>	LC
	Collared peccary	<i>Pecari tajacu</i>	LC
	Deppe's squirrel	<i>Sciurus deppei</i>	MC
	Yucatan squirrel	<i>Sciurus yucatanensis</i>	MC
	White-lipped peccary	<i>Tayassu pecari</i>	LC
	Small rodent spp. ^b	<i>unknown</i>	MC
Birds	Great curassow	<i>Crax rubra</i>	LC
	Little tinamou	<i>Crypturellus soui</i>	LC
	Brown jay	<i>Cyanocorax morio</i>	MC
	Ocellated turkey	<i>Meleagris ocellata</i>	LC
	Parauque	<i>Nyctidromus albigollis</i>	MC
	Spotted wood quail	<i>Odontophorus guttatus</i>	MC
	Plain chachalaca	<i>Ortalis vetula</i>	MC
	Crested guan	<i>Penelope purpurascens</i>	LC
	Great tinamou	<i>Tinamus major</i>	LC
	Dove/pigeon/bird spp. ^c	<i>unknown</i>	MC

^aConsumed by large carnivores (LC), mesocarnivores (MC), or both large and mesocarnivores (B). ^bUnknown rats and other small rodent species, grouped together. ^cPigeons, doves, and other smaller bird species, grouped together.

Landscape-Level Characteristics

To understand seasonal effects at broader spatial scales, I constructed a geographic information system (GIS) in ArcGIS (Environmental Systems Research Institute 2014) using high-resolution aerial photographs and by ground-truthing. I assessed the effects of the absolute distance of sites to both the west (westB) and east (eastB) boundary of the CFR on carnivore distributions. The CFR westB is close to the Guatemalan border and subject to the effects of illegal activities (e.g., illegal immigration, poaching, logging, gold mining, etc.), whereas the eastB is close to the spine of the Mayan Mountain Massif in more remote and rugged terrain. I assessed the effects of waterbodies in the CFR by determining both the absolute distance to both permanent (MajorWU) and ephemeral (MinorWU) water, and the radiating effects of the distance to the nearest water sources (MajorWB and MinorWB; buffered by 2-km). I ground-truthed ephemeral water during both seasons and established that they were dry during the dry season.

Occupancy Estimation

Camera surveys covered 12 weeks of the dry season and 7 weeks of the rainy season. Each survey period comprised 1 week, during which I considered a species as using a site if I captured it ≥ 1 time/survey period. If cameras captured a species at a site ≥ 1 time, the site received a “1,” or “present” for that survey, and a “0” otherwise (MacKenzie et al. 2006).

Parameter Interpretation: p and ψ

Because I interpret “occupancy” as a measure of site-use rather than true occupancy, and because movement in and out of the area is random, I could relax the assumption of closure to changes in occupancy during repeated surveys (Mackenzie et al. 2004, Farris et al. 2015, Mackenzie et al. 2017). I interpret occupancy (ψ) to mean the probability a species will use a site, rather than true occupancy, given that our data represents a “presence-only” data set, and sites are point locations of camera traps (MacKenzie et al. 2003, MacKenzie et al. 2006, Farris et al. 2015). All 5 carnivore species investigated occur in the CFR, but variation in population density and movement patterns affects 1) how they use the landscape, and 2) the frequency and intensity with which we observe species (Rowcliffe et al. 2008, Efford 2012, Burton et al. 2015, Latif et al. 2016). Therefore, when incorporating the effects of variables on detection (i.e., p), the interpretation of this parameter shifts from referring to a simple detection probability of a species at a location, to informing carnivores’ site-use intensity (Ladle et al. 2018). I interpret the results of p and site-use parameters together to understand carnivore distributions within and between seasons.

Model Development

Based on the literature, prior knowledge and field experience, and project goals, I developed sets of a priori single- and multiple-variable candidate models for single-season occupancy analyses (MacKenzie et al. 2006) where I considered the effects of site-specific and landscape factors on jaguar, puma, ocelot, grey fox, and tayra during the dry and rainy seasons. At the

site-specific level, I examined the seasonal effects of variables on carnivore distributions in 4 analyses (i.e., permanent site characteristics, prey availability and cover, vegetation structure, and combined categories). The fourth analysis set the top models from the 3 separate category analyses to compete against one another, following the recommendations of Arnold (2010; i.e., solution 5). My goal was to see what category was most important in determining carnivore distributions during the dry and rainy season and if category importance changed between seasons. I assessed landscape-level and site-specific characteristics separately to 1) reduce confounding effects, and 2) provide clear recommendations at multiple spatial scales for managers. For all analyses, I estimated the effects of variables on site-use intensity (p) and site-use (ψ) simultaneously.

I did not consider models that contained correlated variables ($|r| > 0.70$; Tirpak et al. 2008). I limited individual models to 3 predictor variables per parameter (i.e., p and ψ) to reduce the likelihood of over-fitting. I examined AIC_c values, AIC_c differences (ΔAIC_c), and Akaike weights (w_i) for models with different combinations of predictor variables and considered models with $\Delta AIC_c \leq 2$ supported (Burnham and Anderson 2002). Where multiple models found support, I used model averaging to increase precision of inference. When 85% confidence intervals (CI) around beta values for variables within supported models overlapped with zero, I considered them to be uninformative (Payton et al. 2003, Arnold 2010). When an 85% CI was >0 , I indicate that the variable had positive effects, and negative effects if <0 . I used library “unmarked” for all occupancy and detection analyses, with model averaging for supported models using library “AICcmodavg” in R version 3.4.1 (R Core Team 2017). For brevity and clarity, I report supported models from the 1) final suite of models combining categories at the site-specific level, and 2) landscape-level effects on carnivore distribution.

RESULTS

For jaguars and pumas, I examined 11 models of permanent characteristics; 17 models of prey availability and cover characteristics; and 13 models of vegetation structure during both the dry and rainy season. For ocelot, grey fox, and tayra, I examined 11 models for permanent characteristics; 24 models of prey availability and cover; and 18 models of vegetation structure during both the dry and rainy season. The number of models in the final suite of models differed by species and season, based on models supported in the different category analyses. At the landscape level, I examined 17 models during both dry and rainy seasons for all species (Appendix).

Except for jaguars, the importance of site-specific categories in determining carnivore distribution changed between seasons. Both prey and vegetation categories appeared in supported models more frequently than permanent site characteristics. The harvest status of a

site affected ocelots and grey fox similarly, but in opposing seasons (i.e., during the rainy season for ocelot and the dry season for fox). Jaguar and tayra were the only species for which a single category was important during both seasons (i.e., prey availability and vegetation structure, respectively).

At the landscape level, distance to water sources varied in its effects on jaguar, ocelot, grey fox, and tayra site-use during the dry season and predicted puma site-use intensity. During the rainy season, variables only had meaningful effects on puma and grey fox, suggesting site-use is constant during this period for other species. Constant site-use by jaguar, ocelot, and tayra during the rainy season suggests that the CFR provides quality habitat at this spatial scale for these species. Of the 5 species, variables affected ocelot site-use intensity alone during the rainy season. All other species site-use and site-use intensity were constant during the rainy season.

Jaguar

Site-Specific

Of the 6 models examined during the dry season, only 1 model found support. As mammalian prey (Mprey) availability increased at sites, jaguar site-use intensity decreased, but site-use remained constant. The same model was the only model with support during the rainy season, with similar effects (Tables 4 and 5).

Landscape-Level

Contrasting with site-specific effects on jaguars, site-use intensity was constant for all models during the dry and rainy seasons. During the dry season, 2 models containing distance to water sources had support. Jaguars used sites farther from ephemeral water sources (MinorWU) during the dry season, but distance to major water sources (MajorWU) was uninformative. In contrast, only 1 model had support during the rainy season. The distance to the east boundary (eastB) had uninformative effects on jaguar site-use, suggesting that jaguar use of the CFR during the rainy season is constant at the landscape-level (Tables 6 and 7).

Table 4. Supported models^a of site-specific characteristics affecting rainforest carnivores during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	Dry	p(Mprey ^e) Ψ(.)	3	461.12	0	0.75	-227.3
	Rainy	p(Mprey) Ψ(.)	3	288.7	0	0.92	-141.09
Puma	Dry	p(.) Ψ(%HVO ^f + PalmRich ^g)	4	633.02	0	0.27	-312.08
		p(%CCPalm ^h + PalmRich) Ψ(.)	4	633.45	0.43	0.22	-312.29
		p(%SCVVO ⁱ) Ψ(.)	3	633.92	0.89	0.17	-313.7
		p(.) Ψ(PalmRich)	3	634.12	1.1	0.16	-313.81
	Rainy	p(logs ^j) Ψ(Bprey ^k)	4	301.79	0	0.99	-146.46
Ocelot	Dry	p(%SCVVO + %ForVVO ^l) Ψ(.)	4	638.88	0	0.52	-315
		p(logs) Ψ(Mprey + Bprey)	5	640.12	1.24	0.28	-314.39
	Rainy	p(harvest status ^m) Ψ(.)	4	325.53	0	0.94	-158.33
Grey Fox	Dry	p(harvest status) Ψ(.)	4	352.66	0	0.99	-171.89
	Rainy	p(%SCVVO) Ψ(.)	3	228.14	0	0.53	-110.82
		p(%HVO) Ψ(%SCVVO + %HVO)	5	229.25	1.11	0.3	-108.96
Tayra	Dry	p(.) Ψ(slope ⁿ)	3	281.08	0	0.39	-137.29
		p(%SCVVO) Ψ(.)	3	281.15	0.07	0.38	-137.32
		p(.) Ψ(.)	2	282.19	1.11	0.23	-138.97
	Rainy	p(%CCHW ^o) Ψ(.)	3	144.3	0	0.54	-68.28
		p(%CCPalm) Ψ(.)	3	145.07	0.77	0.36	-69.28

^aAkaike's Information Criterion [AIC]; ΔAIC_c ≤ 2. ^bSite-use intensity (p) and site-use (Ψ) considered simultaneously. ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^eMammalian prey availability at sites, measured as a proportion of mammalian prey capture-events divided by the total number of wildlife capture-events at the site. ^fPercent horizontal visual obstruction. ^gPalm species richness. ^hPercent palm canopy cover. ⁱPercent vertical visual obstruction through site-center. ^jLog (coarse woody debris ≥ 10 cm at midpoint) density (#/ha). ^kAvian prey availability at sites, measured as a proportion of avian prey capture-events divided by the total number of wildlife capture-events at the site. ^lPercent vertical visual obstruction in the surrounding forest. ^mHarvest history: none (i.e., it has not been harvested by a logging concession in the last 15 years, but might be in the future), protection (i.e., the logging concession is not allowed to conduct timber harvest in that area), and harvested (i.e., the site was part of logging operations in the last 15 years). ⁿPercent slope of the site. ^oPercent hardwood canopy cover at the site.

Table 5. Model-averaged coefficients from top models examining site-specific characteristics affecting jaguar, puma, ocelot, grey fox, and tayra during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Parameter ^a	Variable	β^b	Standard Error	85% Confidence Interval	
						Lower	Upper
Jaguar	Dry	p	Mprey ^c	-0.64	0.17	-0.89	-0.4
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
	Rainy	p	Mprey	-0.73	0.22	-1.04	-0.42
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Puma	Dry	p	%SCVVO ^d	-0.34	0.14	-0.54	-0.15
			PalmRich ^e	0.37	0.14	0.17	0.57
			%CCPalm ^f	-0.39	0.17	-0.64	-0.14
		ψ	%HVO ^g	-0.89	0.51	-1.62	-0.15
			PalmRich	-1.54	0.83	-2.74	-0.35
	Rainy	p	logs ^h	0.42	0.17	0.17	0.67
Ocelot	Dry	p	%SCVVO	-0.37	0.13	-0.57	-0.18
			%ForVVO ⁱ	-0.19	0.1	-0.34	-0.04
			logs	-0.3	0.12	-0.47	-0.13
		ψ	Mprey	-0.73	0.42	-1.34	-0.12
			Bprey	6.3	3.59	1.13	11.47
	Rainy	p	status ^k (protection)	-1.18	0.5	-1.9	-0.46
			status(harvested)	-1.43	0.4	-2.01	-0.85
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Grey Fox	Dry	p	status(protection)	-1.2	0.38	-1.75	-0.66
			status(harvested)	-3.51	0.81	-4.67	-2.34
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
	Rainy	p	%SCVVO	-1.95	0.53	-2.71	-1.18
			%HVO	-0.63	0.21	-0.92	-0.33
		ψ	%SCVVO	-2.41	0.9	-3.7	-1.11
Tayra	Dry	p	%SCVVO	-0.41	0.24	-0.76	-0.07
			slope ^l	-0.98	0.69	-1.97	0.01
	Rainy	p	%CCHW ^m	0.77	0.34	0.27	1.26
			%CCPalm	-0.93	0.5	-1.65	-0.22
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>

Table 5. Continued.

^aSite-use intensity (p) and site-use (Ψ). ^bParameter estimates. ^cMammalian prey availability at sites, measured as a proportion of mammalian prey capture-events divided by the total number of wildlife capture-events at the site. ^dPercent vertical visual obstruction through site-center. ^ePalm species richness. ^fPercent palm canopy cover. ^gPercent horizontal visual obstruction. ^hLog (coarse woody debris ≥ 10 cm at midpoint) density (#/ha). ⁱAvian prey availability at sites, measured as a proportion of avian prey capture-events divided by the total number of wildlife capture-events at the site. ^jPercent vertical visual obstruction in the surrounding forest. ^kHarvest history: none (i.e., it has not been harvested by a logging concession in the last 15 years, but might be in the future), protection (i.e., the logging concession is not allowed to conduct timber harvest in that area), and harvested (i.e., the site was part of logging operations in the last 15 years). ^lPercent slope of the site. ^mPercent hardwood canopy cover at the site.

Table 6. Supported models^a of landscape-level characteristics affecting rainforest carnivores during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	Dry	p(.) Ψ(MinorWU ^e)	3	463.32	0.00	0.50	-228.41
		p(.) Ψ(MajorWU ^f + MinorWU)	4	464.23	0.91	0.32	-227.68
	Rainy	p(.) Ψ(eastB ^g)	3	292.48	0.00	0.55	-142.99
Puma	Dry	p(MajorWB ^h) Ψ(.)	3	633.60	0.00	0.28	-313.54
		p(MajorWU) Ψ(.)	3	634.25	0.65	0.20	-313.87
	Rainy	p(.) Ψ(westB ⁱ + eastB)	4	301.26	0.00	0.56	-146.19
Ocelot	Dry	p(eastB) Ψ(MajorWU + MinorWU)	5	637.31	0.00	0.83	-312.99
	Rainy	p(MajorWU) Ψ(.)	3	324.96	0.00	0.39	-159.22
		p(MajorWB) Ψ(.)	3	325.72	0.76	0.27	-159.60
		p(MajorWU + MinorWU) Ψ(.)	4	326.33	1.37	0.20	-158.73
Grey Fox	Dry	p(.) Ψ(MinorWU)	3	370.97	0.00	0.29	-182.23
		p(.) Ψ(MajorWU + MinorWU)	4	372.69	1.73	0.12	-181.91
	Rainy	p(.) Ψ(westB + eastB)	4	245.70	0.00	0.27	-118.42
		p(.) Ψ(MinorWU)	3	246.63	0.93	0.17	-120.06
Tayra	Dry	p(.) Ψ(westB + eastB)	4	279.52	0.00	0.26	-135.33
		p(.) Ψ(MinorWU)	3	280.30	0.78	0.17	-136.90
		p(.) Ψ(eastB)	3	280.76	1.24	0.14	-137.13
		p(.) Ψ(MajorWU + MinorWU)	4	281.40	1.88	0.10	-136.27
	Rainy	p(.) Ψ(MajorWB)	3	139.29	0.00	0.40	-66.39
		p(.) Ψ(MajorWU)	3	139.59	0.30	0.35	-66.54

^aAkaike's Information Criterion [AIC]; ΔAIC_c ≤ 2. ^bSite-use intensity (p) and site-use (Ψ) considered simultaneously. ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^eAbsolute distance to the nearest ephemeral water source. ^fAbsolute distance to the nearest permanent water source. ^gAbsolute distance to the eastern boundary of the Chiquibul Forest Reserve. ^hRadiating effects of the nearest permanent water source, buffered by 2 km. ⁱAbsolute distance to the western boundary of the Chiquibul Forest Reserve.

Table 7. Model-averaged coefficients from top models examining landscape-level characteristics affecting jaguar, puma, ocelot, grey fox, and tayra during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Parameter ^a	Variable	β^b	Standard Error	85% Confidence Interval	
						Lower	Upper
Jaguar	Dry	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	MinorWU ^c	4.52	2.65	0.71	8.34
			MajorWU ^d	-0.62	0.56	-1.42	0.18
	Rainy	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	eastB ^e	77.04	97.24	-62.94	217.02
Puma	Dry	p	MajorWB ^f	-0.24	0.11	-0.4	-0.09
			MajorWU	-0.23	0.1	-0.38	-0.08
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
	Rainy	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	eastB	3.82	1.98	0.96	6.67
			westB ^g	5.24	2.4	1.79	8.7
Ocelot	Dry	p	eastB	0.2	0.1	0.06	0.34
		ψ	MajorWU	-10.06	6.71	-19.72	-0.4
			MinorWU	36.28	28.04	-4.08	76.64
	Rainy	p	MajorWU	-0.57	0.17	-0.81	-0.33
			MajorWB	-0.57	0.17	-0.82	-0.32
			MinorWU	0.15	0.15	-0.06	0.36
		ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Grey Fox	Dry	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	MajorWU	0.25	0.31	-0.2	0.69
			MinorWU	0.76	0.37	0.22	1.3
	Rainy	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	eastB	2.73	1.27	0.91	4.56
			westB	2.52	1.18	0.82	4.22
			MinorWU	0.62	0.37	0.09	1.14
Tayra	Dry	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	westB	41.96	47.22	-26.02	109.93
			eastB	42.38	67.02	-54.09	138.85
			MajorWU	0.52	0.5	-0.2	1.23
			MinorWU	1.27	0.78	0.15	2.39
	Rainy	p	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
		ψ	MajorWU	-91.02	146.06	-301.29	119.24
			MajorWB	-149.04	210.86	-452.58	154.49

Table 7. Continued.

^aSite-use intensity (p) and site-use (Ψ). ^bParameter estimates. ^cAbsolute distance to the nearest ephemeral water source. ^dAbsolute distance to the nearest permanent water source. ^eAbsolute distance to the eastern boundary of the Chiquibul Forest Reserve. ^fRadiating effects of the nearest permanent water source, buffered by 2 km. ^gAbsolute distance to the western boundary of the Chiquibul Forest Reserve.

Puma

Site-Specific

Four of the final 8 models examined during the dry season had support. Vegetation structure affected both puma site-use intensity and site-use. Pumas used sites less intensively as vertical visual obstruction (%SCVVO) increased and as percent palm canopy cover (%CCPalm) increased; however, pumas used sites more intensively as palm species richness (PalmRich) increased. Greater horizontal cover (%HVO) at sites negatively affected puma site-use. In contrast to its effects on site-use intensity, as PalmRich increased, puma site-use decreased. Of the 2 models examined during the rainy season, only 1 model had support. Puma site-use intensity increased as log density increased, but greater avian prey (Bprey) at sites negatively affected site-use (Tables 4 and 5).

Landscape-Level

Two models had support during the dry season whereas, in contrast with jaguars, puma site-use was constant, and site-use intensity was influenced by distance to water sources. As both MajorWU and buffered distance to major waterbodies (MajorWB) increased, puma site-use intensity decreased. Like jaguars, puma site-use intensity was constant during the rainy season, but the distance to both eastB and west boundaries (westB) of the forest reserve affected site-use. As the distance from eastB and westB increased, puma site-use increased, suggesting that pumas use the interior of the reserve during the rainy season (Tables 6 and 7).

Ocelot

Site-Specific

Of the 4 models examined during the dry season, 2 models found support. Ocelots used sites less intensively as both %SCVVO and in the surrounding forest (%ForVVO) increased, but site-use remained constant. Site-use intensity decreased with greater log-density; ocelot site-use decreased as Mprey increased, but site-use increased as Bprey increased. Of the 2 models examined during the rainy season, 1 model found support. Ocelots used sites with both protection and harvested status less intensively than unharvested sites, and site-use remained constant (Tables 4 and 5).

Landscape-Level

One model found support during the dry season. Ocelots used sites more intensively as distance from eastB increased. As the distance from MajorWU increased, ocelot site-use decreased, but distance to MinorWU had uninformative effects on site-use. During the rainy season, distance to water sources affected ocelot site-use intensity in all 3 supported models, and site-use was constant. As distance to MajorWU and MajorWB increased, ocelot site-use intensity decreased, but the distance to MinorWU had uninformative effects (Tables 6 and 7).

Grey Fox

Site-Specific

Only 1 of the 4 models examined during the dry season found support. Grey fox used sites with both protection and harvested status less intensively than unharvested sites during the dry season, and site-use was constant. During the rainy season, 2 of the 5 models examined found support, with vegetation structure affecting both fox site-use intensity and site-use. As %SCVVO increased, both site-use intensity and site-use decreased. However, though %HVO negatively affected fox site-use intensity, greater %HVO had positive effects on fox site-use (Tables 4 and 5).

Landscape-Level

Two models had support during the dry season where site-use intensity was constant, and distance to water sources influenced site-use. As the distance to MinorWU increased, grey fox site-use increased, but the distance to MajorWU had uninformative effects. During the rainy season, 2 models had support where site-use intensity was again constant, but the distance to CFR boundaries and water sources affected site-use. As the distance from eastB and westB increased, grey fox site-use increased. Like its effects on foxes during the dry season, as the distance to MinorWU increased, grey fox site-use increased (Tables 6 and 7).

Tayra

Site-Specific

All 3 of the models examined during the dry season found support, including 1 that suggested tayra site-use intensity and site-use are both constant. As %SCVVO increased, tayra used sites less intensively. During the rainy season, both supported models suggested that canopy cover (i.e., percent hardwood [%CCHW] and %CCPalm) affected site-use intensity, and site-use was constant. Tayra used sites more intensively with increased %CCHW, but less intensively with increased %CCPalm (Tables 4 and 5).

Landscape-Level

Like grey fox, tayra site-use intensity was constant during both the dry and rainy seasons. Four models had support during the dry season, where distance to boundaries and water sources determined tayra site-use. Tayra site-use at sites increased as distance from MinorWU increased; however, the distance to eastB and westB, and MajorWU, had uninformative effects on tayra site-use. Although the 2 models with support during the rainy season suggested that water sources determined tayra site-use, both MajorWU and MajorWB had uninformative effects (Tables 6 and 7).

DISCUSSION

My goal was to understand the seasonal importance of site-specific and landscape-level factors affecting 5 rainforest carnivore species. Of the 3 site-specific categories examined, vegetation structure was an important seasonal determinant of site-use intensity and site-use for all carnivores, except jaguars whose site-use was constant for both seasons at this spatial scale. Landscape-level variables affected all species' site-use in both seasons, except pumas and ocelots that had constant site-use in the dry and rainy season, respectively. Prey availability and cover had seasonally disparate effects on ocelot and puma and was a consistent predictor of jaguar site-use intensity for both seasons. Variables supported in both the site-use intensity and site-use process for a species (i.e., puma and grey fox) frequently had opposing effects on these 2 processes.

Droughty conditions characterize the resource-limiting season (i.e., the dry season) in tropical climates, and thus it is not surprising that access to water sources and prey availability are predictors of carnivore distributions at this time. During the dry season, jaguar, grey fox, and tayra used sites further from ephemeral water sources, suggesting they sought sites where water was present. Because riparian areas hold the only consistent water source in the CFR during the dry season, FCD and the Belize Defense Force patrol these areas most heavily during this period to increase their chances of apprehending illegal immigrants and poachers. Seasonal analyses did not account for this additional human presence, which may have confounded the seasonal effects of riparian areas on jaguar, grey fox, and tayra. However, water generally affected carnivores in a seasonally predictable manner, similar to other studies that describe multiple wildlife species concentrating near these locations during dry periods (Kalle et al. 2014, Sirot et al. 2016, Montalvo et al. 2018, Santos et al. 2019). Ocelots used sites closer to major water sources during the dry season, and increased site-use intensity the farther sites were from the eastern boundary of the forest reserve. Given that one of the major above-ground water sources in the CFR is in the eastern part of the CFR, it makes sense that as ocelots move further from water, they must work harder to find prey and other resources. Ocelot site-use was constant during the rainy season, but similar to their distribution during the dry season, they remained closely associated with riparian areas by using such sites more intensively. Prey no longer need to concentrate around riparian areas during the rainy season due to the greater availability of water on the landscape (Paredes et al. 2017), possibly increasing how intensively ocelots must search for prey.

Prey availability was important to all 3 felids but was the most important predictor of jaguar distribution during both seasons. This corroborates Santos et al.'s (2019) findings that prey availability was the most important factor affecting jaguar distributions, and also had

strong impacts on ocelots. Unlike other studies that describe the importance of rodents and other small mammals to ocelots (de Villa Meza et al. 2009, Porfirio et al. 2016, Nagy-Reis et al. 2018, Santos et al. 2019), ocelots were negatively associated with mammalian prey, but positively associated with avian prey. The low abundance of small mammals in the CFR (Caro et al. 2001) may cause ocelots to alter their foraging behavior to favor sites with more readily available avian prey. It is important to recognize that although ocelots can prey upon larger animals such as agouti (*Dasyprocta punctata*; Konecny 1989, Tewes et al. 1998), these prey may be too large for ocelots to efficiently handle (de Villa Meza et al. 2009). In contrast with ocelots, pumas were unlikely to occur at sites with greater avian prey availability. Large terrestrial-based game birds (e.g., great curassow [*Crax rubra*] and tinamou [*Crypturellus* spp.]) use dense vegetation with coarse-woody debris that may impede puma hunting success, particularly as it relates to their main source of prey (i.e., red brocket deer; Chapter 2, Varela et al. 2010). Red brocket deer are associated with dense forests, yet commonly occur in secondary forests and use man-made trails and openings for foraging (Rossi 2000, Parry 2004, Varela et al. 2010). These cervids alter their behavior in the presence of humans, similar to pumas (Varela et al. 2010, Gaynor et al. 2018, Chapter 2). The fact that pumas used sites interior to the reserve during the rainy season seems to reflect their prey's distribution, with both groups using areas that may be less risky (i.e., no human activity; Chapter 2, Harris et al. 2015).

The deciduous habit of vegetation during the dry season causes seasonal differences in vegetation structure with effects on all species except jaguars. Because the dry season coincides with logging activities in the CFR, during this time it is likely that the human disturbance generated causes both puma and tayra to use sites less intensively, regardless of vegetation structure (Chapter 2). In another area of Belize with active resource extraction, disturbance associated with skidders facilitated palm recruitment (Arevalo et al. 2016). Palms are shade-tolerant and prolific in the understory, and once fully established they suppress and outcompete hardwoods (Denslow et al. 1991, Schnitzer et al. 2000). Unlike deciduous hardwood species, palms retain their leaves and contribute greatly to both horizontal cover and vegetation density, which had negative effects not only on puma site-use intensity, but their use of sites generally. In addition to its effects on pumas, the presence of palms in the canopy negatively affected the intensity with which tayra used sites during the rainy season, whereas they used sites more intensively when hardwoods were present in the canopy. Hardwoods create closed canopies that restrict understory vegetation growth and facilitate subcanopy movements for multiple species (Kricher 1999, Bridgewater 2012), and may provide tayra with greater access to other strata of the forest. As a semi-arboreal species, tayra can use the branching habit and tree trunks of hardwoods to obtain fruit and other prey (Presley 2000) which might be impossible in a palm-dominated forest, as palms do not always achieve a bowl (personal observation). Although mast from palms and hardwoods are prolific during the dry

season, mast from sapodilla species (*Manilkara* spp., *Pouteria* spp., and *Calocarpum mammosum*) and hog plum (*Spondias mombin*; Presley 2000) provide an important food source for tayra during the rainy season.

Vegetation structure and site harvest history are bound together when describing vegetation patterns in the CFR. The protection and harvested status represent 2 extremes in vegetation structure relative to those that could be subject to future harvest. Sites with potential for future harvest might present a balance between protection and harvest status vegetation structures, as these are locations that might have been subject to resource extraction in years past and have had the chance to recover from logging activities (Engilis et al. 2012). Given that ocelot and grey fox co-occur (Chapter 3), it was not surprising that harvest history and vegetation density had similarly negative effects on their site-use intensity. However, both characteristics affected these species in opposing seasons, providing some evidence that ocelot and grey fox partition resources seasonally, with distance to water playing an important role in partitioning. Areas under protection status have closed canopies characteristic of forest interior that provides poor-quality habitat for grey fox (Cypher 2003, Engilis et al. 2012). Although tree falls and major disturbance (e.g., hurricanes) create canopy gaps in these areas, they generally lack openings with varied vegetation structure used by grey fox (Cypher 2003), which could impede their ability to forage for fruit in different forest strata. The rainy season repeats this pattern of association more directly, as grey fox site-use was positively associated with sites providing greater horizontal cover. Information on fox parturition and pup rearing in the tropics is limited, but apparently peaks during the rainy season (LNW personal observation). Greater horizontal cover may provide adults and kits with protection during the day when they are less active (Hallberg and Trapp 1984, Nicholson et al. 1985). Although ocelot and grey fox use similar vegetation structure, riparian areas may have a greater effect on ocelot distribution than grey fox.

Without knowing the system and species' ecology under study, it is easy to develop uninformative models and apply incorrect interpretation. Variables supported in both the site-use intensity and site-use process for a species (i.e., puma and grey fox) frequently had opposing effects. For example, pumas had increased site-use intensity when more palm species were present, but pumas were more likely to use sites when less palm species were present. By including palm species richness in both site-use and site-use intensity parameters to understand how it affects puma distributions, we learned that pumas may not use sites with more palm species because the vegetation is too thick for them to move through easily. Thus, pumas use these areas more intensively to find suitable resources (Van Horne 1983). Yet variables do not always have opposing effects on these processes, which is why a working knowledge on species and systems is necessary for interpretation. Grey foxes displayed a similarly inverse pattern with horizontal cover (i.e., horizontal cover negatively affected grey fox site-use intensity but had positive effects on site-use) as pumas did with palm species richness.

However, vegetation density through the site center negatively affected both fox site-use intensity and site-use. For species such as tayra, we can interpret the effects of variables on site-use intensity in the traditional manner (i.e., negative beta means the species is negatively associated with that characteristic) because site-use at smaller spatial scales was constant during both seasons. However, we should still remain cautious regarding recommendations for this species, until more ecological information is available.

The dry and rainy seasons had different effects on carnivore distributions at both spatial scales examined. There is support for constant site-use at site-specific levels in both seasons in the CFR, whereas variables affected carnivore site-use at broader spatial scales. We can enhance site-specific conditions for several carnivore species by manipulating vegetation structure and composition. Both puma and tayra could benefit from actions that reduce palm density and canopy cover, with additional positive effects for ocelots, as this would reduce overall vegetation density. However, it is necessary to leave some pockets of dense vegetation for grey fox that might appear to use these sites less intensively during the rainy season, but in which they occur more frequently. Although there is some suggestion that puma site-use is constant during the dry season, unlike the other 4 species, this is not the case during the rainy season. This may indicate that pumas are more sensitive than other species to additional changes beyond the effects of season, as they tend to use sites interior to the forest reserve that logging activities infrequently affect. At landscape levels, increasing protection around key features (i.e., riparian areas) during limiting periods could ameliorate additional pressure on carnivores. Pumas and ocelots in particular could benefit from decreased patrolling activities (e.g., using foot patrols without vehicular support) in riparian areas. Future studies should make an effort to enhance our understanding of fox and other carnivore's behaviors during breeding periods, and how that relates to their seasonal distributions.

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APPENDIX

Table 8. All models^a considered at the site-specific level affecting rainforest carnivores during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	Dry	p(Mprey ^e) Ψ(.)	3	461.12	0.00	0.75	-227.30
		p(%SCVVO ^f + %PalmCC ^g) Ψ(.)	4	464.02	2.90	0.18	-227.57
		p(%SCVVO) Ψ(.)	3	467.06	5.94	0.04	-230.27
		p(%PalmCC) Ψ(.)	3	467.7	6.58	0.03	-230.60
		p(slope ^h) Ψ(.)	3	473.83	12.71	0.00	-233.66
		p(.) Ψ(.)	2	475.24	14.12	0.00	-235.50
Puma	Dry	p(Mprey) Ψ(.)	3	288.7	0.00	0.92	-141.09
		p(harvest status ⁱ) Ψ(.)	4	293.64	4.94	0.08	-142.39
		p(.) Ψ(%HVO ^j + PalmRich ^k)	4	633.02	0.00	0.27	-312.08
		p(%PalmCC + PalmRich) Ψ(.)	4	633.45	0.43	0.22	-312.29
		p(%SCVVO) Ψ(.)	3	633.92	0.89	0.17	-313.70
		p(.) Ψ(PalmRich)	3	634.12	1.10	0.16	-313.81
		p(%SCVVO) Ψ(%HVO)	4	636.03	3.01	0.06	-313.58
		p(%PalmCC) Ψ(PalmRich)	4	636.11	3.08	0.06	-313.62
		p(.) Ψ(%HVO)	3	637.32	4.30	0.03	-315.40
		p(slope) Ψ(.)	3	637.84	4.81	0.02	-315.66
	Rainy	p(logs ^l) Ψ(Bprey ^m)	4	301.79	0.00	0.99	-146.46
		p(.) Ψ(.)	2	310.73	8.94	0.01	-153.24
Ocelot	Dry	p(%SCVVO + %ForVVO ⁿ) Ψ(.)	4	638.88	0.00	0.52	-315.00
		p(logs) Ψ(Mprey + Bprey)	5	640.12	1.24	0.28	-314.39
		p(logs) Ψ(Bprey)	4	641.12	2.25	0.17	-316.13
		p(harvest status) Ψ(.)	4	644.95	6.07	0.03	-318.04
	Rainy	p(harvest status) Ψ(.)	4	325.53	0.00	0.94	-158.33
		p(%HVO) Ψ(.)	3	331.15	5.62	0.06	-162.32
Grey Fox	Dry	p(harvest status) Ψ(.)	4	352.66	0.00	0.99	-171.89
		p(Bprey + logs) Ψ(Bprey)	5	363.03	10.38	0.01	-175.85
		p(%PalmCC) Ψ(.)	3	363.68	11.02	0.00	-178.58
		p(.) Ψ(%SCVVO + %AICC ^o)	4	363.98	11.33	0.00	-177.56
	Rainy	p(%SCVVO) Ψ(.)	3	228.14	0.00	0.53	-110.82
		p(%HVO) Ψ(%SCVVO + %HVO)	5	229.25	1.11	0.30	-108.96
		p(%SCVVO) Ψ(%SCVVO)	4	230.42	2.28	0.17	-110.78

Table 8. Continued.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Grey Fox	Rainy	p(logs + stumps ^p) Ψ(.)	4	242.92	14.77	0.00	-117.02
		p(stumps) Ψ(.)	3	244.14	16.00	0.00	-118.81
Tayra	Dry	p(.) Ψ(slope)	3	281.08	0.00	0.39	-137.29
		p(%SCVVO) Ψ(.)	3	281.15	0.07	0.38	-137.32
		p(.) Ψ(.)	2	282.19	1.11	0.23	-138.97
		p(%CCHW ^q) Ψ(.)	3	144.30	0.00	0.54	-68.28
	Rainy	p(%PalmCC) Ψ(.)	3	145.07	0.77	0.36	-69.28
		p(.) Ψ(.)	2	147.64	3.35	0.10	-71.70

^aAkaike's Information Criterion [AIC]; ΔAIC_c < 2. ^bSite-use intensity (p) and site-use (Ψ) considered simultaneously. ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^eMammalian prey availability at sites, measured as a proportion of mammalian prey capture-events divided by the total number of wildlife capture-events at the site. ^fPercent vertical visual obstruction through site-center. ^gPercent palm canopy cover. ^hPercent slope at the site. ⁱHarvest history: none (i.e., it has not been harvested by a logging concession in the last 15 years, but might be in the future), protection (i.e., the logging concession is not allowed to conduct timber harvest in that area), and harvested (i.e., the site was part of logging operations in the last 15 years). ^jPercent horizontal visual obstruction. ^kPalm species richness. ^lLog (coarse woody debris ≥ 10 cm at midpoint) density (#/ha). ^mAvian prey availability at sites, measured as a proportion of avian prey capture-events divided by the total number of wildlife capture-events at the site. ⁿPercent vertical visual obstruction in the surrounding forest. ^oPercent canopy cover at the site. ^pStump (<1.37 m tall and ≥10 cm diameter) density (#/ha). ^qPercent hardwood canopy cover at the site.

Table 9. All models^a considered at the landscape-level affecting rainforest carnivores during the dry and rainy seasons, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	Dry	p(.) psi(MinorWU ^e)	3	463.32	0.00	0.50	-228.41
		p(.) psi(MajorWU ^f +MinorWU)	4	464.23	0.91	0.32	-227.68
		p(anyB) psi(MajorWU+MinorWU)	5	466.14	2.82	0.12	-227.41
		p(MinorWU) psi(.)	3	468.43	5.11	0.04	-230.96
		p(MajorWU+MinorWU) psi(.)	4	470.79	7.47	0.01	-230.96
		p(.) psi(.)	2	475.24	11.92	0.00	-235.50
		p(.) psi(westB ^g +eastB ^h)	4	476.50	13.17	0.00	-233.81
		p(.) psi(MajorWU)	3	477.10	13.78	0.00	-235.29
		p(eastB) psi(.)	3	477.14	13.82	0.00	-235.32
		p(.) psi(MajorWB ⁱ)	3	477.15	13.83	0.00	-235.32
		p(MajorWU) psi(.)	3	477.26	13.94	0.00	-235.38
		p(.) psi(westB)	3	477.34	14.02	0.00	-235.41
		p(westB) psi(.)	3	477.36	14.04	0.00	-235.43
		p(MajorWB) psi(.)	3	477.43	14.11	0.00	-235.46
		p(.) psi(eastB)	3	477.48	14.16	0.00	-235.48
		p(anyB ^j) psi(MajorWB)	4	478.97	15.65	0.00	-235.05
		p(westB+eastB) psi(.)	4	479.12	15.80	0.00	-235.13
	Rainy	p(.) psi(eastB)	3	292.48	0.00	0.55	-142.99
		p(.) psi(westB+eastB)	4	294.78	2.29	0.18	-142.95
		p(.) psi(westB)	3	296.38	3.89	0.08	-144.93
		p(westB+eastB) psi(.)	4	296.93	4.45	0.06	-144.03
		p(westB) psi(.)	3	297.94	5.46	0.04	-145.71
		p(.) psi(MajorWU)	3	299.73	7.25	0.01	-146.61
		p(MinorWU) psi(.)	3	300.41	7.93	0.01	-146.95
		p(eastB) psi(.)	3	300.56	8.07	0.01	-147.02
		p(.) psi(MinorWU)	3	300.67	8.19	0.01	-147.08
		p(MajorWU) psi(.)	3	300.73	8.24	0.01	-147.11
		p(MajorWB) psi(.)	3	300.89	8.41	0.01	-147.19
		p(.) psi(MajorWB)	3	300.91	8.43	0.01	-147.20
		p(.) psi(MajorWU+MinorWU)	4	300.92	8.43	0.01	-146.02
		p(MajorWU+MinorWU) psi(.)	4	301.51	9.03	0.01	-146.32
		p(.) psi(.)	2	301.98	9.50	0.00	-148.87
		p(anyB) psi(MajorWB)	4	302.73	10.25	0.00	-146.93
		p(anyB) psi(MajorWU+MinorWU)	5	302.81	10.32	0.00	-145.74
Puma	Dry	p(MajorWB) psi(.)	3	633.60	0.00	0.28	-313.54
		p(MajorWU) psi(.)	3	634.25	0.65	0.20	-313.87
		p(.) psi(MinorWU)	3	636.12	2.52	0.08	-314.80
		p(MajorWU+MinorWU) psi(.)	4	636.29	2.69	0.07	-313.71
		p(westB+eastB) psi(.)	4	636.42	2.82	0.07	-313.77
		p(westB) psi(.)	3	636.78	3.19	0.06	-315.14

Table 9. Continued.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Puma	Dry	p(.) psi(.)	2	636.86	3.26	0.06	-316.30
		p(eastB) psi(.)	3	638.38	4.79	0.03	-315.93
		p(.) psi(MajorWU+MinorWU)	4	638.47	4.87	0.02	-314.80
		p(.) psi(eastB)	3	638.80	5.20	0.02	-316.14
		p(MinorWU) psi(.)	3	638.86	5.27	0.02	-316.18
		p(.) psi(MajorWU)	3	638.95	5.36	0.02	-316.22
		p(.) psi(MajorWB)	3	638.96	5.36	0.02	-316.22
		p(.) psi(westB)	3	638.98	5.39	0.02	-316.24
		p(anyB) psi(MajorWB)	4	640.52	6.92	0.01	-315.82
		p(anyB) psi(MajorWU+MinorWU)	5	640.69	7.09	0.01	-314.68
	Rainy	p(.) psi(westB+eastB)	4	640.91	7.31	0.01	-316.02
		p(.) psi(westB+eastB)	4	301.26	0.00	0.56	-146.19
		p(MajorWU) psi(.)	3	303.92	2.66	0.15	-148.70
		p(MajorWB) psi(.)	3	305.16	3.90	0.08	-149.32
		p(MajorWU+MinorWU) psi(.)	4	305.61	4.35	0.06	-148.37
		p(.) psi(westB)	3	305.97	4.71	0.05	-149.73
		p(westB+eastB) psi(.)	4	307.41	6.15	0.03	-149.27
		p(.) psi(MajorWU)	3	308.38	7.12	0.02	-150.93
		p(.) psi(MajorWB)	3	308.70	7.45	0.01	-151.10
		p(anyB) psi(MajorWB)	4	309.62	8.36	0.01	-150.37
		p(westB) psi(.)	3	309.83	8.58	0.01	-151.66
		p(.) psi(MajorWU+MinorWU)	4	310.21	8.95	0.01	-150.67
		p(.) psi(eastB)	3	310.48	9.22	0.01	-151.98
		p(.) psi(.)	2	310.73	9.47	0.00	-153.24
		p(eastB) psi(.)	3	310.96	9.70	0.00	-152.22
		p(anyB) psi(MajorWU+MinorWU)	5	310.99	9.74	0.00	-149.83
		p(MinorWU) psi(.)	3	312.26	11.00	0.00	-152.87
		p(.) psi(MinorWU)	3	312.27	11.02	0.00	-152.88
	Dry	p(anyB) psi(MajorWU+MinorWU)	5	637.31	0.00	0.83	-312.99
		p(.) psi(MajorWU+MinorWU)	4	641.03	3.72	0.13	-316.08
		p(.) psi(MinorWU)	3	643.83	6.52	0.03	-318.66
		p(MinorWU) psi(.)	3	647.16	9.85	0.01	-320.32
		p(MajorWU+MinorWU) psi(.)	4	649.49	12.18	0.00	-320.31
		p(.) psi(MajorWB)	3	651.06	13.74	0.00	-322.27
		p(.) psi(MajorWU)	3	651.06	13.75	0.00	-322.27
		p(.) psi(.)	2	651.48	14.17	0.00	-323.61
		p(anyB) psi(MajorWB)	4	652.25	14.94	0.00	-321.69
		p(westB) psi(.)	3	652.38	15.07	0.00	-322.93
		p(MajorWB) psi(.)	3	652.84	15.53	0.00	-323.17
		p(eastB) psi(.)	3	653.08	15.77	0.00	-323.28
		p(MajorWU) psi(.)	3	653.37	16.06	0.00	-323.43

Table 9. Continued.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Ocelot	Dry	p(.) psi(westB)	3	653.60	16.29	0.00	-323.54
		p(.) psi(eastB)	3	653.71	16.40	0.00	-323.60
		p(westB+eastB) psi(.)	4	654.26	16.95	0.00	-322.69
		p(.) psi(westB+eastB)	4	655.73	18.42	0.00	-323.43
	Rainy	p(MajorWU) psi(.)	3	324.96	0.00	0.39	-159.22
		p(MajorWB) psi(.)	3	325.72	0.76	0.27	-159.60
		p(MajorWU+MinorWU) psi(.)	4	326.33	1.37	0.20	-158.73
		p(.) psi(MajorWU+MinorWU)	4	327.67	2.71	0.10	-159.40
		p(anyB) psi(MajorWU+MinorWU)	5	330.12	5.16	0.03	-159.39
		p(.) psi(MajorWU)	3	333.11	8.15	0.01	-163.30
		p(.) psi(MajorWB)	3	333.26	8.30	0.01	-163.37
		p(.) psi(westB)	3	335.92	10.96	0.00	-164.70
		p(.) psi(eastB)	3	335.98	11.03	0.00	-164.74
		p(MinorWU) psi(.)	3	336.09	11.13	0.00	-164.79
		p(westB) psi(.)	3	336.31	11.35	0.00	-164.90
		p(eastB) psi(.)	3	336.37	11.41	0.00	-164.93
		p(.) psi(westB+eastB)	4	338.27	13.31	0.00	-164.70
		p(anyB) psi(MajorWB)	4	339.93	14.97	0.00	-165.53
		p(.) psi(.)	2	340.44	15.49	0.00	-168.10
		p(.) psi(MinorWU)	3	342.70	17.75	0.00	-168.10
		p(westB+eastB) psi(.)	4	344.46	19.50	0.00	-167.79
Grey Fox	Dry	p(.) psi(MinorWU)	3	370.97	0.00	0.29	-182.23
		p(.) psi(MajorWU+MinorWU)	4	372.69	1.73	0.12	-181.91
		p(MajorWB) psi(.)	3	373.11	2.14	0.10	-183.30
		p(.) psi(westB)	3	373.69	2.73	0.07	-183.59
		p(.) psi(eastB)	3	373.97	3.00	0.06	-183.73
		p(.) psi(.)	2	374.09	3.12	0.06	-184.92
		p(MajorWU) psi(.)	3	374.19	3.22	0.06	-183.84
		p(MinorWU) psi(.)	3	374.96	4.00	0.04	-184.23
		p(anyB) psi(MajorWU+MinorWU)	5	375.09	4.13	0.04	-181.88
		p(.) psi(MajorWU)	3	375.67	4.71	0.03	-184.58
		p(MajorWU+MinorWU) psi(.)	4	375.80	4.83	0.03	-183.46
		p(.) psi(MajorWB)	3	376.00	5.04	0.02	-184.75
		p(.) psi(westB+eastB)	4	376.05	5.08	0.02	-183.59
		p(westB) psi(.)	3	376.22	5.25	0.02	-184.85
		p(eastB) psi(.)	3	376.32	5.35	0.02	-184.90
		p(westB+eastB) psi(.)	4	378.25	7.29	0.01	-184.69
		p(anyB) psi(MajorWB)	4	378.32	7.35	0.01	-184.72
	Rainy	p(.) psi(westB+eastB)	4	245.70	0.00	0.27	-118.42
		p(.) psi(MinorWU)	3	246.63	0.93	0.17	-120.06

Table 9. Continued.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Grey Fox	Rainy	p(.) psi(.)	2	247.87	2.17	0.09	-121.81
		p(MinorWU) psi(.)	3	248.46	2.76	0.07	-120.97
		p(.) psi(MajorWU+MinorWU)	4	248.78	3.08	0.06	-119.96
		p(.) psi(eastB)	3	249.52	3.81	0.04	-121.50
		p(westB+eastB) psi(.)	4	249.66	3.96	0.04	-120.39
		p(westB) psi(.)	3	249.70	4.00	0.04	-121.60
		p(.) psi(MajorWU)	3	249.91	4.21	0.03	-121.70
		p(.) psi(MajorWB)	3	249.98	4.28	0.03	-121.73
		p(eastB) psi(.)	3	250.06	4.36	0.03	-121.78
		p(MajorWU) psi(.)	3	250.10	4.40	0.03	-121.79
		p(MajorWB) psi(.)	3	250.11	4.41	0.03	-121.80
		p(.) psi(westB)	3	250.13	4.43	0.03	-121.81
		p(MajorWU+MinorWU) psi(.)	4	250.80	5.10	0.02	-120.97
		p(anyB) psi(MajorWU+MinorWU)	5	251.20	5.50	0.02	-119.94
		p(anyB) psi(MajorWB)	4	252.29	6.59	0.01	-121.71
Tayra	Dry	p(.) psi(westB+eastB)	4	279.52	0.00	0.26	-135.33
		p(.) psi(MinorWU)	3	280.30	0.78	0.17	-136.90
		p(.) psi(eastB)	3	280.76	1.24	0.14	-137.13
		p(.) psi(MajorWU+MinorWU)	4	281.40	1.88	0.10	-136.27
		p(.) psi(.)	2	282.19	2.67	0.07	-138.97
		p(anyB) psi(MajorWU+MinorWU)	5	283.23	3.70	0.04	-135.95
		p(MinorWU) psi(.)	3	283.37	3.85	0.04	-138.43
		p(MajorWB) psi(.)	3	283.97	4.45	0.03	-138.73
		p(westB) psi(.)	3	283.99	4.47	0.03	-138.74
		p(MajorWU) psi(.)	3	284.20	4.68	0.02	-138.84
		p(eastB) psi(.)	3	284.41	4.89	0.02	-138.95
		p(.) psi(MajorWU)	3	284.74	5.22	0.02	-139.12
		p(.) psi(MajorWB)	3	284.90	5.38	0.02	-139.20
		p(.) psi(westB)	3	284.96	5.44	0.02	-139.22
		p(westB+eastB) psi(.)	4	285.11	5.59	0.02	-138.12
		p(MajorWU+MinorWU) psi(.)	4	285.62	6.10	0.01	-138.38
		p(anyB) psi(MajorWB)	4	286.53	7.01	0.01	-138.83
	Rainy	p(.) psi(MajorWB)	3	139.29	0.00	0.40	-66.39
		p(.) psi(MajorWU)	3	139.59	0.30	0.35	-66.54
		p(.) psi(MajorWU+MinorWU)	4	142.28	2.99	0.09	-66.70
		p(anyB) psi(MajorWB)	4	142.44	3.15	0.08	-66.79
		p(anyB) psi(MajorWU+MinorWU)	5	144.59	5.30	0.03	-66.63
		p(MajorWB) psi(.)	3	147.16	7.87	0.01	-70.32
		p(.) psi(westB)	3	147.44	8.15	0.01	-70.46
		p(.) psi(eastB)	3	147.48	8.19	0.01	-70.49

Table 9. Continued.

Species	Season	Model ^b	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Tayra	Rainy	p(.) psi(.)	2	147.64	8.35	0.01	-71.70
		p(MajorWU) psi(.)	3	148.07	8.78	0.00	-70.78
		p(MinorWU) psi(.)	3	148.35	9.06	0.00	-70.92
		p(.) psi(MinorWU)	3	148.89	9.60	0.00	-71.19
		p(MajorWU+MinorWU) psi(.)	4	149.12	9.83	0.00	-70.13
		p(eastB) psi(.)	3	149.13	9.84	0.00	-71.31
		p(westB) psi(.)	3	149.30	10.01	0.00	-71.39
		p(.) psi(westB+eastB)	4	149.77	10.48	0.00	-70.45

^aAkaike's Information Criterion [AIC]; ΔAIC_c < 2. ^bSite-use intensity (p) and site-use (Ψ) considered simultaneously. ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set.

^eAbsolute distance to the nearest ephemeral water source. ^fAbsolute distance to the nearest permanent water source.

^gAbsolute distance to the eastern boundary of the Chiquibul Forest Reserve. ^hAbsolute distance to the western boundary of the Chiquibul Forest Reserve. ⁱRadiating effects of the nearest permanent water source, buffered by 2 km. ^jAbsolute distance to the nearest boundary (i.e., east or west).

CHAPTER II
EFFECTS OF TRAILS AND LOGGING STRUCTURES ON RAINFOREST
CARNIVORES

ABSTRACT

Timber harvest can provide an important form of disturbance in tropical systems that require large canopy gaps for regeneration. Despite the knowledge that carnivores will use trails and logging roads (hereafter: pathways) made for resource extraction, it is unknown how site-specific (e.g., width, vegetation structure, vehicular traffic, etc.) and landscape-level (e.g., logging road density) characteristics associated with these pathways influence carnivore distributions. Therefore, I investigated both site-specific and landscape-level effects of trails and logging roads on 5 commonly captured carnivores in the Chiquibul Forest Reserve (CFR) using occupancy estimation. Except for pumas, top models for carnivores at the site-specific level confirmed the hypothesis that trails and logging roads impact carnivore site-use intensity, but not site-use. At least 2 of the 3 site-specific categories predicted how intensively species used these pathways. Top models at the landscape-level also confirmed that characteristics had different impacts on carnivores' site-use intensity on trails and logging roads, and some suggested that different covariates affected jaguar, puma, grey fox, and tayra site-use in the CFR. However, like site-specific results, landscape-level characteristics had weak effects on species site-use. Carnivores appear to be tolerant of trails and logging roads, as evidenced by the positive responses of tayra and ocelot to sites with greater vehicular traffic, and the fact that all species investigated were likely to use these pathways. Allowing logging roads to lie fallow post logging operations may provide sensitive species (i.e., pumas) with places to retreat during the next year's logging season. Leaving some slash and logging debris on trails and logging roads would benefit tayra in areas with high vehicular activity, but too much vegetation will cause tayra and puma to reduce their intensity of use of these sites.

KEY WORDS: Carnivores, logging, movement pathways, occupancy modeling, vegetation structure.

INTRODUCTION

Populations of mammalian carnivores are declining due to practices that decrease habitat and increase landscape fragmentation (Woodroffe and Ginsberg 1998, Cardillo et al. 2004, Ripple et al. 2014). In the tropics, clearing land to raise livestock leads to habitat loss for many species and causes negative interactions between humans and carnivores (e.g., jaguars [*Panthera onca*]; Michalski et al. 2006, Cavalcanti and Gese 2010) searching for resources (e.g., food, mates) in a degraded landscape. Such land clearing typically leads to deforestation, followed by the loss of prey (Novack et al. 2005) and inter- and intraspecific spatial competition (Foster et

al. 2010). Beyond livestock rearing and agricultural production, poorly planned and implemented timber harvest can lead to habitat degradation and presents a major threat to tropical wildlife (Paviolo et al. 2009, Mayor et al. 2015).

Critics of tropical forestry practices equate timber harvest with deforestation. Because of this association, the negative perceptions of timber harvest effects on wildlife are common, yet some forms of timber harvest provide an important form of disturbance in tropical systems (Lussetti 2017). Closed canopies that restrict understory vegetation growth and facilitate subcanopy movements characterize tropical forests (Kricher 1999, Bridgewater 2012). Although these systems are by no means static, they lack the structural diversity exhibited in forests that experience regular disturbance. Selective logging creates canopy gaps that provide sunlight to a previously sparse and shaded understory, facilitating understory growth via a rapid increase in stem density as species compete for sun and space (Johns 1985, Pinard et al. 1996). Plant species diversity increases in these systems as previously dormant species (e.g., mahogany [*Swietenia macrophylla*]) compete with pioneer species for regeneration space (Lussetti 2017). Not only does this necessary disturbance promote a new stand of trees for future harvest, but the roads created for timber extraction may have positive effects on wildlife communities and facilitate species' use of the landscape (Roopsind et al. 2017, Tobler et al. 2018).

Although there is evidence that roads and trails built to facilitate human access to areas for resource extraction increase poaching (Kerley et al. 2002, Peres and Lake 2003, Paviolo et al. 2009, Kleinschroth and Healey 2017, Morato et al. 2018) and negatively affect species sensitive to edge (Balme et al. 2009, Morato et al. 2018), the direct effects on carnivores are equivocal (Roopsind et al. 2017). Trails and logging roads (hereafter: pathways) may have long-term positive effects on carnivores by facilitating movement across the landscape, reducing energy costs associated with wide-ranging habits, and providing greater access to resources that might not otherwise be readily available (Mohamed et al. 2013). Yet, these pathways also may have negative effects. Kerley et al. (2002) reported Amur tigers (*Panthera tigris altaica*) had reduced survivorship and foraging efficiency in protected areas with road networks and Linkie et al. (2008) determined Sumatran tigers (*Panthera tigris sumatrae*) used sites farther from public and logging roads. Whatever their effects, these pathways act as travel corridors for many carnivore species, a characteristic exploited by researchers (Silver et al. 2004, Wegge et al. 2004, Foster and Harmsen 2012, Sollmann et al. 2013, Wearn et al. 2013). The greater capture success of felids on roads and trails suggests that some carnivores purposefully use these pathways over forest interior when possible (Harmsen et al. 2009). Furthermore, the recent findings of both Roopsind et al. (2017) and Tobler et al. (2018) indicated that multiple species and taxa used logged areas and associated structures more than both forest interior and trails.

This suggests that under certain conditions the overall impacts of logging structures on wildlife communities are positive.

However, although carnivores will use trails and logging roads, it is unknown how different characteristics (e.g., width, vegetation structure, etc.) affect carnivore distributions. Logging concessionaires following reduced-impact logging practices that require the development of pre-planned skid trails could use this knowledge to minimize negative effects on wildlife. Furthermore, the effects of human presence (i.e., human settlements, vehicular traffic, and foot travel) on carnivores likely differs among species (Paviolo et al. 2009, Morrison et al. 2014, Morato et al. 2018). Different characteristics of logging structures (e.g., width, vehicular traffic) may determine how carnivores use these paths generally and during periods of active resource extraction. This may have major implications for carnivore success during the dry season, when logging activities occur, and species are already stressed due to resource limitations.

Therefore, my goal was to examine the effects of different pathways on 5 commonly captured carnivores (i.e., jaguar, puma [*Puma concolor*], ocelot [*Leopardus pardalis*], grey fox [*Urocyon cinereoargenteus*], and tayra [*Eira barbara*]) in the Chiquibul Forest Reserve (CFR), Belize. I investigated both site-specific and landscape-level effects of these structures on each of the 5 species. Because all 5 carnivore species occur throughout the CFR, I expected pathways to have limited effects on site-use. Additionally, I hypothesized that carnivores would use roads more intensively than hiking trails.

METHODS

I examined the effects of trails and logging roads on jaguar, puma, ocelot, grey fox, and tayra via camera surveys and vegetation assessment at 47 sites in the CFR from January 2016 to August 2016. The survey period covered 12 weeks of the dry season, 3 weeks of the transition period between the dry and rainy season, and 7 weeks of the rainy season.

Study Area

The CFR (59,822 ha) is in southwestern Belize in the Maya Mountain Massif, adjacent to the Caracol Archaeological Reserve (CAR; 10,339 ha). With the Chiquibul National Park (CNP; 106,838 ha) surrounding the CFR and CAR, this is the largest protected area in Belize (Association of Protected Areas Management Organizations 2011; Arevalo 2011). The CFR has a subtropical climate with a dry (February–June) and rainy (July–January) season, with the rainy season coinciding with the hurricane season (Salas and Meerman 2008). Although the

dominant ecosystem is tropical broadleaf rainforest, there is a small pocket of submontane pine forest at the reserve's center (Meerman and Sabido 2001).

The network of dirt roads and hiking trails in different stages of neglect found throughout the forest reserve are a result of the CFR's history of multiple use, including recreation, gold mining, research, and logging activities. Currently, there is a single logging concession in the reserve with exclusive rights to extract timber, a position it has held since 2006. The CFR is divided into 80 blocks of ~468 ha, with up to 1000 ha/year (i.e., 2 blocks) selectively logged from March–May. The concession follows reduced-impact logging practices to minimize its impacts on the forest's resources. Important commercial timber species includes mahogany, Spanish cedar (*Cedrela odorata*), nargusta (*Terminalia amazonia*), and sapodilla (*Manilkara zapota*).

Camera Surveys

As part of a larger wildlife monitoring effort in the CFR, I systematically established a 2.25 x 2.25-km grid of trail cameras (Moultrie M-880 Mini Game Camera, Moultrie Feeders, EBSCO Industries, Inc., Alabaster, AL) with infrared (IR) abilities. I used a subset of these cameras (N = 47) lying on pathways (i.e., main dirt road into the CFR, logging tracts, and human trails) to determine the effects of these structures on rainforest carnivores. I recorded each site's UTM coordinates with a handheld GPS unit under the North American Datum of 1927 (NAD27) geodetic reference system. To reduce the chances of data loss from 1) camera malfunction or 2) missing an animal as it walked by, I placed 2 cameras on opposing trees at each site. Cameras were set >3 m from the center of sites on trees or other suitable objects (e.g., wooden stake) >5cm dbh. I avoided facing cameras in an east-west facing direction when possible. I offset opposing cameras by 0.3 m to prevent cameras from triggering each other (Silver et al. 2004). To avoid accidental triggering of cameras (e.g., waving grass; Kelly et al. 2013), I cleared vegetation between and within 1 m of each camera. I set cameras to take 3 photos/event, with a 5-sec delay between picture events to facilitate my ability to capture potentially cryptic species (e.g., tayra). Additionally, I set the function "Motion Freeze" to "On" to maximize image clarity at night, and had cameras imprint each photo with its associated name, date, time, temperature (Celsius), and moon phase.

Site-Specific Characteristics

Pathway Structure

To characterize pathway structure, I identified the type (i.e., main road, logging road, hiking trail; Type). The main roads and logging roads in the CFR are suitable for vehicular traffic and composed of dirt; the main difference between the 2 is that regular maintenance occurs on the main roads, whilst regular maintenance of logging roads continues only until the end of the logging season. At the end of the logging season, these structures lie fallow, and rarely see

human or vehicular traffic thereafter. In a 0.1-ha circular plot centered on the camera site (Fig. 6), I counted the number of intersecting trails through the trail or road center along a 35.6-m transect. Along this same transect, I measured trail/road width at 8 different points (i.e., 0, 5, 10, 15, 20, 25, 30, 35 m). I used these measurements to derive average width (avgwidth) and variance in width (varwidth). Finally, as an index of vehicular impacts on pathway structure, I assessed how rutted the site was from vehicular traffic (ruts) and assigned it to 1 of 3 categories as an index of disturbance: 0 (no ruts), 1 (some ruts), 2 (extremely rutted).

Human Disturbance

I assessed total human disturbance at each site by dividing the number of human foot-traffic (PPNhuman) and vehicular traffic (PPNvehicle) capture-events by the total number of capture-events for the site. Although I counted the number of individual people and vehicles captured during each event, I did not factor the number of individuals into human and vehicular traffic metrics. Additionally, I investigated survey-specific effects of human disturbance by determining the frequency of human foot-traffic (humanOBS) and vehicular traffic (vehicleOBS) per survey period. For each traffic category, I divided captures during a survey period by the total number of capture events for that period at that site (e.g., survey 1 vehicular traffic capture events/survey 1 total capture events). Finally, I noted if the given survey period fell within the logging season (loggingS; yes/no).

Pathway Vegetation Assessment

To characterize vegetation structure along pathways, I recorded site-specific vegetation characteristics. I measured vertical visual obstruction (VVO) with a 2-m cover pole (Griffith and Youtie 1988) by holding the cover pole at plot center (i.e., between the two cameras; Fig. 6), and viewing the cover pole from a height of 1 m in either pathway direction at distances of 5.6 m and 17.8 m. I used these measurements to derive variance in vertical visual obstruction within 5.6 m and 17.8 m of the site (varVVO5.6m and varVVO17.8m), and to estimate percent vertical visual obstruction within 5.6-m and 17.8-m of the site (%VVO5.6m and %VVO17.8m). To quantify horizontal visual obstruction (%HVO; i.e., horizontal cover), I used the line-intercept method (Hays et al. 1981) along a single 35.6-m transect through the pathway. I held a 50-m tape 1 m above the ground on 1 transect through the site (Fig. 6) and measured the horizontal spread (cm) of vegetation (e.g., herbaceous growth, palms, etc.) 0.5-1.0 m tall that hit the line. I assessed canopy cover along this same transect with a yes/no densitometer every 2 m, viewed from a height of 1 m. I used these measurements to estimate percent canopy cover (%CC).

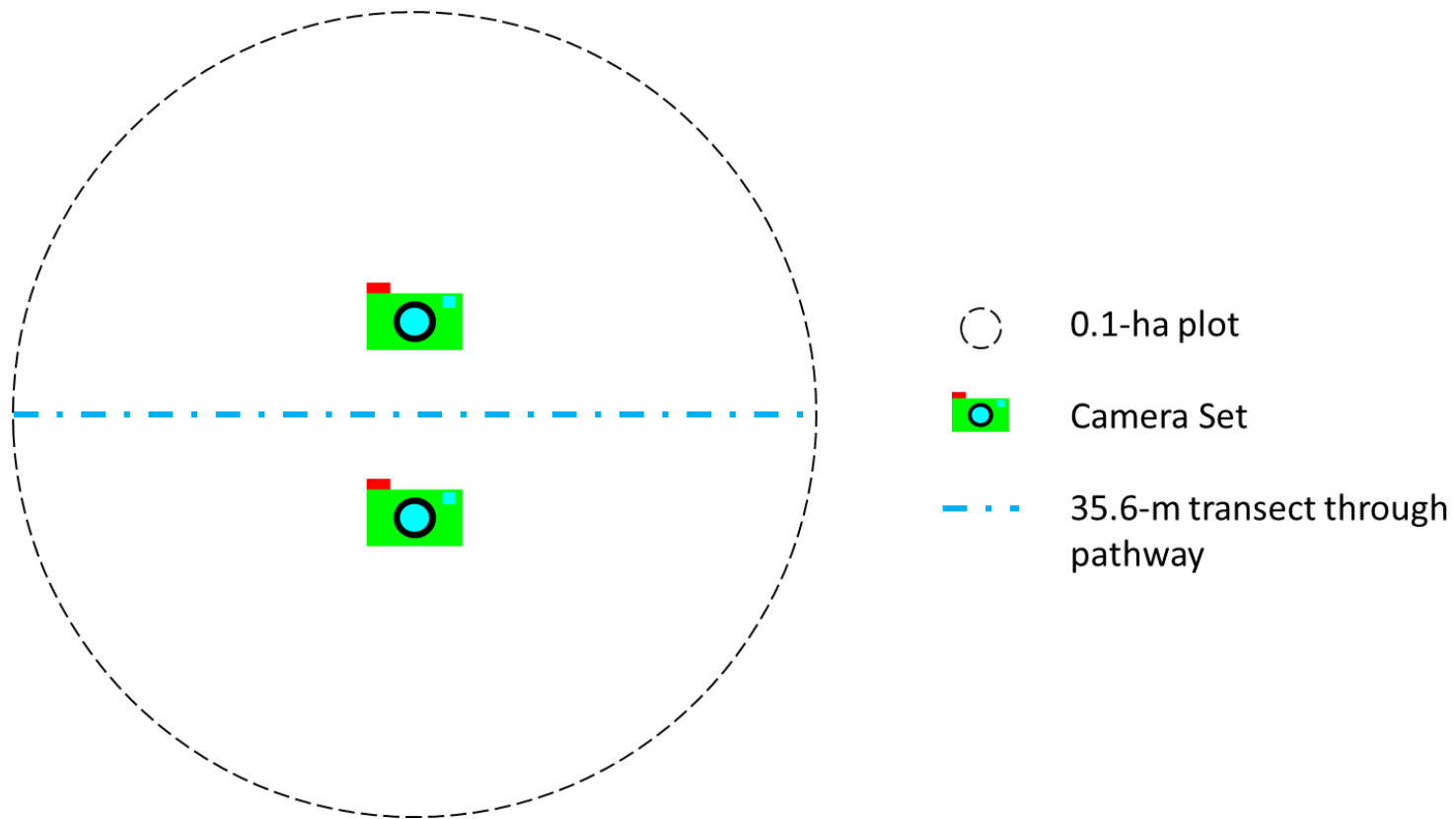


Figure 6. Camera site sampling plots, Chiquibul Forest Reserve, Belize, Central America, 2016.

Landscape-Level Characteristics

To understand the effects of pathways on rainforest carnivores at broader spatial scales, I constructed a geographic information system (GIS) in ArcGIS (Environmental Systems Research Institute 2014) using high-resolution aerial photographs and by ground-truthing. Because the western boundary of the CFR is close to the Guatemalan border and subject to the effects of illegal activities (e.g., illegal immigration, poaching, logging, gold mining, etc.), I examined how the absolute distance (westB) and radiating effects of categorical distances (westBC; within 1 km of west boundary, within 3 km of west boundary, within 5 km of west boundary, >5 km from west boundary) to this boundary affected carnivores. I assessed the effects of the few permanent human settlements in the CFR by determining both the absolute distance to (HSu) and the radiating effects of (HSb; buffered by 2 km) the distance to the nearest human settlement. Finally, I determined the combined density of trails and logging roads within 2 km of each site (Dens).

Occupancy Estimation

Each survey comprised 1 week, during which I assigned each species a binary capture history code (i.e., if a camera captured a carnivore of interest at a site ≥ 1 time/survey period the site received a “1,” for that survey and a “0” otherwise [MacKenzie et al. 2006]). Condensing these periods is biologically relevant, as carnivores have activity “bursts” where they intensively use an area for a short time before moving to a new area. Using more detection periods could bias parameter estimation.

Parameter Interpretation: p and ψ

Because I interpret “occupancy” as a measure of site-use, rather than true occupancy, and because movement in and out of the area is random, I could relax the assumption of closure to changes in occupancy during repeated surveys (Mackenzie et al. 2004, Farris et al. 2015, Mackenzie et al. 2017). I interpreted occupancy to mean the probability a species would use a site (hereafter: site-use), rather than true occupancy, given that my data represented a “presence-only” data set, and sites were point locations of camera traps (MacKenzie et al. 2003, MacKenzie et al. 2006, Farris et al. 2015). All 5 carnivore species investigated are in the CFR, but variation in population density and movement patterns can determine 1) landscape use and 2) the observability of species (i.e., site-use intensity; Rowcliffe et al. 2008, Efford 2012, Burton et al. 2015, Latif et al. 2016). Therefore, when incorporating the effects of variables on detection (i.e., p), I interpret p as informing the effects of covariates on pathway site-use intensity instead of as a simple detection probability (Ladle et al. 2018).

Model Development

I developed sets of *a priori* single- and multiple-variable candidate models for single-season occupancy analyses (MacKenzie et al. 2006), where I considered the effects of site-specific and landscape-level characteristics of different pathways on jaguar, puma, ocelot, grey fox, and tayra. I examined the effects of these pathways on carnivore distributions using 3 distinct categories (i.e., pathway structure, human disturbance, and vegetation structure). I analyzed each category in 2 stages, where I first assessed the effects of variables in a category on species site-use intensity (p), with species site-use (ψ) held constant. The initial assumption of constant ψ (i.e., probability a species uses a site is constant) for these 5 species is reasonable given their detection histories (i.e., I captured several species at nearly every site). Additionally, pathways do not determine if the species are present in the CFR but should affect species site-use intensity as some species will be more sensitive than others to the disturbance generated by these structures. A new suite of models combined top p models investigating the effects of variables on p and ψ simultaneously, using the informative variables from the p analysis only. By conducting this second analysis where ψ was not constant, my goal was to see if the initial hypothesis (i.e., pathways determine species site-use intensity) had support. A final suite of models combined top models from the p and simultaneous p and ψ analyses for each category, including models combining informative variables from the first 3 categories (e.g., $p[\%VVO + \text{Type}] \psi[\text{PPNhuman}]$), following the recommendations of Arnold 2010 (i.e., solution 5). I assessed landscape-level metrics separately from site-specific characteristics to 1) reduce confounding effects, and 2) provide clear recommendations for managers at multiple spatial scales.

I excluded models with correlated variables ($|r| > 0.70$; Tirpak et al. 2008) from consideration. To reduce the likelihood of overfitting models, I limited individual models to 3 predictor variables per parameter (i.e., p and ψ). I considered models with $\Delta\text{AIC}_c \leq 2$ supported, and examined AIC_c values, AIC_c differences (ΔAIC_c), and Akaike weights (w_i) for models with different combinations of predictor variables (Burnham and Anderson 2002). Where multiple models found support, I increased the precision via model averaging. When 85% confidence intervals (CI) overlapped with zero for variables in supported models, I considered them to have an inconclusive effect and thus uninformative (Payton et al. 2003, Arnold 2010). I indicate that a variable had positive effects when an 85% CI was >0 , and negative effects if <0 . I used library “unmarked” for all occupancy estimation, and library “AICcmodavg” for model averaging in R version 3.4.1 (R Core Team 2017). For brevity and clarity, I report supported models from the 1) final suite of models combining categories and 2) landscape-level characteristics.

RESULTS

Except for pumas, where there was some suggestion that pathway structure positively influenced site-use, top models for carnivores at the site-specific level confirmed the hypothesis that pathway characteristics was related to carnivore site-use intensity, but not site-use. For each of the 5 species, at least 2 of the 3 pathway categories predicted carnivore site-use intensity. Jaguar and puma had opposing responses to the same variable at site-specific levels. Top models at the landscape-level also confirmed that pathway characteristics were related to carnivore site-use intensity, and some suggested that different covariates affected how jaguars, pumas, grey fox, and tayra use sites in the CFR. However, like site-specific results, landscape-level characteristics had weak effects on species site-use.

Jaguar

Site-Specific

All 3 pathway categories impacted jaguar site-use intensity, with different effects. Movement-pathway type had support in all models for jaguars. Main access roads in the CFR had positive effects on site-use intensity relative to hiking trails, but logging roads had no detectable impact relative to hiking trails. The logging season decreased jaguar site-use intensity, but %VVO17.8m was uninformative. For all models, site-use was constant (Table 10 and 11).

Landscape-Level

Distance to the west boundary of the CFR was important to all models of jaguar site-use intensity. Jaguar site-use intensity decreased further from the west boundary of the CFR, but the distance to the nearest human settlement had no detectable impact. There was some suggestion that pathway density within 2 km of sites affected jaguar site-use, but results were also uninformative (Table 12 and 13).

Table 10. Supported models^a of site-specific pathway characteristics affecting rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	p and Ψ	p(Type ^e + loggingS ^f) Ψ (.)	5	870.09	0.00	0.32	-429.31
		p(Type) Ψ (.)	4	870.40	0.31	0.27	-430.72
		p(Type + %VVO ^g 17.8m + loggingS) Ψ (.)	6	870.85	0.77	0.22	-428.38
		p(Type + %VVO17.8m) Ψ (.)	5	871.03	0.94	0.20	-429.78
Puma	p and Ψ	p(vehicleOBS ^h + varwidth ⁱ) Ψ (avgwidth ^j)	5	1057.55	0.00	0.27	-523.05
		p(varwidth + intersecting trails) Ψ (.)	4	1058.29	0.73	0.19	-524.67
		p(varwidth + intersecting trails ^k) Ψ (avgwidth)	5	1058.41	0.85	0.17	-523.47
		p(%VVO5.6m) Ψ (avgwidth)	4	1058.97	1.41	0.13	-525.01
		p(%VVO5.6m) Ψ (.)	3	1059.06	1.51	0.13	-526.25
		p(loggingS + varwidth) Ψ (avgwidth)	5	1059.22	1.67	0.12	-523.88
Ocelot	p and Ψ	p(ruts ^l + vehicleOBS + loggingS) Ψ (.)	6	1032.11	0.00	0.5.6m	-509.00
		p(vehicleOBS + ruts) Ψ (.)	5	1032.77	0.66	0.40	-510.65
Grey Fox	p and Ψ	p(Type + intersecting trails) Ψ (.)	5	665.96	0.00	0.67	-327.25
		p(Type + intersecting trails + PPNvehicle ^m) Ψ (.)	6	667.39	1.43	0.33	-326.65
Tayra	p and Ψ	p(PPNvehicle + %VVO5.6m + %VVO17.8m) Ψ (.)	5	412.23	0.00	0.60	-200.38
		p(%VVO5.6m + %VVO17.8m) Ψ (.)	4	413.16	0.93	0.38	-202.10

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c \leq 2$. ^bSite-use intensity (p) and site-use (Ψ). ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^ePathway type (i.e., hiking trail, logging tract, or main road through the forest reserve) the site was located on. ^fSurvey period occurred during or outside of the logging season (yes/no). ^gPercent vertical visual obstruction within 5.6-m or 17.8-m of the site. ^hFrequency of vehicular traffic within a survey period. ⁱVariance in pathway width. ^jAverage pathway width. ^kThe number of trails intersecting sites. ^lHow rutted pathways were from vehicular traffic, serving as an index of disturbance (i.e., 0 [no ruts], 1 [some ruts], 2 [extremely rutted]). ^mTotal vehicular traffic at sites, measured as a proportion of vehicular traffic events divided by total capture events at site.

Table 11. Model-averaged coefficients from top models examining site-specific movement pathway characteristics affecting rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter ^a	Variable	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
Jaguar	p	Type ^c (logging)	0.33	0.38	-0.22	0.88
		Type(road)	1.43	0.39	0.87	1.99
		loggingS ^d (yes)	-0.30	0.18	-0.55	-0.04
		%VVO ^e 17.8m	-0.21	0.15	-0.43	0.01
	ψ	n/a	n/a	n/a	n/a	n/a
Puma	p	varwidth ^f	-0.21	0.09	-0.34	-0.08
		intersecting trails ^g	0.17	0.09	0.04	0.29
		loggingS(yes)	0.28	0.16	0.05	0.51
		vehicleOBS ^h	-0.17	0.08	-0.29	-0.06
		%VVO5.6m	-0.21	0.10	-0.35	-0.07
	ψ	avgwidth ⁱ	1.11	0.74	0.05	2.17
Ocelot	p	ruts(1)	1.05	0.19	0.78	1.33
		ruts(2)	0.82	0.32	0.35	1.28
		vehicleOBS ^j	0.30	0.07	0.19	0.40
		loggingS(yes)	0.30	0.17	0.06	0.54
	ψ	n/a	n/a	n/a	n/a	n/a
Grey Fox	p	Type(logging)	0.55	0.60	-0.32	1.42
		Type(road)	2.57	0.55	1.78	3.37
		intersecting trails	0.27	0.12	0.10	0.43
		PPNvehicle ^k	0.12	0.11	-0.04	0.28
	ψ	n/a	n/a	n/a	n/a	n/a
Tayra	p	%VVO5.6m	0.85	0.28	0.44	1.26
		%VVO17.8m	-1.58	0.56	-2.39	-0.77
		PPNvehicle	0.29	0.15	0.07	0.51
	ψ	n/a	n/a	n/a	n/a	n/a

^aSite-use intensity (p) and site-use (ψ). ^bParameter estimates. ^cPathway type (i.e., hiking trail, logging tract, or main road through the forest reserve) the site was located on. ^dSurvey period occurred during or outside of the logging season (yes/no). ^ePercent vertical visual obstruction within 5.6-m or 17.8-m of the site. ^fVariance in pathway width. ^gThe number of trails intersecting sites. ^hFrequency of vehicular traffic within a survey period. ⁱAverage pathway width. ^jHow rutted pathways were from vehicular traffic, serving as an index of disturbance (i.e., 0 [no ruts], 1 [some ruts], 2 [extremely rutted]. ^kTotal vehicular traffic at sites, measured as a proportion of vehicular traffic events divided by total capture events at site.

Table 12. Supported models^a of landscape-level movement pathway characteristics affecting rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	p and Ψ	p(westB ^e) Ψ(.)	3	909.23	0.00	0.37	-451.34
		p(HSu ^f + westB) Ψ(.)	4	911.13	1.90	0.14	-451.09
		p(westB) Ψ(Dens ^g)	4	911.14	1.91	0.14	-451.10
Puma	p and Ψ	p(HSu + Dens) Ψ(.)	4	1056.25	0.00	0.29	-523.65
		p(HSu) Ψ(.)	3	1056.34	0.08	0.28	-524.89
		p(HSu + Dens) Ψ(HSu)	5	1057.14	0.89	0.19	-522.84
		p(Dens) Ψ(.)	3	1057.96	1.71	0.13	-525.70
		p(HSu + westB) Ψ(.)	4	1058.20	1.94	0.11	-524.62
Ocelot	p and Ψ	p(HSb ^h) Ψ(.)	3	1076.18	0.00	0.36	-534.81
		p(westB) Ψ(.)	3	1076.78	0.60	0.26	-535.11
		p(HSb + Dens) Ψ(.)	4	1077.97	1.79	0.15	-534.51
Grey Fox	p and Ψ	p(westBC ⁱ) Ψ(.)	5	716.93	0.00	0.51	-352.73
		p(westBC) Ψ(HSu)	6	718.65	1.72	0.22	-352.27
Tayra	p and Ψ	p(HSu + Dens) Ψ(.)	4	417.80	0.00	0.42	-204.42
		p(HSu + Dens) Ψ(westB)	5	419.61	1.82	0.17	-204.07

^aAkaike's Information Criterion [AIC]; ΔAIC_c ≤ 2. ^bSite-use intensity (p) and site-use (Ψ). ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^eSite distance (km) to the west CFR boundary. ^fSite distance (km) to nearest human settlement. ^gDensity of pathways within 2-km of the site.

^hDistance to nearest human settlement within 2-km of the site. ⁱCategorical distance to the west boundary (i.e., within 1-km of west boundary, within 3-km of west boundary, within 5-km of west boundary, >5km from west boundary).

Table 13. Model-averaged coefficients from top models examining landscape-level movement pathway characteristics affecting rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter ^a	Variable	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
Jaguar	p	westB ^c	-0.24	0.09	-0.38	-0.11
		HSu ^d	0.07	0.11	-0.08	0.23
	ψ	Dens ^e	0.66	1.07	-0.87	2.20
Puma	p	westB	-0.07	0.09	-0.20	0.07
		HSu	0.20	0.09	0.07	0.33
		Dens	-0.17	0.10	-0.32	-0.02
	ψ	HSu	1.14	1.05	-0.37	2.66
Ocelot	p	westB	-0.13	0.08	-0.24	-0.02
		HSb ^f	-0.15	0.08	-0.26	-0.03
		Dens	-0.06	0.08	-0.18	0.05
	ψ	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>	<i>n/a</i>
Grey Fox	p	westBC ^g (1km)	-0.41	0.46	-1.07	0.25
		westBC(3km)	0.76	0.24	0.41	1.11
		westBC(5km)	-0.30	0.28	-0.70	0.11
	ψ	HSu	0.32	0.34	-0.17	0.80
Tayra	p	HSu	0.53	0.19	0.26	0.80
		Dens	0.56	0.17	0.32	0.80
	ψ	westB	-0.36	0.45	-1.00	0.28

^aSite-use intensity (p) and site-use (ψ). ^bParameter estimates. ^cSite distance (km) to the west CFR boundary. ^dSite distance (km) to nearest human settlement. ^eDensity of pathways within 2-km of the site. ^fDistance to nearest human settlement within 2-km of the site. ^gCategorical distance to the west boundary (i.e., within 1-km of west boundary, within 3-km of west boundary, within 5-km of west boundary, >5km from west boundary).

Puma

Site-Specific

Like jaguars, all 3 pathway categories determined puma site-use intensity, with pathway structural covariates supported in 4 out of 6 of the top models. As variance in pathway width increased, puma site-use intensity decreased, but sites with more intersecting trails increased site-use intensity. Unlike its effects on jaguars, the logging season had positive effects on puma site-use intensity; however, as vehicular traffic increased during survey periods, site-use intensity decreased. Greater vertical visual obstruction in the pathway within 5.6 m of the site had negative effects on site-use intensity. As average pathway width increased, puma site-use also increased (Table 10 and 11).

Landscape-Level

Four of 5 models supported the effects of distance to the nearest human settlement on puma site-use intensity: as site distance from human settlements increased, puma site-use intensity increased. However, this same covariate had uninformative effects on puma site-use. Sites with greater pathway density within 2 km had negative effects on puma site-use intensity. Unlike jaguars, the distance to the west boundary of the CFR was uninformative (Table 12 and 13).

Ocelot

Site-Specific

Unlike jaguars and pumas, vegetation along the pathway had no detectable impact on ocelot site-use intensity, but pathway structure and human disturbance had positive effects. Sites with some ruts from vehicles and heavily-rutted sites had positive effects on ocelot site-use intensity, relative to sites without any ruts. Like pumas, the logging season had positive effects on ocelot site-use intensity; however, unlike pumas, as vehicular traffic increased during survey periods, ocelot site-use intensity also increased. For all models, site-use was constant (Table 10 and 11).

Landscape-Level

Unlike the other 4 carnivore species, ocelot site-use was constant for all landscape-level models. Like jaguars, ocelot site-use intensity decreased farther from the western boundary of the CFR. However, as the buffered distance to the nearest human settlement increased, ocelot site-use intensity decreased. Movement pathway density was uninformative (Table 12 and 13).

Grey Fox

Site-Specific

Like ocelots, vegetation along the pathway had no impact on grey fox, but pathway structural variables had positive effects on grey fox site-use intensity. As with jaguars, models supported the effects of movement pathway type and the number of intersecting trails on fox site-use intensity. Main roads for access in the CFR had positive effects on grey fox site-use intensity and all logging roads had weak effects relative to hiking paths. Like pumas, sites with more intersecting trails increased grey fox site-use intensity. Total vehicular traffic at sites was uninformative. For all models, site-use was constant (Table 10 and 11).

Landscape-Level

All models supported western boundary distance categories for grey fox site-use intensity. Sites within 1 km and 5 km of the western boundary had weak effects on site-use intensity relative to sites >5 km from the boundary. However, grey fox site-use intensity was positive at sites within 3 km of the western boundary, relative to sites >5 km from the boundary. The distance to the nearest human settlement had uninformative effects on grey fox site-use (Table 12 and 13).

Tayra

Site-Specific

Tayra were the only species unaffected by the pathway structure category. As percent vertical visual obstruction along the pathway within 5.6 m of the site increased, tayra site-use intensity also increased. However, as percent vertical visual obstruction along the pathway within 17.8 m of the site increased, tayra site-use intensity decreased. Tayra site-use intensity increased as total vehicular traffic at sites increased. For all models, site-use was constant (Table 10 and 11).

Landscape-Level

All models supported the distance to the nearest human settlement and pathway density for tayra site-use intensity. As the distance from the nearest human settlement increased, tayra site-use intensity increased. Sites with greater pathway density within 2 km also increased tayra site-use intensity. There was some suggestion that the distance from the CFR west boundary affected tayra site-use, but results were uninformative (Table 12 and 13).

DISCUSSION

My goal was to understand how site-specific and landscape-level pathway characteristics affected 5 rainforest carnivore species. Except for pumas, pathway characteristics did not determine carnivore site-use, and each species displayed varying sensitivity to pathways. Surprisingly, tayra responded positively to human disturbance, whereas jaguar and ocelot responded as expected (i.e., negative and positive, respectively), puma response varied, and the human disturbance was unimportant to grey fox site-use intensity. The network of roads and trails does not affect carnivore species occurrence in the CFR, but certain characteristics impact carnivore site-use intensity.

Logging structures are often used as indicators of tropical forest degradation (Lewis et al. 2015). However, forest management practices may mitigate the negative effects of these structures (Putz et al. 2012). Conservationists and the public typically view hiking trails more favorably than logging infrastructure (i.e., main access roads and logging trails) because they provide humans with access that cannot support industrial-scale operations (i.e., logging). However, both grey fox and jaguars used main roads more intensively than hiking trails in the CFR, which also had support at broader spatial scales, with jaguars and foxes using sites closer to the CFR's western boundary more intensively than sites more interior to the forest reserve. Historically, there were more pathways in the western part of the reserve for logging activities that spanned both Belize and Guatemala. These same pathways now facilitate patrols for illegal activities along the Guatemalan border, and some of the older, overgrown logging roads were reopened for access to the CNP and for the 2015 logging season. Not only is it likely that these used and unused roads aid jaguars' long-range movements (Harmsen et al. 2009), but prey items consumed by jaguars and other carnivores, to some extent, use these structures for movement (Weckel et al. 2006, Harmsen et al. 2009, Tobler et al. 2018). Although the logging season likely tempered jaguar road-use intensity because of increased vehicular traffic, the effects of vehicular traffic on grey fox were equivocal. More intersecting pathways from other pathways and wildlife trails at sites may allow foxes to quickly escape vehicular disturbance, a trend also supported for pumas.

Despite the ecological plasticity that allows pumas to occur in human-dominated landscapes (Nowell and Jackson 1996, Michaliski et al. 2006, Morrison et al. 2014, Guerisoli et al. 2019) and to use pathways (Davis et al. 2011, Tobler et al. 2018), pumas had reduced activity on pathways actively used by humans. Unlike the other 4 carnivore species, wider pathways were positively correlated with puma site-use, a characteristic observed by Harmsen et al. (2009) in the Cockscomb Basin Wildlife Sanctuary. Sites with wider pathways and less variation in width may enhance puma maneuverability (Laundre 2010), particularly as they try to avoid

detection, whereas greater variation and more narrow pathways could decrease puma agility when attempting to avoid vehicles. Wider roads also have increased sun exposure that creates more forage for deer and other prey used by pumas. Denser vegetation in pathways may have similar effects, as evidenced by pumas reducing how intensively they used such sites, regardless of factors influencing site-use. Although pumas used sites more intensively when more intersecting trails were present, at broader spatial scales sites with greater pathway density were used less intensively. This behavioral disparity reflects the fact that other wildlife created most trails intersecting with pathways, which may be indicative of species richness at sites, a metric that is positively correlated with puma distributions in other studies (Negroes et al. 2010, Tobler et al. 2018, Guerisoli et al. 2019). Additionally, based on puma avoidance of humans in this and other studies (Foster et al. 2010, Davis et al. 2011, Morrison et al. 2014, Guerisoli et al. 2019), these trails may provide a means for pumas to escape vehicles. Pumas avoided human disturbance at broader spatial scales by reducing how intensively they used sites with greater pathway density (i.e., remained interior to the reserve; Chapter 1) and sites close to human settlements. This tendency to use the CFR interior more intensively supports the suggestion that not only do pumas alter their activities to reduce their interactions with humans (Foster et al. 2010, Morrison et al. 2014, Guerisoli et al. 2019), but may require increased land area in protected area interiors (Paviolo et al. 2009).

It is well documented that when roads are incorrectly built for resource extraction, they can facilitate forest degradation by increasing erosion (Swanson and Dyrness 1975, Williamson and Neilsen, 2000), particularly when logging roads are unmaintained (i.e., they will degrade with continued vehicular use and weather). Vehicles driven on these structures during the consistent and heavy rains that often occur in the CFR churn up the road substrate, and create ruts in the soupy mud, particularly in low-lying areas with poor drainage. The ruts that remain during the dry season can be a few inches to several feet deep and will hold water from rain that infrequently occurs during the dry season. Although rutted pathways may be indicative of human disturbance, these ruts may provide an important source of water for many species throughout the year. Indeed, ocelots are a species associated with riparian areas (Chapter 1) uncommon in the CFR and used sites with ruts more intensively than sites without ruts. Ruts in the CFR may act in a similar manner to “watering holes,” bringing in prey for ocelots (Vaughan & Weis 1999, Montalvo et al. 2019). Corroborating other studies (Roopsind et al. 2017, Satter et al. 2018, Tobler et al. 2018), ocelots are tolerant of human disturbance in the CFR, as evidenced by increased site-use intensity during the logging season relative to the non-logging season, and with increased survey-specific vehicular traffic. Ocelot tolerance extends to broader spatial scales, where they used sites more intensively within 2 km of human settlements, and occurred at sites closer to the western boundary than sites in the forest reserve’s interior, contrasting with other studies that suggest occurrence is greater in more protected areas (Bruner et al. 2001, Nagy-Reis et al. 2017).

Whereas ocelots may tolerate human disturbance that generates favorable vegetation structure and conditions for their prey, vegetation structure drives tayra tolerance of vehicular traffic. Denser vegetation along pathways facilitated tayra site-use intensity, particularly where there was more vehicular traffic. However, tayra avoided sites with denser vegetation, providing evidence that, without vehicular traffic, tayra will use sites with less dense understory more intensively. Although tayra are semi-arboreal mustelids (Presley 2000), when terrestrial-bound, their primary method of locomotion is a bounding gait (Ercoli and Youlatos 2016). Dense vegetation hampers tayra movement efficiency and thus increases energy costs for this wide-ranging mesocarnivore (Kaufmann and Kaufmann 1965, Presley 2000, Ercoli and Youlatos 2016). Furthermore, sites with more vegetation cover overall might hinder tayra attempting to escape vehicular disturbance, compared with sites that have less dense vegetation. Tayra can forage more efficiently in less dense understory where it is easier to see fruiting species and quickly approach prey (Presley 2000, Ercoli and Youlatos 2016). Yet, there is an apparent balance between how much human disturbance tayra will tolerate, as at broader spatial scales they used sites farther from human settlements but with greater pathway density within 2 km more intensively. The desire to be farther from humans while also using pathways to reduce energy costs is a characteristic tayra share with wolverines, another wide-ranging mustelid (May et al. 2006, Gardner et al. 2010).

Carnivores are more tolerant of pathways than previously suggested. Recent studies in other selectively logged areas suggest the act of logging itself does not negatively impact wildlife (Putz et al. 2012, Mayor et al. 2015) and that the infrastructure created to facilitate tree extraction has positive effects on carnivores and other wildlife species using the landscape (Roopsind et al. 2017, Tobler et al. 2018). Indeed, both ocelots and tayra responded positively to sites with greater vehicular traffic, in contrast to expectations (Davis et al. 2011). All species investigated were likely to occur on pathways, although puma site-use appeared to require more specific conditions, which may be indicative of puma specialization in the CFR in the presence of different pathways. Even with puma sensitivity to human disturbance, the species responded positively to wider pathways that others might perceive as evidence of forest degradation (Lewis et al. 2015). However, despite the generally positive effects of pathways on carnivores, both puma and tayra responses provided evidence that some buffer against human disturbance may be important, and reserve planning and design should consider using buffers (Bruner et al. 2001, Paviolo et al. 2009, Burton et al. 2012, Nagy-Reis et al. 2017).

Some logging concessions in the tropics, including the CFR, follow reduced-impact logging practices that require pre-planned skid trail systems (Putz et al. 2012, Kleinschroth et al. 2016, Roopsind et al. 2017, Tobler et al. 2018). Reduced-impact logging recommends allowing logging structures to lie fallow at the end of a season and reopening old logging roads for the new harvest when possible. Although these deeply rutted networks with unaddressed treefalls

are unusable by vehicles once abandoned, these structures benefit a variety of wildlife species. Pathways left fallow may mimic major canopy gaps caused by natural disturbance (e.g., fire, hurricanes, etc.), contributing to vegetation regeneration and the vegetation mosaic used by the wildlife community. Additionally, because humans can only access these reclaimed areas with great difficulty (Kleinschroth et al. 2016, LeGros et al. 2017, Kleinschroth and Healey 2017), allowing logging structures to lie fallow can provide carnivores, such as puma and tayra, with a refuge away from people and actively logged areas. Indeed, the majority of the pathways located in the western portion of the CFR are unused by people except for infrequent foot patrols, which likely contributed to jaguar, ocelot, and grey fox intensively using the area. Furthermore, carnivores, like tayra and jaguar, can navigate these abandoned structures to areas otherwise energetically costly to access. I observed jaguars in the CFR following these linear pathways for a period before hopping off into the forest, a behavior documented in other studies (Harmsen et al. 2009, Foster et al. 2010).

Given the propensity of large, wide-ranging carnivores to use these structures, it should not be surprising that pathways have positive effects on rainforest carnivores and the intensity with which they use such structures. The fact that we are now beginning to frame studies to question the direct effects of these practices reflects an understanding that not only is resource extraction unlikely to end any time soon, but there is a need to find ways for humans and wildlife to coexist as best possible. Understanding how animals use the landscape in areas of resource extraction can help managers plan and structure these practices to not only minimize negative effects on wildlife but enhance wildlife success. Logging concessionaires should allow logging structures to lie fallow at the end of the season to provide species sensitive to human disturbance (i.e., pumas) with places to retreat during the next year's logging season. Leaving some slash and logging debris along pathways would benefit tayra, particularly in areas with high vehicular activity. However, both tayra and puma will reduce how intensively they use such structures with too much vegetation cover. The effects of the CNP as a buffer around the CFR should be a subject of future investigation, with studies framed to understand if the current buffer functions as it should.

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APPENDIX

Table 14. All models^a considered at the site-specific level for effects of trails and logging structures on rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	p and Ψ	p(Type ^e + loggingS ^f) Ψ (.)	5	870.09	0.00	0.29	-429.31
		p(Type) Ψ (.)	4	870.40	0.31	0.25	-430.72
		p(Type + %VVO17.8m ^g + loggingS) Ψ (.)	6	870.85	0.77	0.20	-428.38
		p(Type + %VVO17.8m) Ψ (.)	5	871.03	0.94	0.18	-429.78
		p(Type + PPNvehicle ^h) Ψ (.)	5	872.91	2.82	0.07	-430.72
		p(PPNvehicle + %VVO17.8m) Ψ (.)	4	888.23	18.14	0.00	-439.64
		p(%VVO17.8m) Ψ (.)	3	889.55	19.47	0.00	-441.50
		p(PPNvehicle + loggingS) Ψ (.)	4	905.70	35.62	0.00	-448.38
		p(PPNvehicle) Ψ (.)	3	906.02	35.93	0.00	-449.73
Puma	p and Ψ	p(vehicleOBS ⁱ + varwidth ^j) Ψ (avgwidth ^k)	5	1057.55	0.00	0.19	-523.05
		p(varwidth+ intersectingtrails ^l) Ψ (.)	4	1058.29	0.73	0.13	-524.67
		p(varwidth+ intersectingtrails) Ψ (avgwidth)	5	1058.41	0.85	0.13	-523.47
		p(%VVO5.6m ^m) Ψ (avgwidth)	4	1058.97	1.41	0.10	-525.01
		p(%VVO5.6m) Ψ (.)	3	1059.06	1.51	0.09	-526.25
		p(loggingS + varwidth) Ψ (avgwidth)	5	1059.22	1.67	0.08	-523.88
		p(varwidth) Ψ (.)	3	1059.90	2.34	0.06	-526.67
		p(PPNvehicle + loggingS) Ψ (avgwidth)	5	1061.35	3.80	0.03	-524.94
		p(PPNvehicle + loggingS) Ψ (.)	4	1061.40	3.85	0.03	-526.23
		p(PPNvehicle + loggingS) Ψ (PPNhuman ⁿ)	5	1061.53	3.98	0.03	-525.04
		p(vehicleOBS + loggingS) Ψ (avgwidth)	5	1061.72	4.17	0.02	-525.13
		p(vehicleOBS + loggingS) Ψ (.)	4	1061.76	4.21	0.02	-526.40
		p(PPNvehicle) Ψ (PPNhuman)	4	1061.89	4.34	0.02	-526.47
		p(PPNvehicle) Ψ (.)	3	1061.91	4.36	0.02	-527.68
		p(loggingS) Ψ (.)	3	1062.16	4.61	0.02	-527.80
		p(vehicleOBS) Ψ (.)	3	1062.30	4.75	0.02	-527.87
Ocelot	p and Ψ	p(ruts ^o + vehicleOBS + loggingS) Ψ (.)	6	1032.11	0.00	0.56	-509.00
		p(vehicleOBS + ruts) Ψ (.)	5	1032.77	0.66	0.40	-510.65
		p(ruts + %VVO5.6m + %VVO17.8m) Ψ (.)	6	1037.55	5.44	0.04	-511.73
		p(loggingS + ruts) Ψ (.)	5	1045.34	13.23	0.00	-516.94
		p(ruts) Ψ (.)	4	1045.93	13.82	0.00	-518.49
		p(%VVO5.6m + %VVO17.8m) Ψ (.)	4	1053.70	21.59	0.00	-522.37
		p(vehicleOBS + loggingS) Ψ (.)	4	1059.90	27.80	0.00	-525.48

Table 14. Continued.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Ocelot	p and Ψ	p(vehicleOBS) $\Psi(.)$	3	1060.64	28.53	0.00	-527.04
Grey Fox	p and Ψ	p(Type + intersectingtrails) $\Psi(.)$	5	665.96	0.00	0.63	-327.25
		p(Type + intersectingtrails + PPNvehicle) $\Psi(.)$	6	667.39	1.43	0.31	-326.65
		p(PPNvehicle + Type) $\Psi(.)$	5	670.81	4.85	0.06	-329.67
		p(%HVO ^p) $\Psi(.)$	3	678.19	12.23	0.00	-335.81
		p(PPNvehicle + HVO) $\Psi(.)$	4	679.26	13.30	0.00	-335.15
		p(PPNvehicle) $\Psi(.)$	3	711.43	45.47	0.00	-352.43
		p(intersectingtrails + PPNvehicle) $\Psi(.)$	4	713.35	47.39	0.00	-352.20
		p(PPNvehicle + %VVO5.6m + %VVO17.8m) $\Psi(.)$	5	412.23	0.00	0.60	-200.38
Tayra	p and Ψ	p(%VVO5.6m + %VVO17.8m) $\Psi(.)$	4	413.16	0.93	0.38	-202.10
		p(ruts + PPNvehicle) $\Psi(.)$	5	419.90	7.67	0.01	-204.22
		p(ruts) $\Psi(.)$	4	422.32	10.09	0.00	-206.68
		p(PPNvehicle) $\Psi(.)$	3	423.15	10.92	0.00	-208.30

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c < 2$. ^bSite-use intensity (p) and site-use (Ψ). ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^ePathway type (i.e., hiking trail, logging tract, or main road through the forest reserve) the site was located on. ^fSurvey period occurred during or outside of the logging season (yes/no). ^gPercent vertical visual obstruction within 17.8-m of the site. ^hTotal vehicular traffic at sites, measured as a proportion of vehicular traffic events divided by total capture events at site. ⁱFrequency of vehicular traffic within a survey period. ^jVariance in pathway width. ^kAverage pathway width. ^lThe number of trails intersecting sites. ^mPercent vertical visual obstruction within 5.6-m of the site. ⁿTotal human foot traffic at sites, measured as a proportion of human foot traffic events divided by total capture events at site. ^oHow rutted pathways were from vehicular traffic, serving as an index of disturbance (i.e., 0 [no ruts], 1 [some ruts], 2 [extremely rutted]). ^pPercent horizontal visual obstruction within through the pathway.

Table 15. All models^a considered at the landscape-level for effects of trails and logging structures on rainforest carnivores, Chiquibul Forest Reserve, Belize, Central America, 2016.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Jaguar	p and Ψ	p(westB ^e) Ψ(.)	3	909.23	0.00	0.37	-451.34
		p(HSu ^f + westB) Ψ(.)	4	911.13	1.90	0.14	-451.09
		p(westB) Ψ(Dens ^g)	4	911.14	1.91	0.14	-451.10
		p(westB) Ψ(HSb ^h)	4	911.28	2.05	0.13	-451.17
		p(westB) Ψ(Hsu)	4	911.45	2.22	0.12	-451.25
		p(westB) Ψ(HSu + Dens)	5	912.94	3.71	0.06	-450.74
		p(westB) Ψ(westBC ⁱ)	6	915.01	5.78	0.02	-450.45
		p(westB) Ψ(westBC + Dens)	7	917.19	7.96	0.01	-450.16
Puma	p and Ψ	p(HSu + Dens) Ψ(.)	4	1056.25	0.00	0.23	-523.65
		p(HSu) Ψ(.)	3	1056.34	0.08	0.22	-524.89
		p(HSu + Dens) Ψ(Hsu)	5	1057.14	0.89	0.15	-522.84
		p(Dens) Ψ(.)	3	1057.96	1.71	0.10	-525.70
		p(HSu + westB) Ψ(.)	4	1058.20	1.94	0.09	-524.62
		p(HSu + Dens) Ψ(westB)	5	1058.41	2.15	0.08	-523.47
		p(Dens) Ψ(Dens)	4	1058.47	2.22	0.08	-524.76
		p(Dens) Ψ(HSu + Dens)	5	1060.63	4.37	0.03	-524.58
		p(Dens) Ψ(HSu + westB)	5	1061.16	4.91	0.02	-524.85
Ocelot	p and Ψ	p(HSb) Ψ(.)	3	1076.18	0.00	0.36	-534.81
		p(westB) Ψ(.)	3	1076.78	0.60	0.26	-535.11
		p(HSb + Dens) Ψ(.)	4	1077.97	1.79	0.15	-534.51
		p(HSu + Dens) Ψ(Dens)	5	1078.35	2.17	0.12	-533.44
		p(HSu + Dens) Ψ(westB)	5	1080.21	4.03	0.05	-534.38
		p(HSu + Dens) Ψ(HSu)	5	1080.23	4.05	0.05	-534.38
		p(Dens) Ψ(HSu + Dens)	5	1082.30	6.12	0.02	-535.42
Grey Fox	p and Ψ	p(westBC) Ψ(.)	5	716.93	0.00	0.51	-352.73
		p(westBC) Ψ(HSu)	6	718.65	1.72	0.22	-352.27
		p(westBC) Ψ(Dens)	6	719.49	2.56	0.14	-352.70
		p(westBC) Ψ(westBC)	8	720.05	3.12	0.11	-350.13
		p(westBC) Ψ(westBC + Dens)	9	722.91	5.98	0.03	-350.02
Tayra	p and Ψ	p(HSu + Dens) Ψ(.)	4	417.80	0.00	0.42	-204.42
		p(HSu + Dens) Ψ(westB)	5	419.61	1.82	0.17	-204.07
		p(HSu + Dens) Ψ(Dens)	5	420.23	2.44	0.12	-204.38
		p(HSu + Dens) Ψ(Hsu)	5	420.28	2.48	0.12	-204.41
		p(HSu + Dens) Ψ(HSu + westB)	6	420.50	2.71	0.11	-203.20

Table 15. Continued.

Species	Parameter Estimated ^b	Model	K ^c	AIC _c	ΔAIC _c	w _i ^d	Log-Likelihood
Tayra	p and Ψ	p(HSu + Dens)	6	422.46	4.66	0.04	-204.18
		Ψ(HSu + Dens)					
		p(Dens) Ψ(Dens)	4	424.90	7.11	0.01	-207.97
		p(HSu) Ψ(Dens)	4	426.73	8.93	0.00	-208.89

^aAkaike's Information Criterion [AIC]; ΔAIC_c < 2. ^bSite-use intensity (p) and site-use (Ψ). ^cNumber of parameters estimated in the model. ^dWeight of evidence in favor of the model being the best approximating model in the set. ^eDistance to the west boundary. ^fDistance to nearest human settlement. ^gDensity of pathways within 2-km of the site. ^hDistance to nearest human settlement within 2-km of the site. ⁱCategorical distance to the west boundary (i.e., within 1-km of west boundary, within 3-km of west boundary, within 5-km of west boundary, >5km from west boundary).

CHAPTER III
CORRELATES OF RAINFOREST CARNIVORE COMMUNITY STRUCTURE AND
DYNAMICS

ABSTRACT

Interactions among species are important components of ecosystem function and there has been a shift toward examining entire communities and the influence of environmental factors (e.g., vegetation structure) on shaping community dynamics. As an example, margay and coati are 2 mesocarnivores that use trees for travel, feeding, and sleeping, and their populations may be similarly affected by changes in vegetation structure if they co-occur at sites. I investigated the structure and dynamics of carnivores found in the Chiquibul Forest Reserve (CFR) in Belize, Central America in 5-species groups (i.e., jaguar, puma, ocelot, grey fox, and tayra; margay, coati, jaguarundi, striped hog-nosed skunk, and opossum; grey fox, tayra, coati, striped hog-nosed skunk, and opossum; and jaguar, puma, ocelot, margay, and jaguarundi), and their relationship with a number of environmental correlates. I collected data via camera trapping and site-specific vegetation sampling (i.e., horizontal and vertical visual obstruction in the forest surrounding sites, variance in forest vertical visual obstruction), and used a Geographic Information System to extract forest infrastructure (e.g., road and trail density) metrics. I used occupancy estimation methods to directly model species interactions and the effects of environmental covariates on carnivore site-use and site-use intensity. Of the interactions examined, only ocelot and grey fox exhibited positive co-occurrence at sites; site use by all other species did not depend on the presence of other carnivores. Neither vegetation structural variables nor road and trail density affected carnivore site-use, but percent vertical visual obstruction was an important predictor of species site-use intensity. Vegetation density was positively correlated with site-use intensity by providing cover that allowed different carnivore species to use the same sites, irrespective of other carnivore species present. Because carnivore site-use was constant for all analyses, it appears that the non-homogeneous, but well-structured, vegetation mosaic prevents competition, and thus allows for the co-existence of many different carnivore species in the CFR.

KEY WORDS: Carnivores, forest infrastructure, interactions, multiple-species occupancy estimation, vegetation structure.

INTRODUCTION

Studies of Neotropical mammalian carnivores have historically focused on large charismatic species (i.e., jaguar [*Panthera onca*] and puma [*Puma concolor*]), or specific taxonomic guilds (i.e., felids). Although we have increased our baseline knowledge regarding habitat associations, spatial dynamics, and demographic parameters for smaller felids such as ocelots

(*Leopardus pardalis*) and margay (*Leopardus wiedii*; Nagy-Reis et al. 2017, Penido et al. 2017, Paolino et al. 2018, Satter et al. 2018), we have a limited understanding of how these felids and other less-studied carnivores (e.g., striped hog-nosed skunk [*Conepatus semistriatus*], tayra [*Eira barbara*], grey fox [*Urocyon cinereoargenteus*]) interact.

Typically, efforts to observe the interactions of >1 carnivore species or taxon focus on a few easily “captured” species (Davis et al. 2011, Weckel et al. 2006), with continued emphasis in the tropics on large felids (Harmsen et al. 2009a, Ramesh et al. 2012, Foster et al. 2013). However, as wildlife research has shifted towards a more holistic understanding of the role species play in ecosystems, less-studied members of mesocarnivore communities are gaining attention. For example, Nagy-Reis et al. (2017) assessed landscape use and co-occurrence patterns of 3 meso-felids in Brazil that are relatively common, believed to be suffering from population declines, and about which basic information for proper management is lacking: ocelots, margay, and oncilla (*Leopardus guttulus*). Their findings suggested that human disturbance, in the form of roads and human accessibility, and the protection status of the sites within which these species occurred, were predictive of these species’ site use, while prey availability and intraguild competition were not. Nagy-Reis et al. (2017) delineated the effects of prey availability and the protection-status of the site in facilitating not only each species’ presence, but the drivers of species interactions, and thus the operation of a mesocarnivore community on the landscape. This study and others (e.g., Van der Weyde et al. 2018) represent an important advancement in how we think about wildlife community function, but we are still missing information regarding how species representing different guilds interact.

Without an understanding of species interactions and the influence of the environment on these interactions, efforts to conserve and manage entire communities cannot succeed. Knowing the structure and dynamics of a carnivore community has important implications for how the community is best managed. As some studies suggest (Richmond et al. 2010, Rota et al. 2016, Nagy-Reis et al. 2017, Murphy et al. 2018), when we ignore interspecific associations, inference regarding species’ habitat associations and distributions may be incorrect. The presence of another species, whether a symbiont, competitor, or a predator, can change how a focal species uses a site, even if the full suite of habitat components is present for that focal species (Richmond et al. 2010, Waddle et al. 2010, Krohner and Ausband 2018, Ladle et al. 2018, Murphy et al. 2018). In addition, changes in vegetation structure can have predictable effects on wildlife species and community use of sites (Barras and Seamans 2002, McAdoo et al. 2004, Wan et al. 2018). In the Neotropics, we have some understanding of the effects of vegetation structure and forest infrastructure (e.g., roads and trails) on individual carnivore species (Weckel et al. 2006, Davis et al. 2011, Carrerra-Trevino et al. 2018), but there is a paucity of knowledge on how these same factors affect community dynamics. Knowing how vegetation structure affects carnivore presence and detection, and how site-use changes in

response to the presence of other carnivores, can enhance our ability to predict changes in community trends. For example, margay and coati [*Nasua narica*] are 2 mesocarnivores that use trees extensively for travel, feeding, and sleeping (Gehrt 2003, de Oliveira et al. 2015). If these species use similar vegetation structure and co-occur at sites, changes in vegetation structure might have similar and predictable effects on their populations. Without the combined knowledge of species' interactions with one another and their environment, we have a limited understanding of species presence on, and use of, the landscape.

Developments in computer software programs such as Presence (USGS Patuxent Wildlife Research Center) and MARK (Colorado State University) have allowed for more direct investigations of species co-occurrence, competition, and site-use based on covariates such as vegetation structure, human disturbance indices, and spatial location. Program PRESENCE can model occupancy probabilities and obtain a value called a "species interaction factor" (SIF; MacKenzie et al. 2004) that attempts to quantify the degree of dependence in probability of occurrence between 2 species. A second approach used by both Program PRESENCE and MARK assumes that where 2 species co-occur, interactions are asymmetric – that is, one species is dominant over the other (Richmond et al. 2010, Waddle et al. 2010, Nagy-Reis et al. 2017). Both approaches facilitate our understanding of species interactions, yet they have some important limitations. When MacKenzie et al. (2004) attempted to obtain a SIF that modelled the effects of covariates on 2 salamander species, their models failed to converge due to restrictions on the value that the SIF can take (i.e., species must co-occur at a minimum and a maximum number of locations, but not none or all), particularly when including covariates on parameters (MacKenzie et al. 2017). The methods produced by Waddle et al. (2010) and Richmond et al. (2010) force ecologists to assume a dominant species, which is problematic for more exploratory studies that lack baseline information needed for such hypotheses. Additionally, to use either method, ecologists must fit multiple 2-species models if they wanted to look at an entire community, making these methods an inefficient and time-intensive venture, particularly for large-scale ecological monitoring programs. Rota et al. (2016) created a flexible method allowing for the investigation of >2 interacting species in a single model that others have used with success (Ladle et al. 2018, Parsons et al. 2018). This method generalizes the single-season occupancy model, does not require *a priori* assumptions of asymmetric interactions, and provides explicit conditions for interspecific independence without the need to include additional parameters (i.e., as with SIF). As in other advancements in occupancy modeling, Rota et al.'s (2016) method models species interactions and an individual species' probability of detection as a function of covariates. The incorporation of the detection process and occupancy-state delineates the biological and sampling processes and leads to a process-driven estimate of species distributions (Iknayen et al. 2014, Rota et al. 2016).

Therefore, using the methods developed by Rota et al. (2016), my goal was to understand correlates of a rainforest carnivore community's structure and dynamics by 1) establishing if carnivore species occur independently of other carnivore species, and 2) how vegetation structure and forest infrastructure affects carnivore independence, co-occurrence, and site-use intensity. I expect ocelots and grey fox to use similar vegetation structure, but to use similar sites in opposing seasons. Additionally, based on morphological and behavioral differences, I expect jaguars to use sites with more dense vegetation less intensively, but to occur at these sites, with the opposite effects on pumas. As both margay and coati are semi-arboreal species that may use similar vegetation structure to carry out their daily activities, I hypothesize that they will use similar sites, and exhibit positive co-occurrence because margay are obligate carnivores and coati are more omnivorous. Because both coati and striped hog-nosed skunks are omnivores that feed on insects and mast, they may compete for sites with similar vegetation structure; therefore, I hypothesize that they will avoid sites used by each other.

METHODS

I examined rainforest carnivore community dynamics via camera surveys, and vegetation structure and forest infrastructure assessment in the Chiquibul Forest Reserve (CFR) at 51 sites. Camera surveys occurred from January 2016 to August 2016, comprising 12 weeks of the dry season, 3 weeks of the transition period between the dry and rainy season, and 7 weeks of the rainy season.

Study Area

The Chiquibul Forest Reserve (CFR; 59,822 ha) is in the Maya Mountain Massif, adjacent to the Caracol Archaeological Reserve (CAR; 10,339 ha), Belize. The Chiquibul National Park (CNP; 106,838 ha) surrounds both reserves and represents the largest protected area in Belize (Association of Protected Areas Management Organizations 2011; Arevalo 2011). The CFR has a subtropical climate with 2 distinct seasons: dry (February–June) and rainy (July–January), the latter coinciding with the hurricane season (Salas and Meerman 2008). Tropical broadleaf rainforest is the dominant ecosystem, but a small pocket of submontane pine forest exists at the reserve's center (Meerman and Sabido 2001). The CFR has a long history of multiple use, including recreation, gold mining, research, and logging activities, which have left a network of dirt roads and hiking trails throughout the reserve in various states of use and neglect. Currently, the CFR is subject to selective logging practices from March–May each year by Bull Ridge Limited, the single logging concession in the reserve. The logging concession organized

the CFR into 500-ha blocks, and the Belize Forest Department allows them to conduct logging operations in up to 2 of these blocks (i.e., 1000 ha) each year.

Camera Surveys

To evaluate the effects of vegetation and forest infrastructure on rainforest carnivore distributions, I established a grid of Moultrie M-880 Mini Game Camera trail cameras (Moultrie Feeders, EBSCO Industries, Inc., Alabaster, Alabama, USA) with infrared (IR) abilities. Each camera received a blank SanDisk Ultra 16GB SD card, allowing for the collection of up to 9,999 photos. I systematically placed cameras throughout the CFR on a 2.25 x 2.25-km grid, beginning with a site established at the center of the reserve. From that first site, I established other camera sites every 2.25 km by moving east and west, followed by north and south. Due to the dense network of roads and trails throughout the reserve, the majority of camera sites landed on one of these pathways. A handheld GPS unit under the North American Datum of 1927 (NAD27) geodetic reference system recorded each site's UTM coordinates.

I established camera sites along logging tracts, trails (human and animal; Kelly 2003), and streams, and in interior forest (i.e., not bisected by roads/trails/natural movement pathways; >30 m from any human-built pathway). Each site received 2 cameras, placed on trees on opposing sides of the site, to reduce the chances of data loss from 1) camera malfunction or 2) missing an animal as it walked by. I avoided facing cameras in an east-west facing direction when possible. Cameras were set >3 m from site-center on trees or other suitable objects (e.g., wooden stake) >5 cm dbh. I offset cameras by 0.3 m so that they were not directly opposite of one another to prevent camera IR or flash from triggering the opposite camera. I recorded the height, orientation, and distance between cameras (Silver et al. 2004, Kelly et al. 2013). Due to camera motion-detection sensitivity, I cleared vegetation between and within 1 m of cameras to avoid accidental triggering (e.g., waving grass; Kelly et al. 2013). Additionally, I held a card to each camera with the site number, date, and time to document site set-up and site-check/reset (Kelly et al. 2013).

Once triggered, I set cameras to take 3 photos/event, with a 5-second delay between picture events, should an animal remain in range after the initial capture. This facilitated my ability to capture potentially cryptic species (e.g., tayra). I re-visited sites every 2–3 weeks to avoid data loss. The function “Motion Freeze” was set to “On” to maximize image clarity at night by adjusting exposure time to reduce blur associated with motion. Each photo was imprinted with the associated camera's name, date, time, temperature (Celsius), and moon phase.

Vegetation Structure and Forest Infrastructure Assessment

To characterize vegetation structure at each site, I recorded site-specific vegetation characteristics in a 0.1-ha circular plot centered on the camera site (Fig. 7). I measured vertical

visual obstruction with a 2 m cover pole (Griffith and Youtie 1988) in the surrounding forest (ForVVO). To obtain ForVVO, I set the cover pole at plot center (i.e., between the 2 cameras), and viewed the cover pole from 5.6-m away at a height of 1 m at 5 points along 2 parallel 35.6-m transects (N = 10 points). These 2 transects were oriented parallel to each other and the camera sets. I used these measurements to derive total variance in vertical forest cover (VarForVVO), and to estimate total percent forest cover (%ForVVO), at each site. Along these same 2 parallel transects, I used the line-intercept method (Hays et al. 1981) to quantify horizontal cover in the forest to provide a refined perspective of horizontal visual obstruction (%ForHVO). To obtain %ForHVO, I held a 50-m tape 1 m above the ground and measured the horizontal spread (cm) of vegetation 0.5–1.0 m tall that hit the line.

I used a geographic information system (GIS) in ArcGIS (Environmental Systems Research Institute 2014) to derive landscape attributes associated with camera sites. Using high-resolution aerial photographs and by ground-truthing, I calculated pathway density within 2 km of sites.

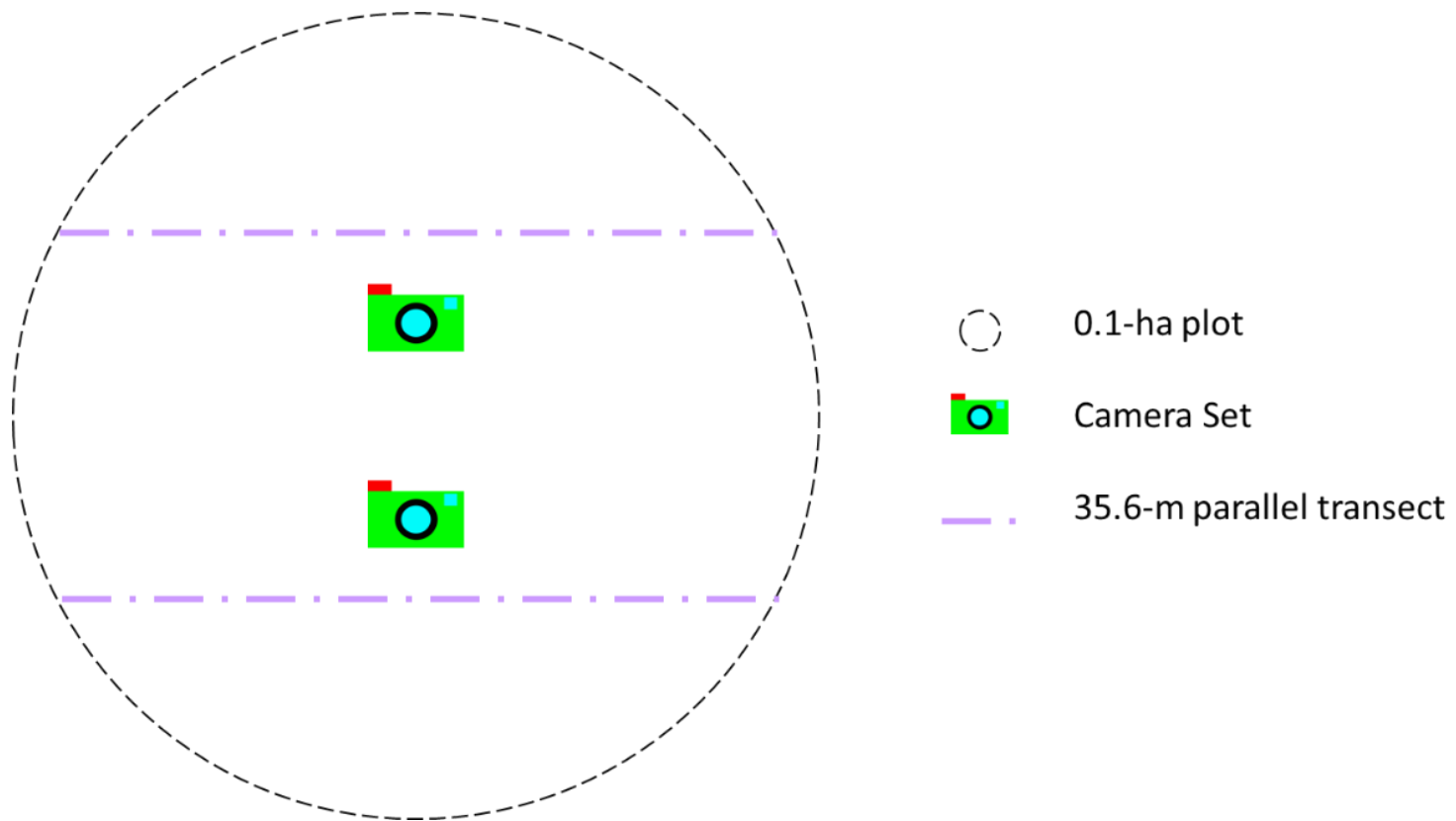


Figure 7. Camera site vegetation plots, Chiquibul Forest Reserve, Belize, Central America, 2016.

Carnivore Dynamics

For multi-species occupancy analyses, I used Program MARK's Multiple-Species Occupancy Estimation, based on methods described by Rota et al. (2016). This method allows you to estimate the natural parameter (f ; Rota et al. 2016) for each species, and every combination of species considered. However, there are a few limitations to this method: it is possible to examine interactions between only 6 species at a maximum; you can see the direction of species dependence (i.e., positive or negative), but not who is influencing whom; and the presence or absence of any other species cannot affect estimates of detection (p). In all analyses, I assumed that p varies by species, but is the same within species for each survey period.

Therefore, I grouped carnivores into the following communities to understand how greater community is structured, and the dynamics between species. Jaguar, puma, ocelot, grey fox, and tayra were the most frequently captured true carnivores, and form the basis for species-specific analyses in Chapters 1 and 2. Incidentally, these species also acted as “representatives” of their respective genera, and possibly exhibit competitive interactions. Jaguars and pumas are the 2 large carnivores in the CFR and rainforest system. Their similar body-sizes and some behaviors have led to assumptions that 1 species outcompetes the other where they co-occur, but limited evidence of this competition exists. Ocelots are another felid in the CFR, a species that appears to be indifferent to the presence of jaguars and pumas (Davis et al. 2011) but may be a “top” mesocarnivore where it occurs. Grey fox are the only canid representative in the system (however, coyotes are becoming more common throughout Belize, and showing up in the CFR), and ocelots might displace them from sites. Tayra are a common, wide-ranging, little-studied mustelid, and a prominent member of the mesocarnivore community.

Margay, coati, jaguarundi (*Puma yaguaroundi*), striped hog-nosed skunk, and opossum (*Didelphis* spp.) are all mesocarnivores that are common in the system (Fig. 8). It is unlikely that the mesocarnivore community competes with the larger carnivores for resources due to different body sizes that would naturally preclude them from using the same prey items, and the fact that most of the mesocarnivore species are omnivores. Although both margay and jaguarundi are obligate carnivores, they likely do not compete for resources as margay are semi-arboreal, and jaguarundi are more closely associated with open areas. However, margay and coati, and coati and skunks, may use similar vegetation structure for foraging activities. Opossums are nocturnal and likely occur independently from coati, jaguarundi, and skunks as opossum would be active when the other species are resting.

The final group examines all 5 species of cats (i.e., jaguar, puma, ocelot, margay, and jaguarundi) in the CFR. Each species exhibits morphological and behavioral differences that allow them to occupy different ecological niches (Davis et al. 2011, Rosenzweig et al. 2013),

leading to the possibility that species occur in sympatry. Jaguar and puma may occur in sympatry due to differences in vegetation structure that affect ease of movement and foraging ability. Although ocelot may be diurnal in certain areas of the CFR and thus overlap with jaguarundi in terms of activity patterns, jaguarundi are typically associated with more open systems than ocelots and so it is unlikely that the 2 species compete for resources.

Occupancy Estimation

Because sites are point locations of camera traps, I interpret occupancy to mean the probability of a species using a site, rather than true occupancy, given that my data represents a “presence-only” data set (MacKenzie et al. 2003, MacKenzie et al. 2006, Farris et al. 2015). This interpretation allows me to relax the assumption of closure to changes in occupancy during repeated surveys, particularly because movement in and out of the area is random (Mackenzie et al. 2004, Farris et al. 2015, Mackenzie et al. 2017, Nagy-Reis et al. 2017).

Each survey period ($N = 22$) comprised 1 week, during which I considered a species as using a site if I captured it on camera ≥ 1 time/survey period. If I captured a carnivore of interest at a site ≥ 1 time, the site received a “1,” indicating that the species was observed using the site on that occasion, and a “0” otherwise, and made no effort to distinguish between individuals (MacKenzie et al. 2006). All carnivores investigated occur in the CFR, but variation in population density and movement patterns affects 1) how they use the landscape, and 2) the frequency and intensity with which they are observed (Rowcliffe et al. 2008, Efford 2012, Burton et al. 2015, Latif et al. 2016). Therefore, when incorporating the effects of variables on p , the interpretation of this parameter shifts from referring to a simple detection probability of a species at a location, to informing carnivores’ site-use intensity (Ladle et al. 2018). I interpret the results of site-use intensity and site-use parameters together to understand carnivore community models.

Based on the literature, prior knowledge and field experience, and project goals, I developed sets of *a priori* single- and multiple-variable candidate models for single-season occupancy analyses (MacKenzie et al. 2006) where I considered the effects of site-specific variables and forest infrastructure on carnivore dynamics. I did not use correlated variables ($|r| > 0.70$; Tirpak et al. 2008) in models. I limited individual models to 3 predictor variables per parameter (i.e., p and ψ) to reduce the likelihood of over-fitting. I examined AIC_c values, AIC_c differences (ΔAIC_c), and Akaike weights (w_i) for models with different combinations of predictor variables and considered models with $\Delta AIC_c \leq 2$ supported (Burnham and Anderson 2002). I fit models assuming all species occur independently, then added species interactions to models one by one to increase model estimation precision. After examining the effects of variables on model performance, I found only %ForVVO to have informative effects. Thus, following the recommendations of Arnold (2010; i.e., solution 5), I developed a final suite of models to

understand how %ForVVO affected species dynamics in the presence of other carnivores (e.g., the effects of %ForVVO on jaguar and puma interactions when ocelot, grey fox, and tayra are present, and then in the presence of ocelot, margay, and jaguarundi).

When 85% confidence intervals (CI) for variables within supported models or species interactions overlapped with zero, I considered them to have an inconclusive effect and to be uninformative (Payton et al. 2003, Arnold 2010). When an 85% CI was >0 , I indicate that the variable had positive effects, and negative effects if <0 . Similarly, for species interactions, if an 85% CI was >0 , I indicate that species co-occurred, or avoided each other <0 . Program MARK's Multiple-Species Occupancy Estimation was used to analyze these data.

RESULTS

All analyses provide evidence that carnivores use sites independently from other species, except for ocelot and grey fox that co-occur at sites. Although neither site-specific nor landscape-level covariates were predictors of independence or co-occurrence, percent vertical visual obstruction (%ForVVO) was an important predictor of species site-use intensity. Unlike other systems where species interactions drive communities, these analyses provide evidence that species occur independently in the CFR.

Ocelot and grey fox are likely to co-occur at sites, whereas jaguar, puma, and tayra site-use was independent from other species. Due to the uninformative nature of grey-fox independence, and the fact that ocelots exhibit independence from other species, it appears that grey fox drive co-occurrence (Table 16 and 17). Sites with greater %ForVVO in the surrounding forest decreased jaguar, ocelot, grey fox, and tayra site-use intensity, but had uninformative effects on puma site-use intensity (Table 17).

Table 16. Supported models^a evaluating interactions between carnivores (i.e., jaguar, puma, ocelot, grey fox, and tayra), Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	K ^b	AIC _c	Delta AIC _c	w _i ^c	Model Likelihood	Deviance
f(independent, ocelot:grey fox) p(all %FVVO)	16	4462.90	0.00	0.43	1.00	4414.90
f(independent, no interactions) p(all %FVVO)	15	4463.02	0.13	0.40	0.94	4419.31
f(independent, jaguar:puma) p(all %FVVO)	16	4466.7	3.8	0.06	0.15	4418.7
f(independent, jaguar:ocelot) p(all %FVVO)	16	4467.21	4.32	0.05	0.12	4419.21
f(independent, jaguar:grey fox) p(all %FVVO)	16	4467.24	4.34	0.05	0.11	4419.24
f(independent %FVVO) p(all %FVVO)	20	3382.27	19.38	0.00	0.00	4414.27
f(independent, ocelot:grey fox) p(all %FVVO)	16	4462.90	0.00	0.43	1.00	4414.90
f(independent, no interactions) p(all %FVVO)	15	4463.02	0.13	0.40	0.94	4419.31
f(independent, jaguar:puma) p(all %FVVO)	16	4466.7	3.8	0.06	0.15	4418.7
f(independent, jaguar:ocelot) p(all %FVVO)	16	4467.21	4.32	0.05	0.12	4419.21

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c \leq 2$. ^bNumber of parameters estimated in the model. ^cWeight of evidence in favor of the model being the best approximating model in the set.

Table 17. Coefficients from the top models examining interactions between jaguar, puma, ocelot, grey fox, and tayra in the Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	Parameter ^a	Species	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
f(independent, ocelot:grey fox) p(all %FVVO) ^c	f	Jaguar	2.81	0.72	1.77	3.85
		Puma	2.25	0.48	1.55	2.95
		Ocelot	0.90	0.49	0.19	1.61
		Grey Fox	-1.08	0.83	-2.27	0.12
		Tayra	0.94	0.49	0.22	1.65
		Ocelot:Grey Fox	1.75	0.89	0.46	3.03
	p	Jaguar	-1.62	0.09	-1.74	-1.49
		Jaguar (%ForVVO) ^e	-0.21	0.08	-0.33	-0.09
		Puma	-1.21	0.08	-1.32	-1.10
		Puma (%ForVVO)	0.11	0.08	0.00	0.23
		Ocelot	-1.05	0.07	-1.16	-0.94
		Ocelot (%ForVVO)	-0.19	0.07	-0.29	-0.08
		Grey Fox	-1.47	0.11	-1.62	-1.31
		Grey Fox (%ForVVO)	-0.27	0.09	-0.40	-0.13
		Tayra	-2.51	0.18	-2.77	-2.24
		Tayra (%ForVVO)	-0.34	0.15	-0.56	-0.13
f(independent, no interactions) p(all %FVVO) ^d	f	Jaguar	2.81	0.72	1.77	3.85
		Puma	2.25	0.48	1.55	2.95
		Ocelot	1.69	0.39	1.13	2.25
		Grey Fox	0.40	0.29	-0.02	0.82
		Tayra	0.94	0.49	0.22	1.65
	p	Jaguar	-1.62	0.09	-1.74	-1.49
		Jaguar (%ForVVO)	-0.21	0.08	-0.33	-0.09
		Puma	-1.21	0.08	-1.32	-1.10
		Puma (%ForVVO)	0.11	0.08	0.00	0.23
		Ocelot	-1.05	0.08	-1.16	-0.94
		Ocelot (%ForVVO)	-0.19	0.07	-0.29	-0.08
		Grey Fox	-1.47	0.11	-1.62	-1.31
		Grey Fox (%ForVVO)	-0.27	0.09	-0.40	-0.13
		Tayra	-2.51	0.18	-2.77	-2.24
		Tayra (%ForVVO)	-0.34	0.15	-0.56	-0.13

^aSite-use (f) and site-use intensity (p). ^bParameter estimates. ^cOcelot and grey fox site-use is dependent on the other's presence, but jaguar, puma, and tayra site-use is independent. Species-specific site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^dJaguar, puma, ocelot, grey fox, and tayra site-use are independent. Species-specific site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^ePercent vertical visual obstruction in the surrounding forest.

All mesocarnivores (i.e., margay, coati, jaguarundi, striped hog-nosed skunk, opossum, and tayra) except for grey fox used sites independently from other species (Tables 18–21). Jaguarundi are unlikely to use sites in the CFR generally, whereas margay, coati, striped hog-nosed skunks, and opossums are all likely to use sites in the CFR. Sites with greater %ForVVO decreased coati, striped hog-nosed skunk, grey fox, and tayra site-use intensity, but had uninformative effects on margay, jaguarundi, and opossum (Table 19 and 21).

Finally, there was support for my hypothesis that all felids' site-use was independent. Jaguar, puma, ocelot, and margay likely to use sites, and jaguarundi unlikely to use sites. Vegetation structure had no effect on individual carnivore site-use. Jaguar and ocelot had decreased site-use intensity as vegetation density in the surrounding forest increased, whereas dense vegetation had uninformative effects on puma site-use intensity (Table 22 and 23).

Table 18. Supported models^a evaluating interactions between mesocarnivores (i.e., margay, coati, jaguarundi, striped hog-nosed skunk, and opossum), Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	K ^b	AIC _c	Delta AIC _c	w _i ^c	Model Likelihood	Deviance
f(independent, coati:striped hog-nosed skunk %FVVO) p(coati and striped hog-nosed skunk %FVVO)	14	2325.18	0.00	0.64	1.00	2285.52
f(independent, coati:striped hog-nosed skunk %HVO) p(coati and striped hog-nosed skunk %FVVO)	14	2326.88	1.69	0.28	0.43	2287.21
f(independent) p(all %FVVO)	15	2329.97	4.79	0.06	0.09	2286.26
f(independent, margay:coati:striped hog-nosed skunk:opossum) p(all %FVVO)	16	2333.35	8.17	0.01	0.02	2285.35
f(independent, margay:coati) p(all %FVVO)	16	2334.23	9.05	0.001	0.01	2286.23
f(independent, coati:striped hog-nosed skunk) p(all %FVVO)	16	2334.26	9.08	0.001	0.01	2286.26
f(independent, no interactions) p(constant)	10	2352.22	27.03	0.00	0.00	2326.72
f(independent, margay:coati) p(margay and coati %FVVO)	14	2359.47	34.28	0.00	0.00	2319.8

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c \leq 2$. ^bNumber of parameters estimated in the model. ^cWeight of evidence in favor of the model being the best approximating model in the set.

Table 19. Coefficients from the top model examining interactions between margay, coati, jaguarundi, striped hog-nosed skunk, and opossum in the Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	Parameter ^a	Species	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
f(independent, coati:striped hog-nosed skunk %FVVO) p(coati and striped hog-nosed skunk %FVVO) ^c	f	Margay	1.01	0.55	0.22	1.80
		Coati	0.76	0.82	-0.42	1.94
		Jaguarundi	-1.21	0.56	-2.02	-0.40
		Striped Hog-Nosed Skunk	0.68	0.81	-0.49	1.85
		Opossum	2.16	0.55	1.37	2.95
		Coati:Striped Hog-Nosed Skunk	0.22	1.04	-1.28	1.72
		Coati:Striped Hog-Nosed Skunk (%ForVVO) ^e	0.61	0.45	-0.04	1.26
	p	Margay	-2.66	0.19	-2.93	-2.39
		Coati	-2.58	0.18	-2.84	-2.32
		Coati (%ForVVO)	-0.43	0.15	-0.65	-0.21
		Jaguarundi	-3.03	0.48	-3.72	-2.34
		Striped Hog-Nosed Skunk	-2.49	0.17	-2.73	-2.25
		Striped Hog-Nosed Skunk (%ForVVO)	-0.71	0.12	-0.88	-0.54
		Opossum	-1.83	0.10	-1.97	-1.69
	f	Margay	1.01	0.55	0.22	1.80
		Coati	0.82	0.78	-0.30	1.94
		Jaguarundi	-1.32	0.56	-2.13	-0.51
		Striped Hog-Nosed Skunk	0.72	0.77	-0.39	1.83
		Opossum	2.16	0.55	1.37	2.95

Table 19. Continued.

Model	Parameter ^a	Species	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
f(independent, coati:striped hog-nosed skunk %HVO) p(coati and striped hog-nosed skunk %FVVO) ^d	f	Coati:Striped Hog-Nosed Skunk	-0.13	0.97	-1.53	1.27
		Coati:Striped Hog-Nosed Skunk (%HVO) ^f	-0.36	0.51	-1.09	0.37
	p	Margay	-2.66	0.19	-2.93	-2.39
		Coati	-2.53	0.17	-2.77	-2.29
		Coati (%ForVVO)	-0.37	0.15	-0.59	-0.15
		Jaguarundi	-3.03	0.48	-3.72	-2.34
		Striped Hog-Nosed Skunk	-2.43	0.17	-2.67	-2.19
		Striped Hog-Nosed Skunk (%ForVVO)	-0.67	0.12	-0.84	-0.50
		Opossum	-1.83	0.10	-1.97	-1.69

^aSite-use (f) and site-use intensity (p). ^bParameter estimates. ^cCoati and striped hog-nosed skunk co-occur at sites and depends on percent forest vertical visual obstruction. Coati and skunk site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^dCoati and striped hog-nosed skunk co-occur at sites and depends on percent horizontal visual obstruction. Coati and skunk site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^ePercent vertical visual obstruction in the surrounding forest at the site. ^fPercent horizontal visual obstruction in the surrounding forest at the site.

Table 20. Supported models^a evaluating interactions between mesocarnivores (i.e., grey fox, tayra, coati, striped hog-nosed skunk, and opossum), Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	K ^b	AIC _c	Delta AIC _c	w _i ^c	Model Likelihood	Deviance
f(independent, no interactions) p(%FVVO all)	15	2970.83	0.00	0.61	1.00	2927.11
f(independent, tayra:coati) p(%FVVO all)	16	2973.01	2.18	0.21	0.34	2925.01
f(independent, grey fox:tayra:coati) p(%FVVO all)	16	2974.86	4.04	0.08	0.13	2926.86
f(independent, grey fox:coati) p(%FVVO all)	16	2974.9	4.07	0.08	0.13	2926.90
f(independent, tayra:coati %FVVO) p(%FVVO all)	17	2977.55	6.72	0.02	0.03	2925.00
f(independent, tayra:coati %FVVO) p(tayr and coati %FVVO)	13	3001.83	31.00	0.00	0.00	2965.99
f(independence) p(constant)	10	3005.54	34.71	0.00	0.00	2980.04
f(independent and tayra:coati) p(constant)	11	3005.73	34.90	0.00	0.00	2976.96

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c \leq 2$. ^bNumber of parameters estimated in the model. ^cWeight of evidence in favor of the model being the best approximating model in the set.

Table 21. Coefficients from the top model examining interactions between grey fox, tayra, coati, striped hog-nosed skunk, and opossum in the Chiquibul Forest Reserve, Belize, Central America, 2016.

Parameter ^a	Species	β^b	Standard Error	85% Confidence Interval	
				Lower	Upper
f	Grey Fox	0.31	0.29	-0.11	0.73
	Tayra	0.99	0.51	0.26	1.72
	Coati	0.76	0.43	0.14	1.38
	Striped Hog-Nosed Skunk	0.68	0.39	0.12	1.24
	Opossum	2.19	0.57	1.37	3.01
p	Grey Fox	-1.43	0.11	-1.59	-1.27
	Grey Fox (%ForVVO) ^c	-0.26	0.09	-0.39	-0.13
	Tayra	-2.54	0.18	-2.80	-2.28
	Tayra (%ForVVO)	-0.36	0.15	-0.58	-0.14
	Coati	-2.56	0.18	-2.82	-2.30
	Coati (%ForVVO)	-0.38	0.15	-0.60	-0.16
	Striped Hog-Nosed Skunk	-2.42	0.17	-2.66	-2.18
	Striped Hog-Nosed Skunk (%ForVVO)	-0.68	0.12	-0.85	-0.51
	Opossum	-1.84	0.10	-1.98	-1.70
	Opossum (%ForVVO)	-0.08	0.09	-0.21	0.05

^aSite-use (f) and site-use intensity (p). ^bParameter estimates. ^cPercent vertical visual obstruction in the surrounding forest.

Table 22. Supported models^a evaluating interactions between felids (i.e., jaguar, puma, ocelot, margay, and jaguarundi), Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	K ^b	AIC _c	Delta AIC _c	w _i ^c	Model Likelihood	Deviance
f(independent, no interaction) p(jaguar:ocelot %FVVO)	12	3799.28	0.00	0.60	1.00	3767.07
f(independent, no interaction) p(jaguar, puma, and ocelot %FVVO)	13	3800.67	1.40	0.30	0.50	3764.83
f(independent, jaguar:puma) p(jaguar %FVVO)	12	3805.16	5.89	0.03	0.05	3772.95
f(independent) p(constant)	10	3805.74	6.47	0.02	0.04	3780.24
f(independent, jaguar:puma) p(jaguar and puma %FVVO)	13	3806.56	7.28	0.02	0.03	3770.72
f(independent, jaguar and puma %FVVO) p(jaguar, puma, and ocelot %FVVO)	15	3807.60	8.33	0.01	0.02	3763.89
f(independent, jaguar:puma %FVVO) p(jaguar %FVVO)	13	3807.92	8.65	0.01	0.01	3772.08
f(independent, jaguar:puma) p(constant)	11	3808.35	9.07	0.01	0.01	3779.58

^aAkaike's Information Criterion [AIC]; $\Delta AIC_c \leq 2$. ^bNumber of parameters estimated in the model. ^cWeight of evidence in favor of the model being the best approximating model in the set.

Table 23. Coefficients from top models examining the felid community (i.e., jaguar, puma, ocelot, margay, and jaguarundi) in the Chiquibul Forest Reserve, Belize, Central America, 2016.

Model	Parameter ^a	Species	β^b	Standard Error	85% Confidence Interval	
					Lower	Upper
f(independent, no interaction) p(jaguar and ocelot %FVVO) ^c	f	Jaguar	2.82	0.73	1.76	3.87
		Puma	2.25	0.48	1.55	2.95
		Ocelot	1.69	0.39	1.13	2.26
		Margay	1.20	0.62	0.31	2.09
		Jaguarundi	-1.31	0.56	-2.12	-0.51
	p	Jaguar	-1.62	0.09	-1.75	-1.50
		Jaguar(%ForVVO) ^e	-0.21	0.08	-0.33	-0.09
		Puma	-1.20	0.08	-1.31	-1.09
		Ocelot	-1.06	0.08	-1.17	-0.96
		Ocelot(%ForVVO)	-0.18	0.07	-0.29	-0.08
		Margay	-2.69	0.19	-2.96	-2.41
		Jaguarundi	-3.03	0.48	-3.72	-2.34
f(independent, no interaction) p(jaguar, puma, and ocelot %FVVO) ^d	f	Jaguar	2.82	0.73	1.76	3.87
		Puma	2.25	0.48	1.55	2.95
		Ocelot	1.69	0.39	1.13	2.26
		Margay	1.20	0.62	0.31	2.09
		Jaguarundi	-1.31	0.56	-2.12	-0.51
	p	Jaguar	-1.62	0.09	-1.75	-1.50
		Jaguar(%ForVVO)	-0.21	0.08	-0.33	-0.09
		Puma	-1.20	0.08	-1.31	-1.09
		Puma(%ForVVO)	0.12	0.08	0.00	0.23
		Ocelot	-1.06	0.08	-1.17	-0.96
		Ocelot(%ForVVO)	-0.18	0.07	-0.29	-0.08
		Margay	-2.69	0.19	-2.96	-2.41
		Jaguarundi	-3.03	0.48	-3.72	-2.34

^aSite-use (f) and site-use intensity (p). ^bParameter estimates. ^cSpecies use sites independently. Jaguar and ocelot site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^dSpecies use sites independently. Jaguar, puma, and ocelot site-use intensity depends on percent forest vertical visual obstruction. Site-use intensity varies by species, but is the same within species. ^ePercent vertical visual obstruction in the forest surrounding the site.

DISCUSSION

My goal was to understand the determinants of a rainforest carnivore community's structure and dynamics by establishing if carnivore site-use is affected by the presence of other carnivores, and the effects of vegetation structure on community dynamics. All community analyses provide support for species using sites independently, except for ocelots and grey fox that co-occur at sites, with no evidence of vegetation affecting site-use. When there was evidence for vegetative cover (i.e., vertical cover in the surrounding forest) effects on site-use intensity, it was negative for all species except puma. Denser vegetation appears to facilitate co-occurrence by providing cover that allows different species to use the same sites, while at the same time reducing potentially negative interactions. Unlike other less species-rich systems with communities driven by interactions between a few species, this rich carnivore community's structure and dynamics are determined by forest structure.

Jaguars and pumas exemplify the importance of understanding interspecific associations. Both species are habitat generalists, large-bodied, wide-ranging, and apex predators. Such similarities lead to the assumption that jaguars and pumas must compete where their ranges overlap. Yet jaguar and puma occur irrespective of other species present when considered part of a community involving multiple families (i.e., jaguar [Felidae], puma [Felidae], ocelot, grey fox [Canidae], and tayra [Mustelidae]) or in a single-family community (i.e., jaguar, puma, ocelot, margay, and jaguarundi [Felidae]). Although the 2 species are ubiquitous throughout the CFR, site-use intensity is correlated with vegetation structure. Jaguars are ambush predators whose successful hunting strategy depends on remaining camouflaged as they sit and wait for unsuspecting prey (Emmons 1987, Crawshaw and Quigley 1991). Denser vegetation likely provides more cover that facilitates jaguar ambush strategy, and thus reduces their need to search for suitable hunting locations. In contrast, pumas are visual predators that require open systems to see prey and will go on long searches to find prey (Seidensticker et al. 1973, Sweanor 1990, Beier et al. 1995). For a hunting venture to be successful, pumas must be able to see their prey with space enough to allow the long-legged animal to rush and strike unsuspecting quarry (Pierce and Bleich 2003, Harmsen et al. 2009b). In the CFR, pumas tend to use sites with less dense vegetation, in addition to reducing site-use intensity as vegetation density increases (Chapter 1 and 2). These behavioral and morphological difference with the jaguar, with its shorter legs and stocky form helping it to navigate dense vegetation (Harmsen et al. 2009b), facilitates these species sympatry.

Exploitative and interference competition between large felids and canids is a common phenomenon (e.g., scavenging carcasses [Harrison 1990], and wolves (*Canis lupus*) are known to kill pumas [White and Boyd 1989, Boyd and Neale 1992]). However, even though ocelots

and grey fox are 2 similar-sized species belonging to the felid and canid families respectively, there was little evidence for or against their co-occurrence in a study adjacent to the CFR (Davis et al. 2011). Based on this and other studies, I expected ocelots and grey fox would not co-occur at sites in the CFR. Yet, in contrast to these studies and my expectations, ocelots and grey fox were more likely to occur together. Grey fox and ocelots appear to coexist by exploiting vegetation structure that apparently meets both species' needs. The unused logging roads and logging decks throughout the forest reserve contribute to dense structure and variability in vegetation, and offer habitat favored by ocelot and grey fox prey (Blaum et al. 2007, Ofori et al. 2016, Satter et al. 2018). The pockets of non-homogeneous, but well-structured vegetation cover throughout the CFR may provide similar conditions as agricultural areas that support small-mammal populations (Schmid-Holmes and Drickamer 2001, Pardini 2004), and thus are attractive to ocelots. Although there likely is some overlap in food resources consumed, ocelots are obligate carnivores, and grey fox are omnivores and can therefore use other items to meet their dietary needs. I frequently captured grey fox on camera carrying snakes, lizards, and different seasonally available fruits (e.g., Sapotaceae), as described in Davis et al. (2011).

Of the 5 most commonly captured species, tayra are the least studied. As a wide-ranging medium-sized mustelid (Konecny 1989, Sunquist et al. 1989), they may require larger tracts of land than expected relative to their size, like wolverines (*Gulo gulo*) in the Northern hemisphere. However, wolverines compete with larger carnivores where ranges overlap (Khalil et al. 2014), impacting their space-needs. Tayra, however, occur throughout the CFR irrespective of the presence of other carnivores. Tayra are more omnivorous than wolverine and consume similar items as grey fox (Hall and Dalquest 1963, Konecny 1989, Emmons and Freer 1990, Sáenz-Bolaños et al. 2018). Because both tayra and grey fox are capable tree-climbers, they can each use varying levels of the forest strata to forage (e.g., hard and soft mast, amphibians, and reptiles) and partition resources used. Although both grey fox and tayra use diverse vegetation structure provided by disturbed forests and agricultural systems (Emmons and Freer 1990, Davis et al. 2011), tayras larger ranges may provide enough resources to reduce competitive interactions with grey fox.

Some mesocarnivores may be susceptible to predation by other carnivores. For example, coati are omnivores that will follow seasonally available resources (Kaufmann et al. 1976, Kaufmann 1982, Russell 1982, Delibes et al. 1989) and exist in a variety of ecosystems ranging from the tropics (Valenzuela and Ceballos 2000) to pinon-oak juniper woodlands in Arizona (Kaufmann et al. 1976, Lanning 1976). Because coati can obtain resources for survival and reproduction in a variety of ecosystems, predation is the limiting factor for coati populations (Gehrt 2003). Although coati do sometimes forage in trees, most foraging occurs on the ground, increasing coati susceptibility to predation (Currier 1983, Rabinowitz and

Nottingham 1986, Valenzuela and Ceballos 2000). Solitary males lack the protection afforded by being in a group of many alert individuals, whereas the larger groups of females with new offspring and juveniles are noisier and thus present as obvious targets. Predators looking down from the trees (e.g., primates [Fedigan 1990] and birds of prey [Kaufmann et al. 1976, Glanz 1991, Jorgensen and Redford 1993]) will have a difficult time observing coati in denser vegetation (Camp et al. 2013). With more vegetation cover at sites, these mesocarnivores can forage safely, and hear predators approaching sooner than at more open sites. Like coati, striped hog-nosed skunks are also omnivores that can occur in a variety of ecosystems. Invertebrates, such as insects and arachnids, and vegetation, such as nuts and fruits, comprise an important component of both coati (Gehrt 2003) and skunk (Leopold 1965, Patton 1974) diets. Logging activities create holes in the canopy and promote rapid growth of previously dormant plant species, producing brushy and shrubby sites used by these species (Brokaw 1985, Johns 1985, Whitmore 1989, Finegan 1996). Such conditions encourage insect and other invertebrate populations (Stephen and Sanchez 2014), providing an ideal food source for coati and skunks. Greater vertical vegetation cover gives coati another stratum in which to forage, leaving the ground and lower reaches of the understory available for use by skunks.

As with all carnivores in the CFR except for jaguarundi, margay are likely to occur throughout the forest. Margay are highly adapted to arboreal life, but they are not a strictly arboreal species (de Oliveira et al. 2015). Rather, margay partition their activities between both terrestrial and arboreal sites (e.g., travel and resting; Konecny 1989, de Oliveira et al. 2015), and terrestrial species comprise much of their prey consumption (Oliveira 1998, Wang 2002, Oliveira and Cassaro 2005, Bianchi et al. 2011). Additionally, margay are known to use highly disturbed forest, abandoned plantations and other agroforestry systems, if there is adequate tree cover (Oliveira et al. 2010, Tortato et al. 2013). Although selective logging practices leave plenty of tree cover in the CFR, there are areas where trees are not close enough to facilitate margay movement through the canopy. It is likely that the vertical cover metric inadequately explains margay site-use intensity because of this species arboreal and terrestrial habits. This metric had a similarly uninformative effect on jaguarundi, but likely for differing reasons. Jaguarundi are typically associated with naturally open systems, such as savannas and old fields, and along riparian corridors that provide distinctly different vegetation structure where 2 ecosystems meet (Konecny 1989). Although logging activities and the roads and trails present in the CFR do provide conditions that are used by jaguarundi, dense forest cover dominates the CFR, and there is little constant above-ground water, providing poor quality habitat overall for jaguarundi.

Because there are a diversity of resources that facilitate the presence of the many carnivore species in the CFR, and all carnivores in the CFR are generalists, a dominance hierarchy may not exist. Competition occurs when 1) resources are limiting, and 2) >1 species

attempt to use the same resource in the same place at the same time. The carnivores in the CFR may have specialized hunting strategies, but no species is a habitat or prey-species specialist. Competitive exclusion and dominance in species interactions occurs when 1 species successfully outcompetes another for that desired resource (Hardin 1960). Human induced (i.e., logging) and natural (i.e., hurricane) disturbances that leads to dynamic vegetation cover occur regularly in the CFR; this, in turn, provides a variety of species with the full suite of resources they require, such as hiding and foraging cover, and prey habitat. Even ocelots and grey fox co-occur at sites, when I expected them to exhibit avoidance to reduce negative interactions; if either species was a specialist, it is unlikely that evidence of co-occurrence could exist. Although there is potential for temporal segregation (Chapter 1) between ocelot and grey fox, the community analyses were unable to detect this as affecting ocelot and fox interactions in a community setting.

When using occupancy estimation in long-term studies to understand changes in population trends, it is important to recognize that patterns of site-use may reflect individual animals' habits, rather than act as a reflection of the population's abundance (Mackenzie et al. 2017). The many pockets of non-homogeneous vegetation in the CFR appear to support its diverse carnivore community, yet this same characteristic may support only low abundances of individual species. Studies on the small mammal community in the CFR reflect this characteristic (i.e., Caro et al. 2001, Kelly and Caro 2003), a pattern that is likely repeated in the meso- and large-carnivore communities. Smaller populations place less pressure on available resources, allowing the community to remain stable. Additionally, it is possible that logging activities in the forest provide periods of surplus prey for carnivores, as others have documented that selective logging increases small mammal abundance in the tropics (Delany 1971, Malcom 1995, and Struhsaker 1997). Resource availability and patterns of predictability (e.g., small mammals in selectively logged areas, seasonally and spatially available mast [Janzen 1973, van Schaik et al. 1993, Zimmerman et al. 2007]) means carnivores do not need to fight for or defend resources, and can co-exist with minimal negative interactions.

East of the CFR and within the same mountain chain, is the Cockscomb Basin Wildlife Sanctuary (CBWS), also a protected area, but one that operates under a "preservation" management regime. This mandate means that CBWS must rely on natural disturbance (e.g., hurricanes) to alter the system, as there are only a few established hiking trails, and 1 road into the sanctuary. Not only has this passive management regime led to less structural diversity in the forest, but also a less species-rich and carnivore-diverse system (Bridgewater 2012). Jaguars and pumas are the main carnivores present in the CBWS, with a much reduced mesocarnivore community compared to the CFR (Bridgewater 2012). The CBWS is an island for some jungle species due to the pressure placed on the surrounding human-dominated landscape (Foster et al. 2010), and it is possible that a dominance hierarchy exists under these

conditions. Indeed, it is under these conditions that jaguars and pumas alter their habits spatially and temporally to avoid contact (Harmsen et al. 2009a, Harmsen et al. 2009b, Foster et al. 2010, Foster et al. 2013). Studies suggest that the CBWS holds a high density of jaguars relative to other areas in Belize (Silver et al. 2004, Harmsen 2006); however, as Van Horne (1983) discussed, a dense population of a species in one place versus another is not an indication of prime habitat quality. Contrasting the CFR, the small size of the CBWS and a matrix unfriendly to jaguar and puma dispersal (Foster et al. 2010) could mean these 2 large carnivores exert greater pressure on resources. Changes in a dominance hierarchy could signal that the site is no longer supporting 1 of its species, the loss of which could completely change the dynamics of that system.

Although the analyses I used limit explicit inference on patterns of species dependence, except for grey fox and ocelots, there is little evidence supporting a need to examine this community for a dominance hierarchy. It is necessary to interpret p and ψ parameters simultaneously to understand observed patterns in the carnivore community, and how covariates affect community dynamics. Except for jaguarundi, vegetation structure facilitates the positive occurrence of all carnivores in the CFR. Not only will this knowledge inform future study designs seeking to understand the distribution of these tropical species and communities, but it can guide management actions that manipulate vegetation to provide for the needs of an entire community of species. Furthermore, logging concessionaires hoping to gain certification by reducing negative impacts of logging on wildlife can use this information to inform logging protocols. This study represents an important step in understanding not only the dynamics of a carnivore community, but the role vegetation structure plays in facilitating species coexistence.

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CONCLUSION

My goal was to determine the factors affecting carnivore coexistence and individual species distributions in a managed forest reserve in Belize, Central America. Using an occupancy-modeling framework, I came up with different models to explain the 1) seasonal effects of factors on carnivore distribution throughout the CFR, 2) importance of different pathways and their characteristics in determining how carnivore site-use intensity in the CFR, and 3) coexistence among carnivores. Variables generally failed to affect carnivore site-use, but percent vertical visual obstruction was an important predictor of species site-use intensity. The importance of site-specific categories in determining carnivore distributions changed between seasons for all species except jaguars. Top models for carnivores at both site-specific and landscape levels suggest that pathway characteristics affected carnivore site-use intensity, but not general site-use. Except for ocelot and grey fox, and where grey fox are part of other communities, all analyses provided evidence that carnivores used sites independently from other species.

Carnivores occur independently in the CFR, with species co-occurrence apparently driven by the variable vegetation structure created by logging and other disturbance that affect resource availability and composition. Although grey fox and ocelot broadly exhibited dependence, a refined examination of each species' suggests that coexistence is a result of seasonal partitioning of resources, since the same categories had the same effects on both species, but in opposing seasons. Pumas and jaguars occurred in sympatry, with prey driving patterns of site-use intensity for jaguars in both dry and rainy seasons, and vegetation primarily affecting pumas. Others actively working in the CFR (e.g., researchers, rangers, etc.) have observed pumas are more common than jaguars; however, this may be a factor of the detection process, as pumas may be more detectable because they have to search more intensively for suitable resources in the CFR than jaguars. Pumas were more selective about the vegetation structure used than jaguars. Relative to pumas, vegetation structure minimally impacted jaguar distributions, they were less sensitive to human disturbance, and took greater advantage of the road and trail network present in the CFR. Unlike the other 4 species, few characteristics of the CFR affected tayra. Similar to pumas, vegetation structure and human disturbance (i.e., vehicular traffic) consistently predicted tayra distributions. However, not only did tayra exploit denser vegetation more readily than pumas, they also used sites with more vehicular traffic when denser vegetation was present, suggesting they can be quite resilient to human disturbance.

The non-homogeneous, but well-structured, vegetation mosaic created by both logging activities and natural (e.g., hurricanes) disturbance appears to provide resources that facilitates carnivore presence in the CFR. Knowing that jaguars and pumas likely respond differently to

activities that change forest structure and increase human presence on the landscape has important implications for their continued persistence. Increasing protection around key features (i.e., riparian areas) could help mitigate added pressure on carnivores from human disturbance during limiting periods, and allowing logging structures to lie fallow at the end of the logging season could provide sensitive species with places to retreat when humans are highly active on the landscape. Where vehicles are active, leaving some slash and logging debris in pathways would benefit tayra, but reducing overall vegetation density would have positive effects on tayra, puma, and ocelot. However, leaving pockets of dense vegetation is necessary as this structure likely facilitates jaguars successful ambush strategy while hunting, and grey fox occur around this structure more frequently.

VITA

Lauren Watine is a wildlife biologist whose interests lie in carnivore conservation, predator-prey dynamics, and human-wildlife conflict. As a carnivore scientist, she has conducted a state-wide dietary habits study of coyotes in Florida; worked with Belizean landowners to mitigate jaguar-cattle conflicts; monitored wolves with the Idaho Department of Fish and Game; and managed black bears with Yosemite National Park's bear management team. Before arriving in Tennessee, Lauren completed her Bachelor's and Master's degrees at the University of Florida, with the topic of her M.S. thesis investigating coyote predation effects on white-tailed deer fawns. Lauren's PhD research focuses on understanding the determinants of a rainforest carnivore community in a managed forest reserve in Belize, Central America. More often than not, you can find Lauren somewhere relatively unexplored in the mountains with dirt on her face and critter scat in her pack.