ENVIRONMENTAL DRIVERS OF JAGUAR DISTRIBUTION, ACTIVITY, AND ABUNDANCE IN SANTA ROSA NATIONAL PARK, COSTA RICA

A Dissertation Presented

by

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DEDICATION

To the memory of Alvaro Ugalde Víquez, the father of the National Parks of Costa Rica.

To the untamed God spirits present in all nature creatures.

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ABSTRACT

ENVIRONMENTAL DRIVERS OF JAGUAR DISTRIBUTION, ACTIVITY, AND ABUNDANCE IN SANTA ROSA NATIONAL PARK, COSTA RICA

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Jaguars (*Panthera onca*) are a landscape species persisting in less than 54% of their historical distribution range; thus, the understanding of abiotic and biotic environmental factors affecting ecological interactions of this top predator in seasonal ecosystems such the dry forest is crucial for their conservation. In addition to factors affecting species ecology, some methodological constraints also could affect jaguar study outcomes leading to wrong decision-making. Data gathered from available jaguar peer-reviewed literature showed that there are large number of variables and techniques used to model jaguar distribution that did not contribute substantially to descriptions of jaguar distribution. Using the variables that do correlate with distribution (or better estimates of those variables or what they represent) such as prey abundance, protection level, distance to protected areas, landcover, road variables and vegetation, would improve estimates of jaguar distribution and abundance based on intuitive predictors. Therefore, researchers should better identify and then quantify specific casual factors affecting jaguar distribution and abundance, rather than simply describe it. Camera trap data at waterholes and pathways in Santa Rosa National Park in northwestern Costa Rica were evaluated that included two camera trap designs (50 camera traps at waterholes and on pathways during both dry/wet seasons). For 10 large mammal species (including jaguars) and four large bird species in the dry forest of northwestern Costa Rica, only capuchin monkeys (*Cebus capucinus*), tiger herons (*Trigrisoma mexicanum*), white-tailed deer (*Odocoileus virginianus*), and tapirs (*Tapirus bairdii*) showed interacting effects of location and seasonality, suggesting that these species were the most influenced by waterholes during the dry season. Data from a single female jaguar equipped with a GPS unit, and seasonal sea turtle abundance data and predation rates from track count surveys at Playa Naranjo and Playa Nancite, were analyzed to assess jaguar dependency on nesting turtles. Seasonal movements of this single female were influenced by seasonal sea turtle abundance availability, an overall home range size of 89 km^2 did not differ statistically across turtle and non-turtle seasons, and during turtle seasons this collared female tended to stay mostly near the coastline. With regard to camera placement and seasonality on photo rates of jaguars and nontarget species, from June 2016 to June 2017 I deployed 58 camera traps at trail and off-trail locations in a grid array. I recorded 64 species of amphibians, reptiles, birds and mammals for which I calculated and compared relative abundance indexes (RAI: no. of independent photos/100 trap nights). For jaguars, I identified a high RAI of males at trail locations and high rates of female jaguars at off trail locations. Analysis of predator and prey interactions indicated temporal avoidance at trail locations. Density estimation using spatial capture-recapture models registered 19 jaguar individuals (11 males; 8 females), and a population density of 2.6/100 km^2 (95% [CI] 1.7-4.0) jaguar females and 5.0/100 km^2 jaguar males (95% [CI]

3.4-7.4). Camera location placement might bias sex individual detections and subsequent estimates based on telemetry and camera trap data. Long-term studies of jaguar populations might give more realistic and useful insights to conservation if researchers paid more attention to species' behavior and interactions that could be biasing results. Thus, it is important to continuously rethink the "what?" and "how?" of the things we are doing in conservation science to effectively understand ecological processes. Additional observations from this study suggest some large herbivores are more sensitive to changes of climate than other species; therefore, jaguar studies should continue to tackle the effects of climate variability on prey species and their relationships with large predators in a unique ecosystem such the tropical dry forest.

PREFACE

The jaguar (*Panthera onca*) is the largest felid in the Neotropics and many populations have been gradually extirpated from their natural range. The jaguar is classified as “near threatened” and only occurs in 54% of its historic geographic range due to fragmentation, reduction of its natural prey, poaching, deficient protection, isolation, and killing in retaliation for livestock depredation. Jaguar populations persisting in the Neotropics are more threatened than they appear due the lack of assessments at the subpopulation level where area-specific factors vary.

Jaguars play a key role in the dynamics of ecosystems by preying on and likely controlling populations of herbivores and frugivores. Therefore, regular evaluation of jaguars and their prey is important to support conservation decision-making both inside and outside of protected areas.

Santa Rosa National Park (SRNP) in northwestern Costa Rica encompasses some of the last relicts of seasonal dry forest ecosystems in the Neotropics. These critically endangered ecosystems, owing to the scarcity of water during the dry season, enhance habitat heterogeneity for vertebrates. Since 1980, SRNP has been undergoing an active restoration process via suppression of anthropogenic fires and recovery of lands previously used for livestock. This forest restoration has resulted in recovering predator and prey communities.

The elusiveness and rarity of jaguars has made it relatively difficult to conduct field studies and in Costa Rica the geographic distribution of jaguar studies is limited. Although knowledge of jaguar ecology has increased, detailed studies still are challenging, and research is lacking in understanding the complexity of jaguar and prey responses in the few outstanding seasonal ecosystems were jaguars still persist.

Since 2011, colleagues and I have gathered camera trap, GPS telemetry, and track survey information to help evaluate how seasonal climatic and environmental factors might influence the distribution and abundance of jaguars, their competitors, and prey in SRNP northern Costa Rica. In Chapter 1 (submitted to Mammal Review), I review published literature in order to identify and assess the importance of various environmental and anthropogenic variables, techniques, scales, and modeling approaches used to model jaguar distribution. In Chapter 2 (published in Journal of Tropical Ecology; https://www.cambridge.org/core/journals/journal-of-tropical-ecology), I analyze camera trap data to elucidate patterns of seasonal use of waterholes and pathways by ten large mammal and four large bird species. In Chapter 3 (published in Biotropica; https://onlinelibrary.wiley.com/journal/17447429), I use jaguar and sea turtle track count surveys, combined with satellite telemetry of one jaguar, to evaluate how much jaguar hunting behavior and movements are influenced by seasonality of sea turtle nesting. In Chapter 4, I assess the effect of camera trap site placement on jaguar and non-target species photo rates to identify methodological implications for further jaguar studies, and in Chapter 5, I estimate the jaguar population density, using sex and camera placement (trail/off trial) as covariates, considering GPS telemetry data from one collared jaguar, and also characterize the jaguar population structure in SRS. Finally, in Chapter 6, I present a summary of my research findings as they pertain to conservation and management.

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CHAPTER 1

A REVIEW OF ENVIRONMENTAL AND ANTHROPOGENIC VARIABLES USED TO MODEL JAGUAR (*Panthera onca*) DISTRIBUTION ACROSS ITS RANGE; DO COMMONLY USED MODELING VARIABLES CORRELATE WITH DENSITY?

Abstract

Jaguars (*Panthera onca*) are a landscape species of conservation importance, and understanding environmental and anthropogenic drivers of jaguar distribution is necessary to develop effective conservation strategies. We reviewed available literature in order to describe the environmental and anthropogenic variables used in various modeling efforts; subsequently, those variables identified as the most significant were tested against jaguar density. We identified 84 documents published from 1980 to 2019 that focused on jaguar distribution, and 39 variable types (21 anthropogenic, 18 environmental) were included in models with a variety of techniques, scales and approaches. These variables were pooled into three anthropogenic (roads, land use, human activities and population) and six environmental subcategories (climate, vegetation, ecological interactions, topographic, water, and others). No single variable was assessed in more than half of the documents, and 21 variables were assessed in only 1 or 2 documents. Twelve variables were reported as not significantly correlating with jaguar distribution, but these all were assessed only 1 or 2 times. Of the remaining 27 "significant" variables, 9 were assessed in only 1 or 2 papers. An additional 8 were identified in >50% of 3-27 papers as significant: these included hunting pressure, human activities, precipitation, temperature, vegetation type, conspecifics, prey, and distance to water. A sort set of most significant variables (i.e., precipitation, temperature, urban development, fresh water, human footprint, vegetation cover, natural resources protection level, peccary relative abundance, deer relative abundance, paca relative abundance, and co-specific relative abundance) were contrasted with jaguar density. Nevertheless, we only found statistical evidence of correlation for peccary relative abundance and natural resources protection level with jaguar density; most variables used in models did not substantially contribute to descriptions of jaguar abundance. Using the variables that do correlate with distribution (or better estimates of those variables or what they represent), such as peccary relative abundance and natural resources protection level, should help researchers produce better models in the future and make better predictions in areas without quantitative jaguar data. More importantly, thoughtful assessment of those variables should direct researchers to better identify and then quantify specific casual factors affecting jaguar distribution and abundance, rather than simply describe it, especially in terms of jaguar reproduction, survival, and dispersal.

Introduction

The jaguar (*Panthera onca*) is the largest felid on the American continent (Seymour 1989) whose populations have been gradually extirpated from their natural range (Ceballos et al. 2005, Ripple et al. 2011). The species is classified as “Near threatened” (IUCN 2018) and occurs in only 54% of its historic geographic range (Sanderson et al. 2002). Nevertheless, previous jaguar population assessments at the continental scale also showed that the species is declining at a great rate (Rabinowitz and Zeller 2010, Medellín et al. 2016, de la Torre et al. 2017). Still, in the 21st century threats such as trophy hunting, killing as retaliation by livestock predation, habitat loss, human expansion, and poaching of prey continue to cause the species’ downward trend (Medellín et al. 2016, IUCN 2018). Jaguars are landscape species with large home ranges and reside both inside and outside of protected areas and across a variety of ecosystems under a gradient of anthropogenic pressures (Silver et al. 2004). They are an apex predator that functionally helps maintain the balance in ecosystem structure, regulating populations under lower trophic levels to stable states (Estes et al. 2011, MacBride and Thompson 2018). Studying free-ranging jaguars can be challenging due to their elusive behavior, their large home range sizes and low population densities, and the fact that they sometimes live in insolated and difficult-to-access areas (Salom et al. 2007, Carrillo et al. 2009). Therefore, data collection is logistically demanding and expensive. Jaguar presence across the American continent is fairly well known (Rabinowitz and Zeller 2010); however, questions about their distribution and population trends still are a conundrum (Sanderson et al. 2002, de la Torre et al. 2017). Thus, it is important to better understand and help ameliorate the negative threats affecting populations at a local and regional scale (de la Torre et al. 2017b).

Understanding drivers of species distribution under global change scenarios is crucial to developing conservation strategies (Kareiva and Marvier 2015); hence, adequate quantities of usable resources should determine species abundance and distribution, contrary to factors that pose as constrainers of species distribution (Manly et al. 2002). One of the most critical duties for species conservation is to document how environmental and anthropogenic factors allow or limit a species distribution and abundance (Morrison et al. 2006). With regard to jaguar distribution, there are different approaches related to types of data collection, scale, and statistical approaches commonly used; nevertheless, there is a lack of systematic classification of common environmental and anthropogenic factors related to the species modeling approaches. In general, recent studies have argued that some techniques and variables used are unrelated to species abundance which can lead to wrong inferences (Dallas and Hastings 2018). Basic statistic empirical models analyzing or describing summaries of empirical jaguar data usually are based on correlation among variables (Morrison et al. 2006). Deductive models rely on previous knowledge of species-habitat relationships based on literature or expert opinion (Morrison et al. 2006). Presence-only models rely on occurrence records together with environmental variables to represent the ecological-niche of a species (Phillips et al. 2017). Lastly, occupancy models use a mixture of detection/no-detection records with a set of different covariates combination to choose the best models that explain species occupancy across the sites (Mackenzie et al. 2017).

The aim of this study is to summarize and evaluated the relationship among the most significant anthropogenic and environmental variables cited in peer reviewed literature that positively support abundance/occurrence relationships across jaguar range. Therefore, we compiled information on different variables, modeling, and data collection approaches commonly used to model jaguar distribution to test whether the best set of anthropogenic and environmental variables used in peer review literature do really correlate with jaguar abundance. The outcome of this study make call to re-think the use and abuse of meaningless variables for future modeling of jaguar distribution, in order to make it easier and efficient to construct useful models based on biologically reliable variables.

Materials and Methods

A comprehensive literature review of factors influencing jaguar distribution and abundance was conducted using two Internet search engines: *Web of science* and *Google scholar*. The systematic search was temporally delimited from 1980 to 2019 and used the following combination words: “*Jaguar*” + “*Distribution*” + “*Environmental variables*” + “*Prey abundance*” + “*Panthera*”.

For each publication identified as relevant, we identified the methods of analysis used to inform jaguar distribution, the geographic scale of the assessment, and a list of variables included in the assessment. Similar variables with different names were classified into one-name variables, and these were subsequently sorted into sub-categories within the broader categories of anthropogenic and environmental factors. Once the best set of predictor variables summarized the most significant determinants of jaguar distribution, we also gathered relative abundance and jaguar density data from available documents to independently perform a correlation analysis with this set of predictors using the statistical software R Version 3.6.1(R Core Team 2019) in order to test whether these variables positively correlated with jaguar abundance parameters.

Results

We identified 153 peer reviewed documents in our search, but only 84 either tackled issues of jaguar distribution or correlated distribution with anthropogenic or environmental factors. Among these studies we found that the number of jaguar distribution studies recently has increased over time, with almost 87% of the literature being published after 2000 (Fig. 1.1a). Most studies took place in Brazil (n = 25), Mexico (n = 15), and Belize (n = 10; Fig. 1.1b).

Among the studies there were four main modeling approaches (Table 1.1). The most widely used were basic statistic empirical models (n = 36) which usually analyze or describe summaries of empirical data based on correlation among variables (Morrison et al. 2006). Occupancy models (n = 19) use a mixture of detection/no-detection records with a set of different covariates combination to choose the best models that explain species occupancy across the sites (Mackenzie et al. 2017). Niche or presence-only models (n = 19) rely on occurrence records together with environmental variables to represent the ecological-niche of a species (Phillips et al. 2017). Deductive approaches (n = 10) rely on previous knowledge of species-habitat relationships based on literature or expert opinion (Morrison et al. 2006).

A variety of research techniques were used to gather data for assessments of jaguar distribution (Table 1.1). Data from camera trapping was used most often (n = 33), but historic records (n = 21) and telemetry studies (n = 14) were also commonly relied on. There also were also multiple geographic scales used in modeling efforts (Table 1.1). Most were local or study area-specific (n = 55), but a number of papers assessed jaguar distribution at continental (n = 10), regional (n = 12), or country (n = 7) scales.

Our summation of different qualitative and quantitative variables types used to model jaguar distribution identified a total of 39, including 21 classified as anthropogenic and 18 as environmental (Table 1.2). The anthropogenic variables were sorted into four subcategories: road, land use, human activities, and population. Environmental variables were sorted into five subcategories: climatic, vegetation, topographic, water, and other.

Anthropogenic variables

Anthropogenic-based variables are often described as significant groups of variables negatively affecting jaguar presence on their habitats as a result of human infrastructures, population growth, and human behaviors (e.g., Silveira et al. 2014).

Roads have been identified as having a direct effect on jaguar habitat quality, increasing fragmentation and access to pristine areas (Colchero et al. 2010, Gese et al. 2018, Romero-Muñoz et al. 2018), increasing poaching of jaguar and prey (Sanderson et al. 2002), as well as stressing animal’s behavior near highly used roads (Petracca 2010). Studies we reviewed incorporated three “road” metrics in models: distance to roads, distance to railroads, and road density. Nevertheless, only 5 (25%) of the 20 papers that used road variables reported statistical significance (Table 1.2), distance to roads being the most common and only significant metric.

Land use variables often are considered to reflect restriction of jaguar distribution by reducing the resources available for populations in the wild, thus representing a source of perturbation (Cuyckens et al. 2017). Reviewed papers included land cover, distance to forest, and distance to agriculture as modeled variables. Thirteen (50%) of 26 papers that assessed land use variables reported significant correlation patterns involving land cover, land cover type being the most common metric used, but only identified as significant in <50% of the models in which it was included (Table 1.2).

Human activities typically reflect an amount of economic, recreational, or illegal activities carried out by humans that directly affect jaguar presence or biological processes within jaguar range (Jordan et al. 2016, Jędrzejewski et al. 2017, Silva et al. 2018, Ávila-Nájera et al. 2019). For such human activities, 11 metrics were identified, including level of protection, distance to protected areas, cattle density, human activities, hunting pressure, forest loss, human footprint, distance to tourism, number of dams, fires, and indigenous communities. For such group variables, 14 (64%) of 22 papers reported significant influences, but only level of area protection, distance to protected areas, human activities, and hunting pressure were included in >1 paper and identified as significant in ≥50% of the models in which they were included.

Population variables synergistically interact with other factors magnifying the impact of human activities on jaguar distribution (Jędrzejewski et al. 2018). Of the four metrics identified in the 9 (28%) of 32 papers that included population variables, population density was significant in 7 of 11 papers, and distance to settlements in only 4 of 17 papers.

Environmental variables

Environmental drivers of species distribution mostly relate to biotic and abiotic factors essential for species survival (e.g., Ashcroft et al. 2011). Climate variables are widely used to model distribution, especially at macro-scales, and also directly affect seasonal variation resource abundance, thus forcing organisms to move (Astete et al. 2017b, Gese et al. 2018). Three climate metrics were included in 22 papers (seasonality, precipitation, and temperature), but only 8 papers (36%) identified any of them as being significantly correlated with jaguar distribution (Table 1.2).

For jaguars, vegetation can serve as a refuge for resting and reproduction, but also can reflect both the distribution of prey and cover necessary for successful hunting (Zeilhofer et al. 2014, Booker 2016, Dobbins et al. 2017, Souza et al. 2017, De la Torre and Rivero 2019). Of the six vegetation-related variables considered in models (ecosystem type, connectivity, vegetation type, normalized difference vegetation index [NDVI], tree richness, and primary production), 29 (57%) of 51 papers assessing vegetation reported significant correlations. Vegetation type was the only variable used in >2 models, and was identified as significant in most (22/35 = 63%) of those.

Ecological interactions variables focus on available prey resources and potential competitors (Schaller and Crashaw1980, Conde et al. 2010, Astete et al. 2017, Hidalgo-Mihart et al. 2018). Both the prey and/or competitor occurrence/abundance variables were identified as significantly influencing jaguar distribution in 32 (84%) of 38 papers including these ecological interactions. In addition, both variables were identified as significant in the majority of models in which they were assessed (Table 1.2).

Topographic variables derived from terrain structure relate to general habitat associations, therefore defining local species distribution (e.g., Punchi-Manage et al. 2013). Jaguar distribution studies use a variety of such metrics (i.e., average elevation, altitude, roughness) that we pooled into a single elevation variable category, but slope was also a widely used variable. Nevertheless, only 12 (43%) of the 28 papers reported significant correlations with jaguar distribution, elevation being the most common.

Water is crucial resource for wildlife; it shapes ecosystem and community dynamics (e.g., Sirot et al. 2016), and often affects the temporal distribution of both jaguars and their prey (e.g., Cavalcanti 2008). In the 25 papers incorporating distance to water (and once, runoff) into models, only 8 (23%) reported significant correlation with jaguar distribution and this was most true for studies in seasonal ecosystems.

Two studies incorporated three other variables into models (soil, geology, and distance to the beach) of which only distance to beach was identified as a significant metric in explaining jaguar distribution.

Variable inclusion and significance

No single variable was assessed in more than half of the documents, and 21 variables were assessed in only 1 or 2 documents (Table 1.2). Twelve variables were reported as not significantly correlating with jaguar distribution, but these all were assessed only 1 or 2 times. Of the remaining 27 “significant” variables, 9 were assessed in only 1 or 2 papers. We identified a set of 8 variables reported as significant in >50% of the documents and thus important influences of jaguar distribution; these included level of protection, human activities, population density, precipitation, vegetation type, prey, competitors, and distance to water.

Variable correlation with density

Base on the results of the review above, a set of 11 variables (Figure 1.2) were pair-correlated against jaguar relative abundance index (RAI: # jaguar records/100 trap nights) and jaguar density estimates (# individuals/100 km^2) in a correlation matrix. Only two variables showed a Pearson correlation coefficient >50%; protect (Natural resources protection%) and peccaries (RAI: # peccary records/100 trap nights) (Figure 1.2). Single correlation analysis between jaguar RAI and density estimates suggested low correlation ($R^2 = 0.15$; Figure 1.3) and almost no correlation between jaguar RAI and protection level (R^2 =0.007). However, jaguar density showed a positive relationship (R^2 = 0.31) with protection level (Figure 1.4). Jaguar RAI and peccary RAI showed no correlation (Figure 1.5), but jaguar density was positively correlated with peccary (RAI, R^2 = 0.40; Figure 1.5). Multiple correlation analysis including protection level % and peccary RAI with jaguar density estimates indicated an important correlation improvement (Multiple R^2 = 0.58)(Table 1.4).

Discussion

Early jaguar distribution research was limited by available techniques and technologies, making it difficult to understand important influential variables. With the development of techniques such camera trapping in India for tigers (*Panthera tigris*) (Karanth et al. 1995), its use for informing jaguar distribution in the Americas (Silver et al. 2004) increased. Reliable and satellite telemetry equipment furthered research capacity (e.g., Morato et al. 2016). And, the development of higher computer hardware capacity led to increasingly sophisticated analysis techniques such as deductive GIS modeling (Sanderson et al. 2002), occupancy modeling (Makenzie et al. 2017), and niche modeling (Phillips et al. 2017) that has accelerated the efficiency with which jaguar data of various kinds have been used to provide insights into jaguar distribution.

Distribution model reliability likely is affected by scale, survey technique used, and the anthropogenic and environmental metrics available to be included (Boydston and Gonzàles 2005, Torres et al. 2008, Bitetti et al. 2010; Sollmann 2011; De la Torre et al. 2017; Gese et al. 2018). Most of the studies we surveyed were conducted at a local scale and utilized data mostly from camera trap surveys (Michalski et al. 2015, Watkins et al. 2015, Fort 2016, Jordan et al. 2016, Astete et al. 2017). Nevertheless, local-scale camera-trap modeling studies, for example, may sometimes have scale mismatch issues because they only have available coarse, countrywide geographical layers to apply to ecological processes evaluated at fine scale (e.g., Quinones et al. 2018); this is a common issue across modeling approaches independent of particular taxa (MacGarigal et al. 2016).

Relevant evidence of road-based metrics affecting jaguar distribution were observed in a few studies (Colchero et al. 2010, Zeilhofer et al. 2014, Dueñas-Lopez et al. 2015, DeMatteo et al. 2017), presumable as consequence of better access routes that result in increased poaching (Sanderson et al. 2002, Petracca 2010). Distance to roads was a common metric in reviewed documents, perhaps because this variable can be easily built with any basic GIS (geographic information system) software (DeMatteo et al. 2017, Gese et al. 2018), but when included it most often was not identified as a significant variable.

Land use metrics should reflect both exposure to negative human interactions and a limitation of prey resources (Cuyckens et al. 2017). Land cover was identified as a significant metric in many, but not a majority, of studies in which it was assessed, but showed discrepancies in terms of pixel resolution across the studies (Zeller & Rabinowitz 2011, Cuervo-Robayo and Monroy-Vilchis 2012, Cullen et al. 2013, Morato et al. 2014). Though additional exploratory correlation of urban development and jaguar density was not the most significant, likely, this may occur because most of the jaguar distribution studies used national or global land cover layers due to the high expenses incurred getting fine pixel resolution data at local scale (Hansen et al. 2013), such our case that we used global layers.

Human activities may affect jaguar presence or biological processes due to anthropogenic recreational or economic activities in or near jaguar range (Jordan et al. 2016, Jędrzejewski et al. 2017, Morato et al. 2018, Silva et al. 2018, Portugal et al. 2019). The metrics of distance to protected areas and level of protection were significant in only half of the studies where they were assessed, and though these two metrics can be easily built, they do not always reflect the intensity and efficiency in law enforcement which we assume to contribute importantly to wildlife occurrence. Further analysis showed level of protection within protected areas influenced jaguar density as highly significant variable, due is likely the most protected the areas the better conserve prey and predators, acting as shelters for both. Also, hunting pressure was identified as significant on 2 or 3 studies, and though this makes clear sense, it is a variable that is hard to adequately map as well as measure.

Metrics identified in the population subcategory such as population density and distance to settlements were sometimes identified as significant, perhaps magnifying the importance of other factors assessed but also indicating that jaguars can live adjacent to areas where people, and perhaps particularly livestock owners, live and co-exist (Jędrzejewski et al. 2018).

Environmental variables were widely used and mostly described biotic and abiotic factors essentials for species subsistence (Ashcroft et al. 2011). Within the subgroups of variables, we identified a handful of metrics we suspect were autocorrelated. For example, the climate group variables of seasonality, precipitation, and temperature were all significant in some studies, but seasonality is influenced by the interaction of precipitation and temperature, where high temperatures and low precipitation increase droughts that may also increase mortality because when a drought comes, it also diminishes available food (Sirot et al. 2016). Somehow evidence suggested precipitation might influence jaguar density from this study; assuming most rainy areas in the tropics are the most productive in terms of biomass. In addition, we also identified the simultaneous use of derived climatic sub-metrics; i.e., for temperature in the same modeling study authors used variance of temperature, mean of temperature, standard deviation, maximum temperature and minimum temperature, even though all were nested variables derived from temperature.

Vegetation variables were the most used across jaguar studies (Sanderson et al. 2002, Weckel et al. 2006), vegetation type being significant in most. Vegetation type may represent refuge (similar to a forested land cover metric), a source of prey, and stalking or hunting habitat (Zeilhofer et al. 2014, Booker 2016, Dobbins et al. 2017, Souza et al. 2017).

Ecological interactions, when they can be identified and mapped, are both common and highly significant factors influencing jaguar distribution. Prey occurrence and abundance is important to jaguars not only because of their high demand relative to other mammals (Sunquist and Sunquist 2002), but also because prey has such an influence on carnivore demography (Fuller and Sievert 2001). We found prey abundance as high significant driver of jaguar density, hence in places with high prey availability jaguar density is positively correlated. Also, we identify both prey and competing predator distribution and abundance is often simultaneously collected using camera traps, for example, and are thus both available and reasonable metrics to include in models (Weckel et al. 2006; Azevedo and Murray 2007; Petracca 2010; Davis et al. 2010; Harmsen et al. 2011; Rodriguez-Soto et al. 2011; Petracca 2013; Gutiérrez-Gonzàlez and López-González 2017, De la Torre and Rivero 2019).

Topographic variables may affect hunting opportunities (Kruuk 2006), but more likely they are also correlated with other variables such as distribution of humans, protected areas, and land/vegetation cover that are more directly correlated with factors affecting jaguar distribution. Still, elevation may be widely used researchers can easily get this information without advanced training in geographic information technologies.

Even though some carnivores can partially fulfill their nutritional water requirements with prey, hunting places near water could increase predator encounters, especially in seasonal environments (Sirot et al. 2016). Distance to water is a commonly used metric, likely also because researchers can easily get this information without advanced training. Though we did not find evidence suggesting fresh water as driver of jaguar density, we hypothesize in seasonal ecosystems water might be related to prey and therefore to jaguar densities.

Distance to beach was identified once as a significant variable in a place where nesting sea turtles are seasonally abundant, and thus a variable reflecting peaks of prey availability (Carrillo et al. 2009).

Other variables were identified as significant, but only tested in one or two papers; these may be worth considering in future modeling efforts if data are available. Many variables were also not identified as significant, though they could be constrainers of jaguar distribution. It is likely that the metrics assessed are constrained by a variety of issues, including the types of variables available (Jędrzejewski et al. 2017, Silva et al. 2018) or the lack of ease to build them (Colchero et al. 2010, Petracca 2010). Also, variables cannot always be based on or derived for specific effects for which human activities or environmental conditions limit or enhance jaguar presence. Finally, some assessments are constrained by the kinds and/or amounts of data used in modeling. Sample sizes may limit, for example, assessment of sex-, age-, or behavior-specific influences on distribution or abundance.

Our additional analysis testing correlation of the best set of potential predictors based on the previous variables identified as the most significant, showed peccary abundance and the level of protection of wilderness areas were strongly related to jaguar density. Therefore, variables that are shown to correlate with distribution (or better estimates of those variables or what they represent) should help researchers produce better models of jaguar distribution in the future and make better predictions in areas without quantitative jaguar data.

More importantly, thoughtful assessment of those variables should direct researchers to better identify and then quantify specific casual factors affecting jaguar distribution and abundance, rather than simply describe it, especially in terms of jaguar reproduction, survival, and dispersal. Habitat descriptors are useful in understanding a species' niche (Hutchinson 1957), and habitat quality is often inferred from the distribution of species (McLoughlin et al. 2010). Habitat use patterns may provide a link to population dynamics, but such links have not been well identified for jaguars. So, even though linking demographic rates to habitat use is logistically and financially challenging, doing so will provide that demonstrated relationships that are needed to best conserve jaguar populations into the future. Jaguar habitat modeling provides a plethora of hypotheses to test, and demographic data will unveil the mechanisms providing for jaguar population viability.

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Table 1.1 Frequency of (i.e., number of references) modeling approaches, data gathering methods, and geographic scale used to assess jaguar distribution, as tabulated from a review of 83 peer- reviewed papers published between 1980 and 2019 (underline = highlight of highest values).

Model method	**No. of References**	**Percent of References**
Telemetry	14	17
Camera trap	33	41
Genetics	2	2
Historic records	21	25
Sign counts	2	2
Interviews	3	2
GIS	9	11
Model method		
Occupancy	19	22
Niche modeling	19	23
Deductive	10	12
Basic statistic empirical models	36	44
Scale		
Continental	10	12
Regional	11	14
Country	7	9
Local	56	68

Table 2.2 Qualitative and quantitative variable types identified in an assessment of peer-reviewed documents assessing jaguar distribution (n = 83), 1980-2019 (Underlined percentages highlight the highest values).

Variable	Variable classification	No. of metrics	No. of References	Perc. of significant references per variable classification
Anthropogenic	**Road**: *Rai,Roa, Rod*	3	20-- 5*	25
	Land use: *Lco,Dif,Dia*	3	26--13*	50
	Human activities: *Hup,Lpr,Dpa,Hua,Nud,Catt,Fir,Ind,Fol,Hufo,Dit.*	11	22--14*	64
	Population: Pod,Dis,Nuh,Sett	4	32--9*	28
Environmental	**Climatic**: *Sea,Pre,Tem*	3	22--8*	36
	Vegetation: *Eco, Con,Veg, NDVI,Trer,Ppr*	6	51-- 29*	57
	Ecological interactions:*Coe,Prey*	2	38--32*	85
	Topographic: *Ele,slop*	2	28--12*	43
	Water: *Diw, Run*	2	35--8*	23
	Others: *Soil,Geo,Dib*	3	2--1*	50

.*: References reported as significant

Environmental: *Sea:* seasonality, *Pre:* precipitation, *Tem:* temperature, *Eco:* ecosystem type, *Con:* connectivity, *Veg:* vegetation, *NDVI:* normalized difference vegetation index , *Trer*: tree richness, *Ppr:* primary production, *Coe:* Co-especifics, *Prey*, *Ele:* elevation, *slop:* slope, *Diw:* distance to water, *Run:* runoff, *Soil*, *Geo*: geology, *Dib:* Distance to the beach. ***Antropogenic:*** *Rai:* distance to railroads, *Roa:*distance to roads, *Rod*: road density,*Lco*: Land cover, *Dif:* Distance to forest, *Dia:* Distance to agriculture, *Hup:* hunting preasure, *Lpr:* level of protection, *Dpa:* distance to protected areas, *Hua:* Human activities ,*Nud:* number of dams, *Catt:* cattle density, *Fir:* fires, *Ind*: indigenous communities nearby, *Fol:* forest loss, *Hufo*; human foodprint, *Dit*: Distance to tourism, *Pod:* population density, *Dis*: distance to settements, *Nuh*: number of houses, *Sett:* settlements.

Table 1.3 Qualitative and quantitative variable types identified in an assessment of peer-reviewed documents assessing jaguar distribution (n = 83), 1980-2019.

Category	Subcategory	Documents	Variable	No. of times identified as	
				Significant	Not significant
Anthropogenic	Roads	20	distance to roads	5	13
			road density	0	2
			distance to railroads	0	1
	Land use	26	land cover type	12	14
			distance to forest	1	0
			distance to agriculture	1	0
	Human activities	22	level of area protection	5	4
			distance to protected areas	4	4
			cattle density	3	5
			human activities	4	1
			hunting pressure	2	2
			forest loss	1	0
			human footprint	1	1
			distance to tourism	1	0
			number of dams	0	1
			fires	0	1
			indigenous communities nearby	0	1

	Population	32	distance to settlements	4	15
			population density	6	5
			number of houses	1	0
			settlements	0	1
Environmental	Climate	22	seasonality	4	7
			precipitation	5	6
			temperature	3	4
	Vegetation	51	vegetation type	26	16
			connectivity	0	2
			ecosystem type	1	0
			normalized difference vegetation index	1	2
			tree richness	0	1
			primary production	1	1
	Ecological interactions	44	prey occurrence/abundance	21	3
			competitor occurrence/abundance	15	9
	Topographic	28	elevation	12	11
			slope	1	8
	Water	37	distance to water	19	13
			runoff	0	2
	Other	2	distance to the beach	1	0
			soil type	0	1
			geology	0	1

Table 1.4 Summary of multiple regression coefficients assessing the additive relationship of peccary RAI and the protection level on jaguar density (# individuals/ 100 km2).

Coefficients	ß	SE	T value	P value
Intercept	-2.301	2.065	-1.116	0.285
Peccary RAI	0.061	0.035	1.733	0.107
Protection level	0.797	0.023	3.366	0.005**

Note: Multiple R^2 =0.58, F: 9.046, Overall Equation p value = 0.003

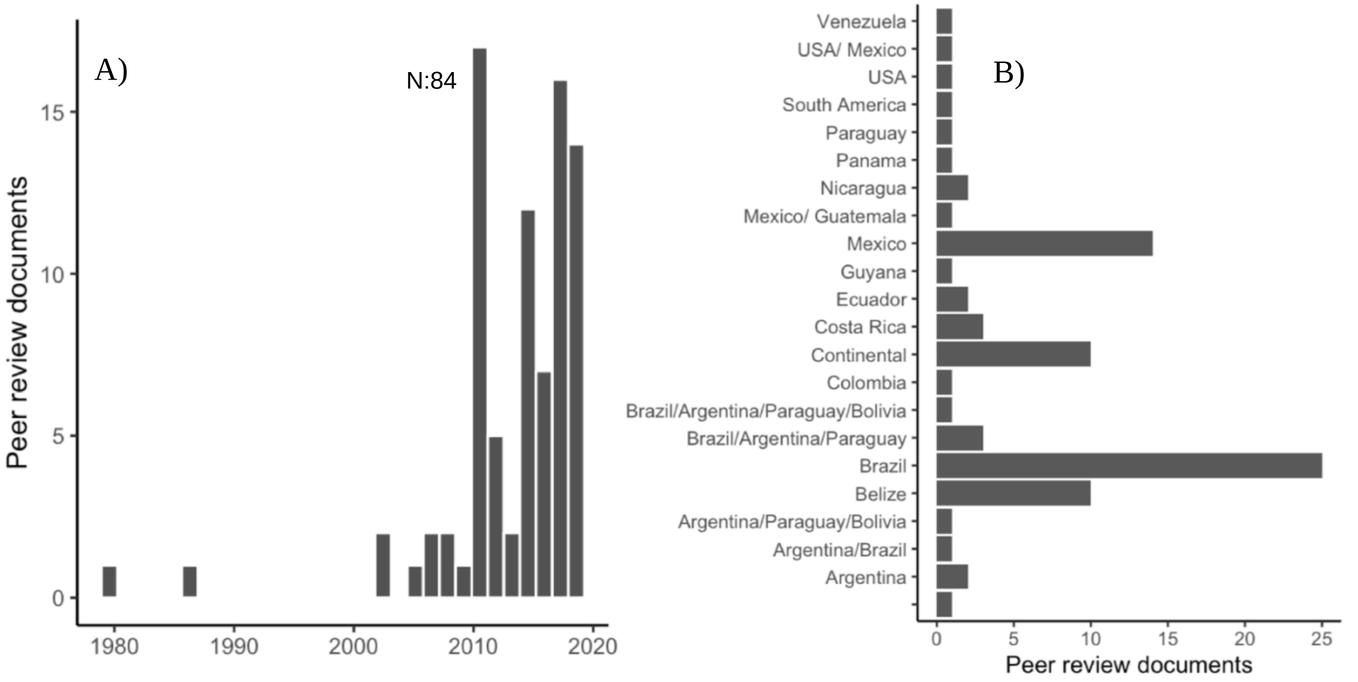

Figure 1.1 A) Annual number of peer-reviewed documents assessing jaguar distribution across its range. B) Country-specific number of peer reviewed documents assessing jaguar distribution.

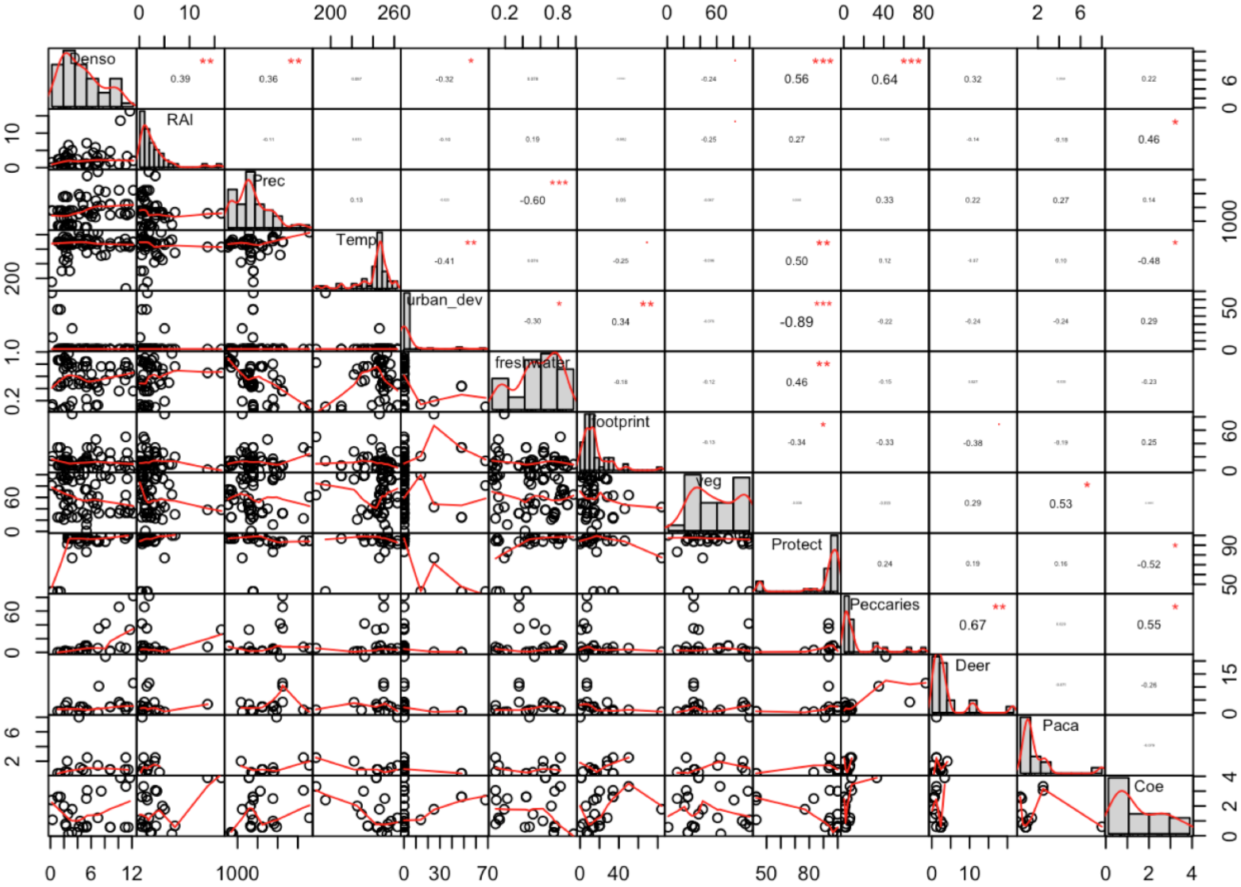

Figure 1.2 Exploratory correlation matrix showing the relationship of jaguar's density (Denso) and jaguar's relative abundance (RAI) with proxies of the most significant anthropogenic and environmental variables identified in peer reviewed documents assessing jaguar distribution (N=83).

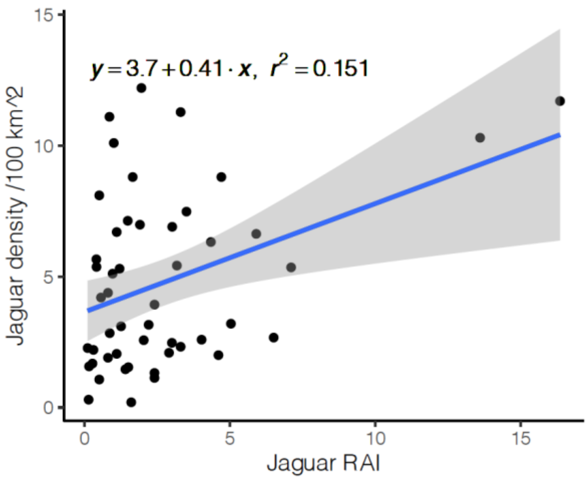

Figure 1.3 Relationship between jaguar density (# individuals/ 100 km2) and jaguar relative abundance index (RAI: # jaguar records/ 100 trap nights) from peer reviewed documents assessing jaguar distribution.

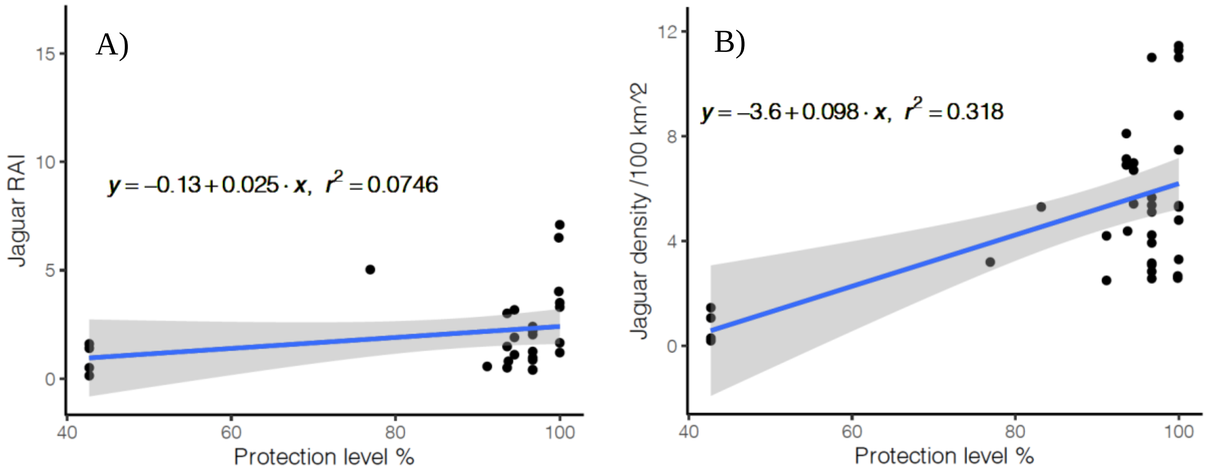

Figure 1.4 A) Relationship between jaguar relative abundance index (RAI: # jaguar records/ 100 trap nights) and protection level from peer reviewed documents assessing jaguar distribution. B) Relationship between jaguar density (# individuals/ 100 km2) and protection level from peer reviewed documents assessing jaguar distribution.

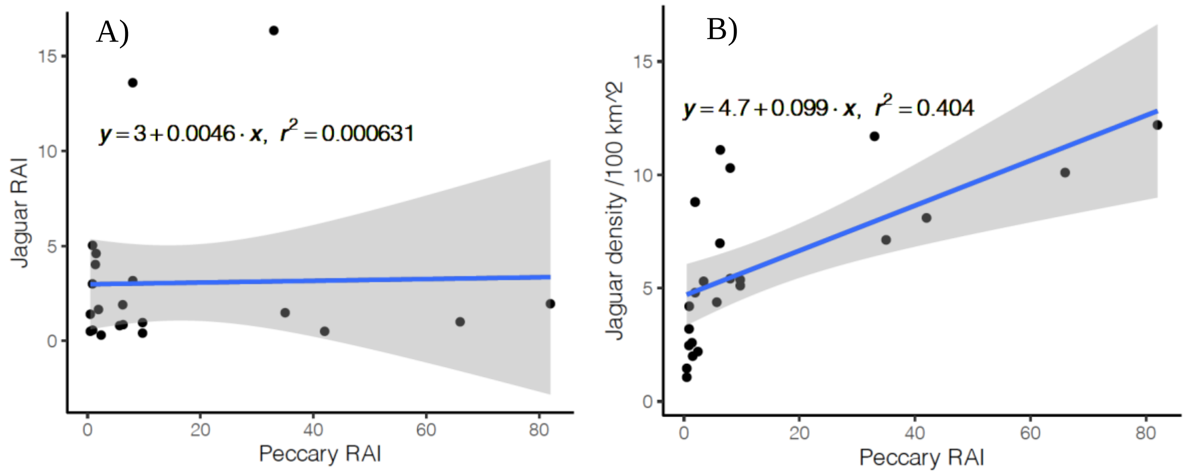

Figure 1.5 A) Relationship between jaguar relative abundance index (RAI: # Jaguar records/ 100 trap nights) and peccary relative abundance RAI (RAI: # Peccary records/ 100 trap nights) in places with data available from review documents. B) Relationship between jaguar's density (# individuals/ 100 km2) and peccary relative abundance RAI (RAI: # Peccary records/ 100 trap nights) in places with data available from review documents.

CHAPTER 2

SEASONAL USE OF WATERHOLES AND PATHWAYS BY MACROFAUNA IN THE DRY FOREST OF COSTA RICA

Abstract

Temporal and spatial scarcity of water in semi-arid and seasonal ecosystems often leads to changes in wildlife movements and behavior, and in the neotropics this dynamic is poorly understood due to logistic and methodological limitations. We used camera trapping to elucidate patterns of seasonal use of waterholes and pathways by 10 large mammal and four large bird species in the dry forest of northwestern Costa Rica. From 2011 to 2015, we deployed trail cameras at 50 locations, including waterholes and three types of pathways (roads, human trails and animal paths). We used Generalized Lineal Models to evaluate the effect of locations and seasonality on photo rates. We found interacting effects of locations and seasonality for capuchin monkeys (*Cebus capucinus*), tiger herons (*Trigrisoma mexicanum*), white-tailed deer (*Odocoileus virginianus*), and tapirs (*Tapirus bairdii*) suggesting that these species were the most influenced by waterholes during the dry season. Comparison of waterholes and specific types of pathways (roads, animal paths and human trials) showed that location influenced the photo rates of almost all species, suggesting a useful insight to avoid bias in camera trap studies. Furthering our ecological understanding of seasonal water regimes and wildlife behaviors allow for better understanding of the consequences of climate on wildlife.

Introduction

Water is an obligatory resource for wildlife, and when free water becomes scarce and temperatures increase, permanent waterholes play an essential role for wildlife survival, especially in semi-arid and seasonal environments (Sirot et al. 2016; Strauch 2013; Valeix 2011).

Accordingly, the spatio-temporal patterns of water availability influence wildlife movements, habitat use, and behavior (Pastorini et al. 2010; Kluever et al. 2017).

Previous research emphasizing herbivore and carnivore interactions in African semi-arid savannahs showed that waterholes promote diversity and shape ecosystem dynamics during periods of water scarcity (Etienne et al. 2016; Harris et al. 2015; Jarman 1972). In the southwestern United States, free water provisioning influences spatial and temporal use of water sites by ungulates and carnivores (Harris et al. 2015; Kluever and Gese 2016). Less is known about the importance of water resource availability in the highly diverse neotropics, (Mandujano and Gallina 1995; Vaughan and Weis 1999) due to logistic difficulties and the fact that typically invasive sampling methods are likely to altering animal behavior (Carrillo et al. 2002). For example, in the late 1990s Cabrera (1999) sampled wildlife use of waterholes throughout direct observations at Santa Rosa National Park in Costa Rica and reported very low occurrence of felid species, as well as other mammals; Cabrera (1999) attributed these low rates to somehow effect of his presence on wildlife behavior.

Whereas direct observational studies may cause behavioral disruptions, camera traps offer a non-invasive method for sampling elusive species in difficult-to-survey landscapes and generate valuable data that can be used to better understand wildlife behavior, activity patterns, abundance, demographic parameters, community metrics richness, and habitat use (O'Connell et al. 2011; Rowcliff and Carbone 2008; Rovero and Zimmermann 2016), and their use at waterholes has proved effective (Harris et al. 2015). We used camera trapping to elucidate patterns of seasonal use waterholes and pathways by 10 large mammal and four large bird species in the dry forest of northwestern Costa Rica. We expected a variety of species-specific responses to season (wet and dry) and locations (waterholes and paths) that would reflect the biology of the species. In particular, we suspected that observations of jaguars (*Panthera onca*) would be most common on trails and roads, regardless of season, and that observations of herbivores would be most common at waterholes in the dry season, especially for tapirs (*Tapirus bairdii*) that have been shown to used freshwater more often in the dry season (Foerster and Vaughan 2002).

Materials and Methods

Study area

This study was conducted in Santa Rosa National Park (SRNP), one of the four national parks within the Guanacaste Conservation Area (GCA) located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza 1992). SRNP encompasses 387 km^2 and is dominated by seasonal dry forest, which is one of the few remaining tropical dry forests in Central America (Gillespie et al. 2000; Janzen 1988). During the early 1900s, forested lands throughout SRNP and the larger GCA were converted to pastures for cattle grazing and a jaragua grass species (*Hyparrhenia rufa*) was introduced as forage. This species became a threat to the remaining old growth forest patches due the high fuel load it presented and the potential of spreading anthropogenic fires inside the SRNP (Janzen and Hallwachs 2011; Jansen 1986). Due the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980's involving, among other things, the recovery of abandoned pastures by active fire suppression (Klemens et al. 2011).

Mean annual rainfall in SRNP totals 1,600 mm but is highly seasonal (monthly averages from 0 mm to 1040 mm); the wet season (months with ≥ 40mm of rain) is May to November, and the dry season (with almost no rain and temperatures over 37°C) is December to April (Figure 2.1). During the dry season, many forest patches lose their leaves and fewer evergreen forest patches retain them. In addition, most of the rivers and streams in the study area run dry up and the remaining waterholes become important providers of free water for wildlife (Campos and Fedigan 2009).

Data collection

During the dry and wet seasons of 2011-2015, automatic trail cameras (Bushnell®, Trophy Cam models 119436, 119446, 119456) were deployed at 50 different sites within SRNP. Half of the cameras (n = 25) were place at waterholes and half on pathways (roads, n = 11; human trails, n = 9; and animal paths, n = 5) that jaguars were likely to use; cameras were deployed for an average of 53 days (range = 34-244). Each camera was attached to a tree at a height of approximately 40 cm and set to be active for 24 h/day in video mode with the minimum delay (1 sec) between consecutive triggers. Once deployed, cameras were checked on average every 22 days to replace batteries and change SD memory cards, if necessary. For each camera deployment, we recorded the location type (waterhole or pathway type), camera operation dates (and therefore, number of trap nights), season (wet or dry), and the number of independent photo events for each species. Photos or videos were considered an independent photo of a species if they were: (1) taken at least 30 minutes apart (e.g., a series of 3 photos of the same species taken in consecutive seconds = 1 photo event); (2) consecutive photos of the same species could be identified as different individuals (spots, scars, horns/antlers, sex) and not part of the same group (e.g., 15 minutes apart, going in opposite directions = 2 photo events); or (3) photos of the same species separated by photos of a different species (e.g., species 1, followed 2 minutes later by a species 2, followed five minutes later by species 1 = 1 species with 2 photo events and 1 species with 1 photo event).

Statistical analysis

To examine and identify potential data issues (e.g., normality, overdispersion, outliers) and fulfill model assumptions, we followed the data exploration protocol suggested by Zuur et al. (2010). The number of independent photos of species at a site were analyzed using generalized linear models (GLM; Zuur et al. 2009) with a log link function, as is customary for count data, implemented using the statistical software R.3.1.3 (R core development team 2016). Due to overdispersion in the counts, we assumed a negative binomial error distribution (Zuur et al. 2009), and to account for variation in effort, we used the log of the number of trap nights as an offset to standardize the counts.

In order to assess the effect of seasonality (Seas) and site location (Loc) on photographic rates (no. of independent photos/100 trap nights*)*, five *a priori* models were developed for each species. One model included the intercept, two each singular predictor, one the additive effect of the two predictors, and one the first order interactions for the two predictors (Table 2.1).

The empirical supports of these five candidate models were evaluated using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002), and throughout the model comparison for each species we determined the most plausible models due the highest Akaike weight (*W;* range = 0 to 1; Anderson 2007). Based on the *W* we assessed the evidence from one model over another (Burnham and Anderson 2002). Because we were particularly interested in those models showing interactions and the additive effects of Season and Location on photo rates, we included in the confidence set of models, based on the *W* value, those for species where the interaction and the additive effect of Seas and Loc differed by <10% from the top model (Thompson and Lee 2000). To better interpret the magnitude of top additive and interacting models, the seasonal mean differences in photographic rates of pathways (roads, human trails and animal paths) and waterholes were contrasted in a response scale, and graphically depicted.

Results

With a total effort of 5,430 trap-nights we recorded 2,681 independent photo events of 64 species of amphibians, birds, mammals, and reptiles. Of these, 14 species (10 mammals and 4 birds) were independently photographed >40 times and included in our analyses (Table 2.2). During the dry season, average photographic rates were more than twice as high on pathways for opossums (*Didelphis marsupialis*) and jaguars, and more than twice as high at waterholes for capuchin monkeys (*Cebus capucinus*), coatis (*Nasua narica*), tapirs, and tiger herons (*Tigrisoma mixicanum*) (Table 2.2). The highest photos rate of any species during the dry season was that for great curassows (*Crax rubra*) at water holes. During the wet season jaguars were photographed on trails at >2 times the rate at waterholes, and capuchin monkeys and tiger herons were photographed at waterholes >2 times the rate on trails (Table 2.2). The highest photo rate of any species during the wet season was that for white-tailed deer (*Odocoileus virginiaus*) at water holes.

Model selection based on *W* showed that the null model was the most plausible for skunks (0.64) and ocelots (*Leopardus pardalis*; 0.60). For opossums (0.48), agoutis (0.44), pumas (*Puma concolor*; 0.71), coatis (0.66), and wood rails (*Aramides cajaneus;* 0.53), the most plausible model included only a seasonal (Seas) effect, whereas for jaguars (0.68), great curassows (0.46) and crested guans (*Penelope purpurascens*; 0.32), location (Loc) had the most influence (Table 3); however, the additive effect of location and season for great currasows (0.44) was very near the top model. The most plausible model for white-tailed deer (0.44), capuchin monkey (0.85) and tiger heron (0.64) included the additive effect of location and season, and for tapirs (0.57) included the interaction of these two predictors.

Capuchin monkey photo rates were significantly higher at waterholes during the dry season compared with any pathway, although during the wet season the rates on pathways increased substantially, though they did not differ from waterholes (Figure 2.2). Tapir photo rates were lower in the dry season on roads, human trails, and animals paths compared to waterholes, and during the wet season, tapir photo rates on human trails and animals paths followed the same pattern but were of less magnitude (Figure 2.2). For white-tailed deer, photo rates were lower during the dry and wet seasons on animal paths. Although empirical evidence based on the *W* (Table 2.3) showed an interaction of season and site location for great curassows, finer analyses differences at human and animal paths, and only marginal differences between seasons (Figure 2.2). On human trails and animal paths tiger heron photo rates were different than at waterholes but with no seasonal effect, though on roads rates were highest at waterholes during the dry season (Figure 2.2).

Discussion

We used camera trapping as a non-invasive technique to assess the effect of climate seasonality on patterns of waterhole use of macrofauna in the tropical dry forest, and hypothesized that seasonality would be most identifiable for species like tapirs that are thought to be water-dependent. We found statistical evidence of interacting effects of season and location for tapirs, and an additive effect for white-tailed deer, capuchin monkeys, tiger herons, and great curassows. In tropical-seasonal ecosystems, megaherbivores frequently increase their use of waterholes during the driest months (Moreira- Ramírez et al. 2016; O'Farrill et al. 2014; Pérez-

Cortez et al. 2012) and our observations suggest that waterholes become rare places that are selected for use due to the favorable microclimate and habitat conditions for megafauna.

During the dry season tapirs and white-tailed deer were found more frequently at waterholes and roads; nevertheless, the results showed some dependency on waterholes, even during the wet season, for both species. Though white-tailed deer marginally increased the use of waterholes during the dry season, they also used roads regardless of the season, perhaps as a strategy to avoid predation in risky places such as waterholes (Valeix et al. 2011). Harris et al. (2015) mentioned that large herbivores could forage temporarily in risky places during periods of resource scarcity due to high energetic rewards, although still using the less vulnerable areas the most. In our area, this might mean road pathways for white-tailed deer where herbivores can easily detect and escape from predators.

Capuchin monkeys are mostly diurnal and arboreal, and seldom have been recorded at camera traps on pathways, but others have noted that during the onset of the dry season, especially during the driest months (March-April), they tend to cluster near waterholes (Campos and Fidegan 2009). We found that capuchin monkeys increased the use of waterholes during the dry season and observed troops sipping at waterholes during the peaks of high daily temperatures, an adaptation to heat stress and water scarcity (Campos and Fidegan 2009).

Waterhole use by carnivores in this study differed from patterns previously reported in other seasonal environments. In arid ecosystems of South Africa and North America, seasonality directly influenced patterns of prey distribution, and as a consequence prey tended to aggregate at waterholes during extended drought periods, thus attracting predators to such places (Kalle et al. 2014; Kluever et al. 2017; Sirot et al. 2016; Valeix et al. 2011). Our data suggest that ocelots use pathways and waterholes alike regardless of season, jaguars used pathways the most regardless of season, and pumas used trails less, especially during the dry season. This could suggest some avoidance of jaguars by pumas, reflecting findings by Harmsen et al. (2010) who hypothesized differential use of trails based on photographic rates. However, Gutierrez-Gonzales and Lopez-Gonzales (2017) found that jaguars and pumas exhibited sympatric behavior based on the abundance and distribution of white-tailed deer.

Evidence of a seasonal difference in observation frequencies were found for opossums, agoutis, and coatis regardless of the location type, suggesting that spatial distribution of water is perhaps not as limiting as the temporal distribution of water. This finding partially supports Alfaro's (2014) insights, describing somehow synchronicity patterns between falling fruits-precipitation regimes and mammal relative abundance in SRNP (Alfaro 2014). In addition to this, Paredes et al. (2017) highlighted the importance of temporal distribution of water as a driver of changes in photo rates of medium-size frugivores-omnivores across a latitudinal gradient. The amount of preformed water contained in juicy fruits could partially augment the amount of free water physiologically required by some mammals during periods of drought.

Photo rates of only tiger herons and great curassows were influenced by seasonality and location, almost always with higher photo rates at waterholes. This pattern in cracids perhaps is a response of their habitat preferences; Parker (2002) described curassows as inhabiting humid and narrow ridge areas with the presence of high ground structures to escape from predators, and based on its diet of fruits, arthropods and a few small vertebrates. Tiger herons seem tied to aquatic habitats and heavily associated with riparian zones, preying small fishes, frogs and crabs (Birdlife International 2016).

Our analysis, as well as other studies in arid ecosystems, suggests that spatial and temporal distribution of water is important to wildlife in the dry forest of SRNP. Tapirs, white-tailed deer, tiger herons, and capuchin monkeys were the most dependent of waterholes during the dry season, but road pathways also played an important role during the wet season, perhaps for movement. Detailed comparison of waterholes and specific types of pathways (roads, animal paths and human trials) showed methodological implications of locations influencing the photo rates of all species, suggesting a factor to account for in camera trap studies. Finally, the ecological link between water/climate regimes and wildlife distribution patterns in seasonal ecosystems should lead to a better understanding of the consequences of changing climate regimes, and future research should consider variables such as evapotranspiration, vegetation dynamics, and detailed resource phenology when considering species distributions.

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Table 2.1 Description of five priori-candidate models evaluating the effect of seasonality (Seas) and site location (Loc) on photographic rates (PR) in Santa Rosa National Park.

Model	Description
1) PR = log(Trap nights)	Intercept only
2) PR = log(Trap nights) + Seas	PR vary by Seas
3) PR = log(Trap nights) + Loc	PR vary by Loc
4) PR = log(Trap nights) + Seas + Loc	PR vary by Seas and Loc in an additive way
5) PR = log(Trap nights) + Seas * Loc	PR vary differently by Seas and Loc

Table 2.2 Photographic rates (no. of independent photos/100 trap nights; no. of trap nights in parentheses) of the most commonly photographed wildlife species at seasonal waterholes and on pathways (roads, human trails, and animal paths) in Santa Rosa National Park in northwestern Costa Rica during 2011-2015.

		Dry Season		Wet Season	
		Pathway	Waterhole	Pathway	Waterhole
Common name	Scientific name	(970)	(1555)	(2249)	(656)
Opossum	*Didelphis marsupialis*	1.55	0.77	0.62	0.46
Capuchin monkey	*Cebus capucinus*	0.00	2.83	0.04	0.46
Agouti	*Dasyprocta punctata*	5.98	5.02	5.51	3.20
Ocelot	*Leopardus pardalis*	1.86	1.93	1.24	1.07
Jaguar	*Panthera onca*	4.64	1.29	3.07	0.76
Puma	*Puma concolor*	1.44	2.19	1.16	1.22

Skunk	*Conepatus semistriatus*	1.86	1.09	1.16	1.98
Coati	*Nasua narica*	0.21	1.41	0.40	1.07
White-tailed deer	*Odocoileus virginianus*	11.44	11.45	6.80	9.45
Tapir	*Tapirus bairdii*	1.55	8.75	0.67	1.22
Great curassow	*Crax rubra*	10.72	16.08	5.02	7.93
Crested guan	*Penelope purpurascens*	0.72	2.25	0.71	0.91
Wood rail	*Aramides cajaneus*	1.65	0.96	0.71	0.61
Tiger heron	*Tigrisoma mexicanum*	0.21	2.51	0.18	0.46

Table 2.3 Model importance weights for10 mammal and 4 bird species, describing the effect of seasonality (Seas) and site location (Loc) on photo rates in Santa Rosa National Park. For the most parsimonious model (*W* = 1), weights indicate the evidence for a given model compared with the other models (i.e., the larger the number [in bold and underlined], the more evidence for that model).

	Model description and AIC Model Weight				
Species	Intercept	Loc	Seas	Loc + Seas	Loc x Seas
Opossum	0.44	0.04	<u>***0.48***</u>	0.04	0
Capuchin monkey	0	0.07	0	<u>***0.85***</u>	0.08
Agouti	0.19	0.09	<u>***0.44***</u>	0.26	0.02
Ocelot	<u>***0.60***</u>	0.09	0.22	0.03	0.06
Jaguar	0	<u>***0.68***</u>	0	0.29	0.03
Puma	0.1	0.05	<u>***0.71***</u>	0.13	0.01
Skunk	<u>***0.64***</u>	0.1	0.22	0.03	0.01
Coati	0.07	0.11	<u>***0.66***</u>	0.13	0.03
White-tailed deer	0.06	0.13	0.35	<u>***0.44***</u>	0.02
Tapir	0.01	0.01	0.01	0.40	<u>***0.57***</u>
Great curassow	0.01	<u>***0.46***</u>	0.01	0.44	0.08
Crested guan	0.2	<u>***0.32***</u>	0.27	0.15	0.06
Wood rail	0.32	0.05	<u>***0.53***</u>	0.1	0
Tiger heron	0	0.26	0.02	<u>***0.64***</u>	0.08

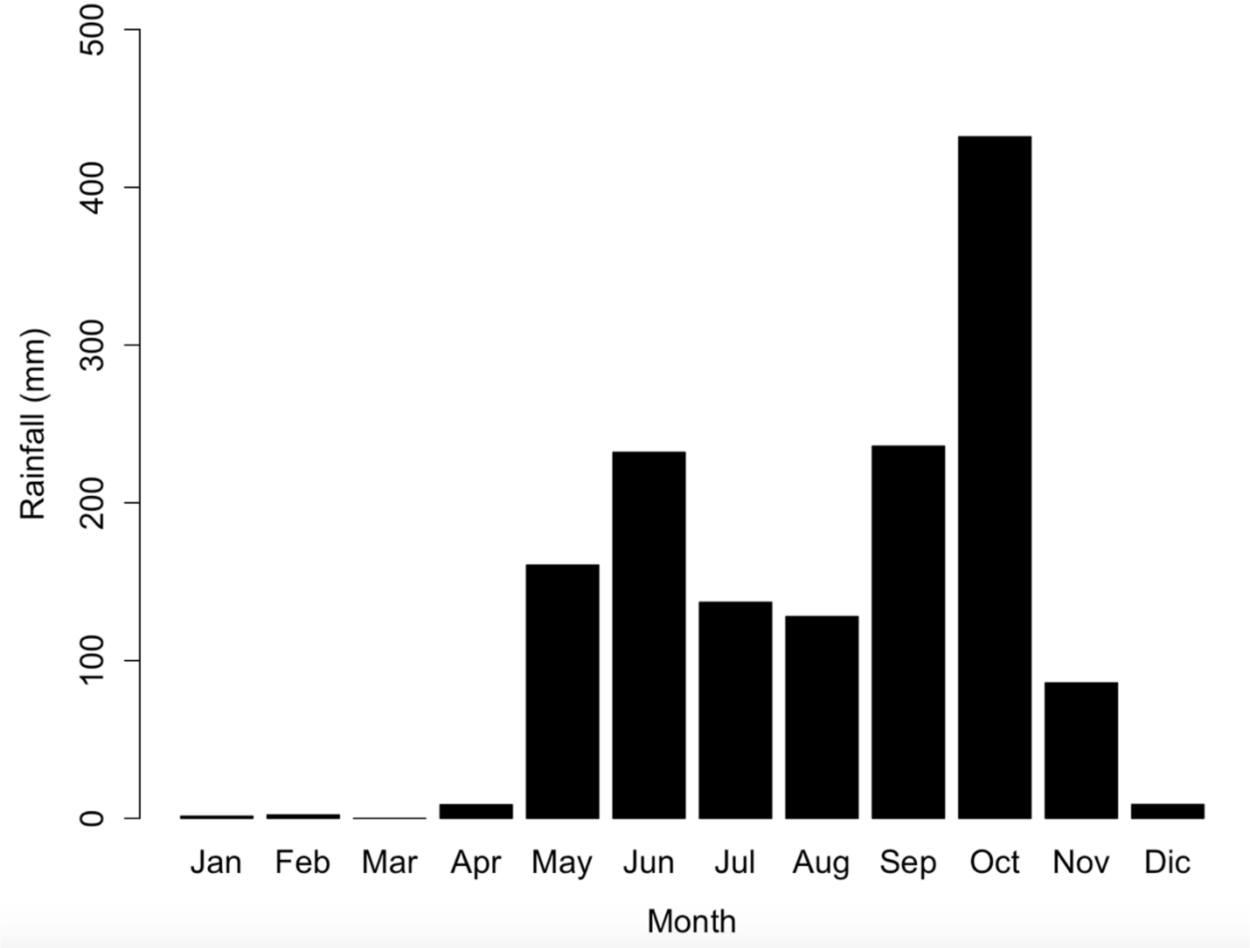

Figure 2.1 Mean monthly rainfall in Santa Rosa National Park in northwestern Costa Rica during 2011-2015.

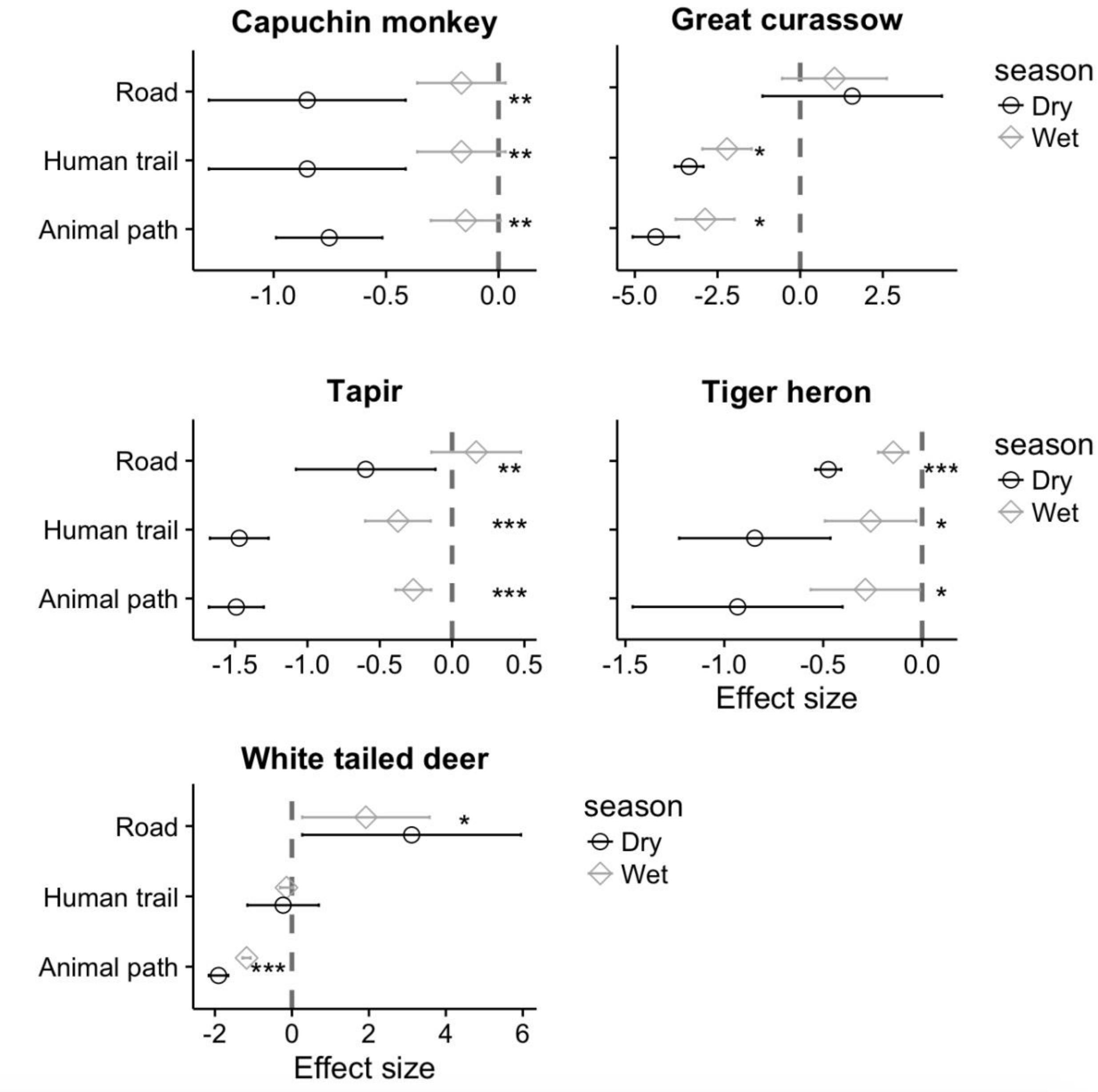

Figure 2.2 Mean differences in photographic rates showing the effect of seasonality (dry/wet) and locations (animal path, human trail, road) among waterholes and three types of pathways in Santa Rosa National Park. Statistical significance p<0.05; [* significant location effect, ** significant seasonal effect, * significant effect of both seasonality and location]. Error bars represent the 95% confidence interval**

CHAPTER 3

INFLUENCE OF SEA TURTLE NESTING ON HUNTING BEHAVIOR AND MOVEMENTS OF JAGUARS IN THE DRY FOREST OF NORTHWEST COSTA RICA

Abstract

Jaguars (*Panthera onca*) are opportunistic predators that prey on large profitable prey items, such sea turtles at nesting beaches. Here we use jaguar and sea turtle track count surveys, combined with satellite telemetry of one jaguar, to evaluate whether jaguar hunting behavior and movements are influenced by seasonality of sea turtle nesting in the Guanacaste region of northwest Costa Rica. We used Generalized Linear Models to evaluate the effect of moon phase and sea surface temperature on olive ridley (*Lepidochelis olivacea*) and green turtle (*Chelonia mydas*) nesting abundance, as well as the combination of these predictors on the frequency of jaguar predation activity (proximity to nesting beaches) and movements. For home range size analyses we calculated Kernel Density Estimates for each season at three different temporal scales. We found evidence of interacting effects of sea surface temperature, moon phase, and season on sea turtle abundance. Sea turtle abundance was related to jaguar locations and predation events, but jaguar home range size (88.8 km^2 overall) showing no statistical difference between turtle nesting seasons or among temporal scales. Environmental conditions influenced sea turtle nesting and, as a consequence, also influenced jaguar movements and foraging activity. Our study defined the home range of a female jaguar in the tropical dry forest and its relationship to seasonally abundant turtles. Additional information related to the effect of tourism on jaguar-sea turtle interactions would improve conservation of these species at unique nesting beaches in the area.

Introduction

Highly seasonal ecosystems present a combination of challenges for wildlife that lead to physiological and behavioral adaptations (Blaum et al. 2007; Stoner and Timm, 2011; Astete et al. 2017). For example, jaguars (*Panthera onca*), which are widely distributed from northern Mexico to northern Argentina (UICN 2019), exhibit seasonal movement patterns related to peaks of prey availability and abiotic factors (Cavalcanti 2008; Carrillo et al. 2009; Guilder et al. 2015). In the Pantanal of Brazil during the dry season, jaguars spend more time foraging near caiman (*Caiman crocodilus*) habitats (Cavalcanti 2008), whereas in Corcovado, Costa Rica jaguars switch activity patterns related to spatiotemporal distribution of white-lipped peccaries (*Tayassu pecari*) and sea turtles (*Lepidochelys olivacea, Chelonia mydas*) (Carrillo 2000).

Jaguars, however, are opportunistic predators preying on as many as 85 species, including most available animals weighing >1kg (Rabinowitz and Nottingham 1986; Carrillo 2000); thus, efforts to understand the relationship of abiotic factors (seasonality and moon phases) and prey on jaguar spatial dynamics are area-specific. By using Global Positioning Satellite (GPS) telemetry, researchers can determine correlations between animals and their habitats, and thus record patterns of space use that likely influence their persistence (Morellett et al. 2013; Gonsalez-Borrajo 2017). Not surprisingly, previous research emphasizing on jaguar spatial dynamics (e.g., Rabinowitz and Nottingham 1986; Carrillo 2000; Cavalcanti 2008; De la Torre et al. 2017; Gese et al. 2018; Morato et al. 2018) has shown that seasonality influences area-specific movements of jaguars.

Santa Rosa National Park (SRNP) in the dry forests of northwestern Costa Rica is likely home to one of the largest recovering jaguar populations in Costa Rica (Montalvo et al. 2015). It also contains two important sea turtle (olive ridley [*Lepidochelys olivácea*] and green turtle [*Chelonia Mydas*]) nesting beaches, one characterized by a rare seasonal sea turtle nesting aggregation (arribada; Nacite Beach), and the other (Naranjo Beach) characterized by year-round but seasonal solitary nesting (Hughes and Richard, 1974; Cornelius 1976; Cornelius and Robinson 1982; Valverde et al. 1998; Behm et al. 2000). Here in particular, we hypothesize that during sea turtle nesting peaks, jaguars spend more time close to the beaches as a foraging strategy. In this study we sought to identify the effect of seasonality and moon phases on jaguar foraging distances to sea turtle nesting beaches; seasonal spatiotemporal changes in jaguar home range size, and patterns of sea turtle predation related to season, sea turtle abundance, and moon phases.

Methods

Study area

This study was conducted in SRNP, one of the three national parks within the Guanacaste Conservation Area (GCA) located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza 1992). SRNP encompasses 387 km^2 and is dominated by the few remaining tropical dry forests in Central America (Janzen 1988; Gillespie et al. 2000), with average annual rainfall of 1,600 mm that is highly seasonal (monthly averages from 0 mm to 1040 mm); the wet season (months with $\geq$ 40mm of rain) is May to November, and the dry season (with almost no rain and temperatures over 37°C) is December to April. Due the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980's involving protected area status, the recovery of abandoned pastures by active fire suppression (Klemens et al. 2011), and protection from many human activities of the Park's two important sea turtle nesting beaches. At Nancite (length = 1.05 km), where thousands of turtles come ashore during the wet months (Valverde et al. 1998; Fonseca et al. 2009), only researchers are allowed visit during the arribada. At Naranjo (length = 5.64 km), there is a staffed ranger station and campground where up to 40 tourists may stay and use the beach year-round, even though there is an increasing pattern of seasonal nesting (Drake et al. 2000).

Data collection

We gathered previous sea turtle nesting data surveys from peer review papers and technical papers for both Nancite Beach (1980-2011) and Naranjo Beach (2013 - 2015). When the raw data from turtle nesting surveys was not available, we used the R package “digitalize” to retrieve data from old figures (Poisot 2011). Opportunistic sea turtle track-count surveys also were conducted at Naranjo Beach during 2013-2015. Each morning we walked along Naranjo Beach at 2 km/hour and registered activity from the previous night; sea turtle track-counts by species, jaguar presence (i.e., jaguar tracks on the beach) and jaguar predation events (i.e., jaguar-killed turtles). Additional information such moon phase (Lazaridis 2014) and sea surface temperature (https://neo.sci.gsfc.nasa.gov) also were gathered for further analysis.

We also monitored the movements of three-year-old jaguar female fitted with a GPS collar (Lotek Engineering, Newmarket, ON, Canada; http://www.lotek.com) programmed to record the jaguar’s position every 2 hours during 577 days (12/1/2014 – 6/30/2016). The jaguar was capture using a foot snare (Frank et al. 2003), and chemically immobilized using a dart projectile (Dan-inject, Kolding, Denmark; https://www.dan-inject.com) with a combination of 5 mg/kg of ketamine (10% ketamine, Bremer Pharma GmbH, Warburg, Germany) mixed with 2mg/kg xylazine (Procin Equus 10%, Pisa Agropecuaria) (Seem and Karesh, 2005). Handling and capture protocols followed the “Guidelines of the American Society of Mammalogists for the use of wild mammals in research” (Sikes et al. 2011) and also were approved by the Environmental Minister of Costa Rica.

Statistical analysis

To fulfill the model assumptions, we followed the data exploration protocol designed by Zuur et al. (2010), by using the statistical software R version 3.1.3 (R Core Team 2015) to perform data analysis. For the turtle count data and the distance data from each jaguar location to the nesting beaches we used generalized lineal models (GLM—) with a log link function (Venables and Ripley 2002), assuming negative binomial error distribution due to overdispersion issues, whereas binomial distribution was used for the jaguar predation data (Forte 2015). For home range analysis we calculate the KDE (Kernel Density Estimate) using both 50% and 95% isopleth contours with the R package "rhr" (Signer and Balkenhol 2015), using season (peak vs. off season) at three different temporal scales (month, week, season) as covariates. Additionally, side fidelity tests also were used to determine whether the animal showed patterns associated to specific areas within SRNP.

Results

Mean normalized peak counts of sea turtles (species combined) at both beaches depicted the same seasonal nesting trend (peak from July to January; Fig. 3.1) throughout the year, with maximum mean sea turtle counts at Naranjo Beach of ~ 212 in September vs. ~2,197 at Nancite Beach in October. Sea turtle abundance was modeled with GLM at Naranjo Beach (N = 270) using sea surface temperature (*SST*), moon phases (*Moon*), and relative turtle seasonality (*Seas*). The most plausible model (Table 1; Δ AIC > 60 and AIC $\omega = 1$) that included the interaction of *SST* by *Moon* and *Seas* showed strong evidence of sea turtle nesting seasonality.

We also collected 5,924 GPS locations of the collared jaguar during December 2014 – June 2016. GLM modelling testing for Seas and Moon effects on jaguar distances to the closest nesting beach produced a top model with the interaction of Moon and Seas

(Table 3.2; AIC ω = 1) markedly influencing jaguar location distances to nesting beaches. As expected, the collared jaguar was farther (~1.06 km) from nesting beaches during non-peak nesting season (Fig. 3.2). With regard moon phase, during peak nesting season the collared jaguar stayed closer to nesting beaches on waxing and waning moon phases, whereas during the non-peak season the closest mean distances registered for this jaguar were on full and waning moon phases (Fig. 3.2).

The overall home range (95% HR) size of the collared jaguar was 88.8 km^2, and the HR estimates for the non-peak (50% HR: 17.6 km^2, 95% HR: 72.3 km^2) and peak nesting seasons (50% HR: 18.1 km^2, 95% HR: 68.2 km^2) were similar, though the spatial distribution of the 50% HRs varied (Fig. 3.3). We observe more aggregation at Naranjo and Nancite Beaches during the nesting peak season (Fig. 3.3), whereas during the non-peak nesting season 50% HR was concentrated in the middle of SRNP and a small section of Nancite Beach (Fig. 3.3). Further analysis of site fidelity indicated that the mean square distance from the center of activity (6.8 km; CI 95%: 4.01–9.08), as well as the linearity index (0.050; CI 95%: 0.015–1.55) did not show statistical evidence of site fidelity. With regard to spatiotemporal variation of the GPS-collared jaguar's HR sizes, we did not find statistical evidence between monthly (t = 0.20, df =14.83, p = 0.84) and weekly (t = 0.8, df = 50, p = 0.4) HR sizes (Fig. 3.4), but during the non-peak nesting season the HRs were larger (Fig. 3.4)

The GLM modeling of the occurrence of predation events at Naranjo Beach showed turtle abundance as the top model (Table 3; AIC ω = 0.6), as well as the interaction of peak nesting season (Table 3.3; AIC ω = 0.39). Jaguar predation hotspots at both beaches showed a specific pattern of aggregation at Naranjo with most of the sea turtle carcasses at the southern section (Fig. 3.5), whereas predation hotspots at Nancite beach were evenly distributed, with the highest carcass concentrations at both north and southern sections (Fig. 3.5). GPS locations of the collared jaguar matched the pattern of predation hotspots determined from carcasses (Fig. 3.5).

Discussion

We used track count surveys of sea turtles and GPS telemetry of a female jaguar to evaluate the influence of turtle nesting season on jaguar home range size and distribution of locations. Our results indicated a seasonal increase in sea turtle availability (Cornelius and Robinson 1982; Valverde et al. 1998; Behm et al. 2000; Fonseca et al. 2009) that shaped ecological interactions. We found statistical evidence suggesting that moon phase, sea surface temperature, and the time of the year influence the number of sea turtles that come ashore, perhaps due to sea surface temperature affecting the internal physiology of sea turtle, as well as constraining sea grass nutrition quality in need to prepare clutches to laying (Hamann et al. 2003; Houtan et al. 2015). Additionally, observations by us and others (Carrillo et al. 2009; Houtan et al. 2015; Herrera 2016) indicate sea turtles likely to choose specific moon phases to nest, perhaps due to the amount of energy intake and time spent to come ashore and nest, as well as because the moon brightness might make sea turtles more vulnerable to predators.

Jaguar location distances from nesting beaches were frequently closer on the peak-nesting season, interacting with moon phases, similar to the finding of previous studies (e.g., Carrillo 2000; Carrillo et al. 2009); this suggests a seasonal foraging strategy by jaguars to maximize their energy budget. Jaguars may also synchronize births with peaks of sea turtle abundance as a strategy to increase offspring survival and recover body mass after birthing (Bergstrom et al. 2017; Campos et al. 2017); we have recorded frequent field sightings of females with offspring at nesting beaches during peak nesting (unpublished information).

Early telemetry studies described seasonal responses on jaguar home range sizes owing to prey abundance peaks on time (Carrillo 2000; Cavalcanti 2008; Astete et al. 2016; Gese et al. 2018). Though we found no statistical evidence of seasonal changes in home ranges sizes, seasonal core areas changed location from one season to another, concentrating mostly on nesting beaches during sea turtle peak season and matching with locations of predated sea turtle carcasses (Alfaro et al. 2016; Escobar-Lasso et al. 2017). Changes in prey distribution over time and though space has consequences for predators, because if prey respond to environmental changes, predators follow the same trend (Sunquist and Sunquist, 2002). For example, in the Kalahari Desert when large prey are dispersed, the home range size of a lion (*Panthera leo*) pride increases 5 times the regular home range size (Sunquist and Sunquist, 1989). Elsewhere, analysis of jaguar predation events upon sea turtles showed a strong positive relationship between turtle abundance and the frequency predation events (Guilder et al. 2015).

In summary, our results provide strong evidence of jaguar behavioral responses linked to peaks of seasonal availability of sea turtles in the dry forest ecosystem. Climate and environment conditions directly influenced biology of sea turtle nesting and as a consequence it also constrains jaguar movements and to foraging activity. Optimal foraging theory predicts that predators seek out prey in terms of energy (MacArthur and Pianka 1966), and our study partially fulfilled this prediction. Even though our study only used GPS telemetry data from one individual, our results were consistent with the sea turtle track and carcass count surveys and previous data. Finally, knowledge of jaguar home range sizes and its variation with prey in seasonal ecosystems might contribute to improve conservation especially in places such Naranjo Beach with dual value for conservation of endangered species and tourism; our study defines a base-line home range size for jaguars in the tropical dry forest, and focuses the importance of seasonal sea turtle availability as is influences the terrestrial dynamics of large predators.

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Table 3.1 Sea turtle abundance (Tur: olive ridley *Lepidochelis Olivacea,* and green turtle *Chelonia mydas*) at Naranjo beach in Santa Rosa National Park, northwestern Costa Rica, as modeled using season of relative turtle abundance (Seas), sea surface temperature (SST), and moon phase (Moon).

Model	df	AIC	Δ AIC	ω
Tur = SST x Moon x Seas	16	1613	0	1
Tur = SST+ Moon + Seas	6	1673	60	<0.001
Tur = SST	2	1754	141	<0.001
Tur = Seas	2	1755	142	<0.001
Tur = Moon	4	1786	173	<0.001
Tur = Intercept	1	1806	193	<0.001

Table 3.2 Models describing the effect of Turtle abundance season (Turtle season) and moon phases (Moon) on distances of a GPS-collared jaguar to the closest nesting beach (Dist. beach) in Santa Rosa National Park in northwestern Costa Rica.

Model	df	AIC	Δ AIC	ω
Dist. beach = Turtle season × Moon	9	106419	0	1
Dist. beach = Turtle season + Moon	6	106435	16	< 0.001
Dist. beach = Turtle season	3	106450	31	< 0.001
Dist. beach = Moon	5	106789	369	< 0.001
Dist. beach = 1	2	106809	389	< 0.001

Table 3.3 Models describing the effect of Sea turtle abundance (Tur), seasonality (Seas) and moon phase (Moon) on jaguar predation events (Pred. Events; i.e., jaguar-killed turtles) at Naranjo Beach in Santa Rosa National Park in northwestern Costa Rica.

Model	df	AIC	Δ AIC	ω
Pred. events = Tur	2	228	0	0.60
Pred. events = Tur x Turtle season	4	229	1	0.39
Pred. events = Tur x Moon	1	237	9	0.007
Pred. events = Tur x Moon + Seas	8	239	11	0.002
Pred. events = Intercept	1	137	16	0.001

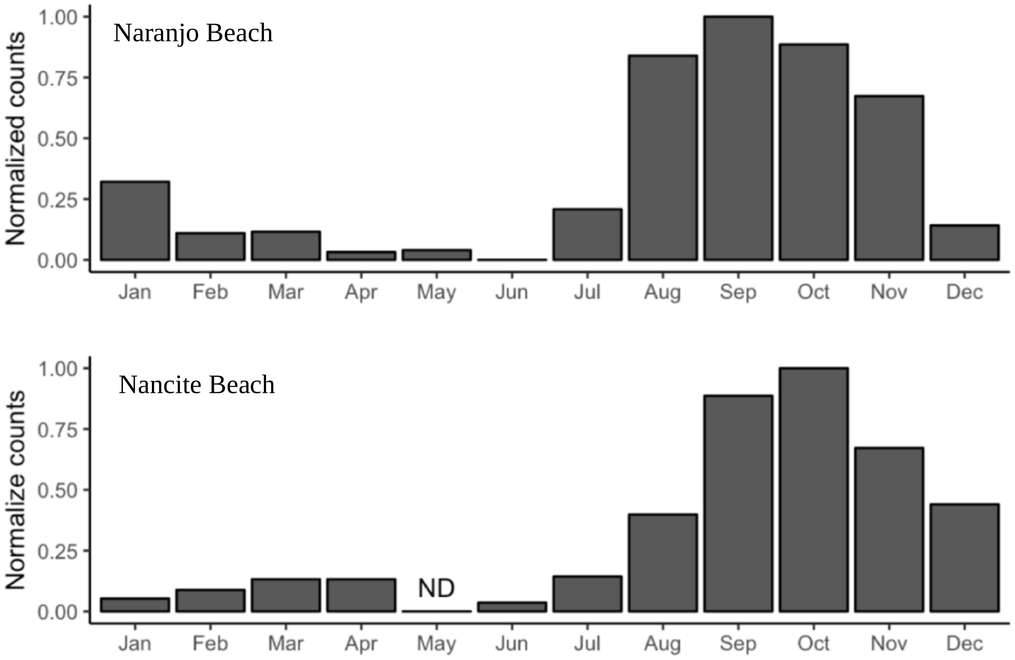

Figure 3.1 Monthly mean-normalized counts of sea turtles (olive ridley *Lepidochelis olivacea,* and green turtle *Chelonia mydas*) at Naranjo Beach (2013-2015) and Nancite Beach (1980-2011) in Santa Rosa National Park in northwestern Costa Rica. Actual average peak counts were 212 nesting turtles at Naranjo in September vs. 2,197 at Nancite in October.

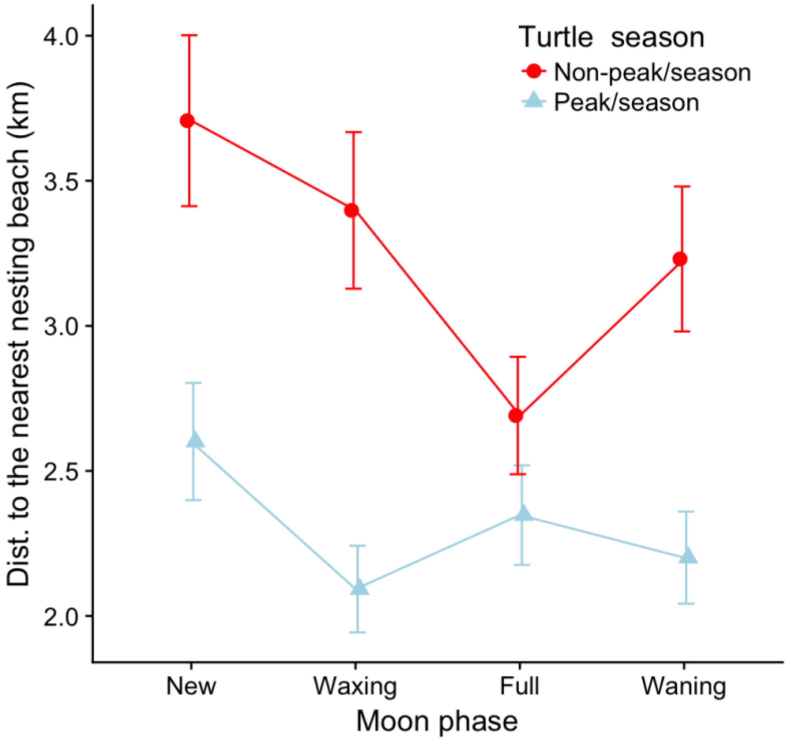

Figure 3.2 Mean GPS-collared jaguar distances (km) to the nearest turtle nesting beach [mean ± 95% confidence interval] as influenced by moon phase and season of relative turtle abundance in Santa Rosa National Park in northwestern Costa Rica.

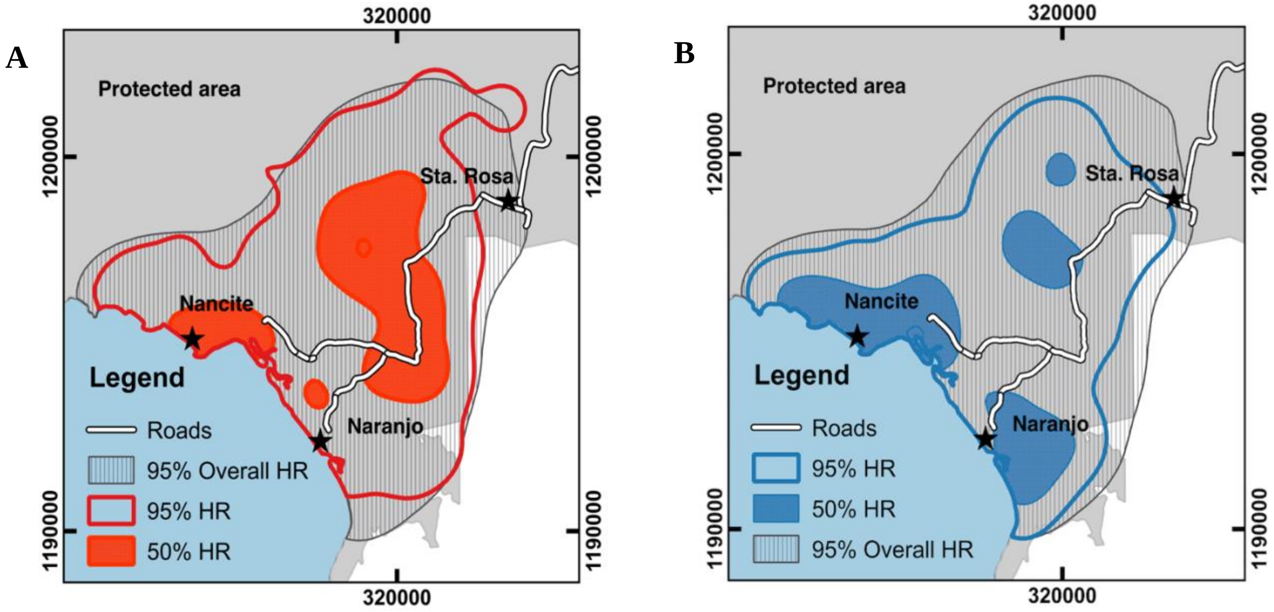

Figure 3.3 Seasonal home range sizes (km^2) of a GPS-collared female jaguar during the non-peak (A) and peak season of sea turtle nesting (B) at Santa Rosa National Park in northwestern Costa Rica.

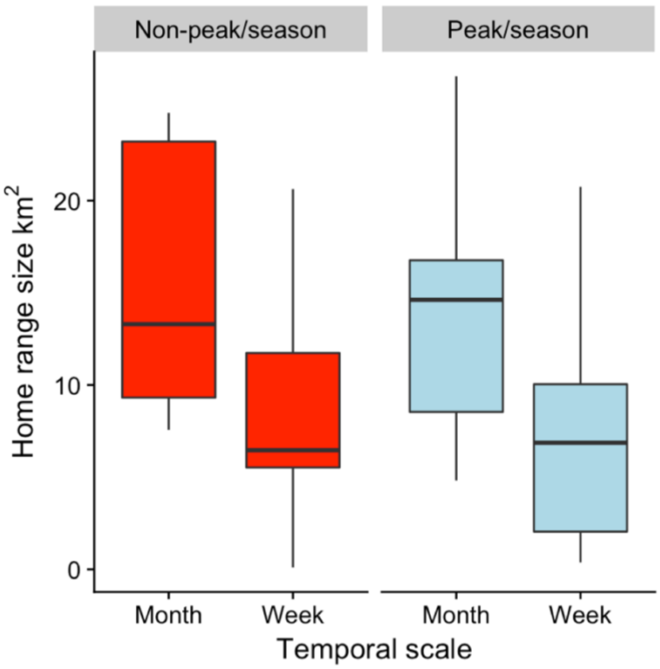

Figure 3.4 Spatiotemporal variation of a GPS-collared jaguar's monthly and weekly home range sizes (km^2) between seasons of differing turtle abundance at Santa Rosa National Park in northwestern Costa Rica.

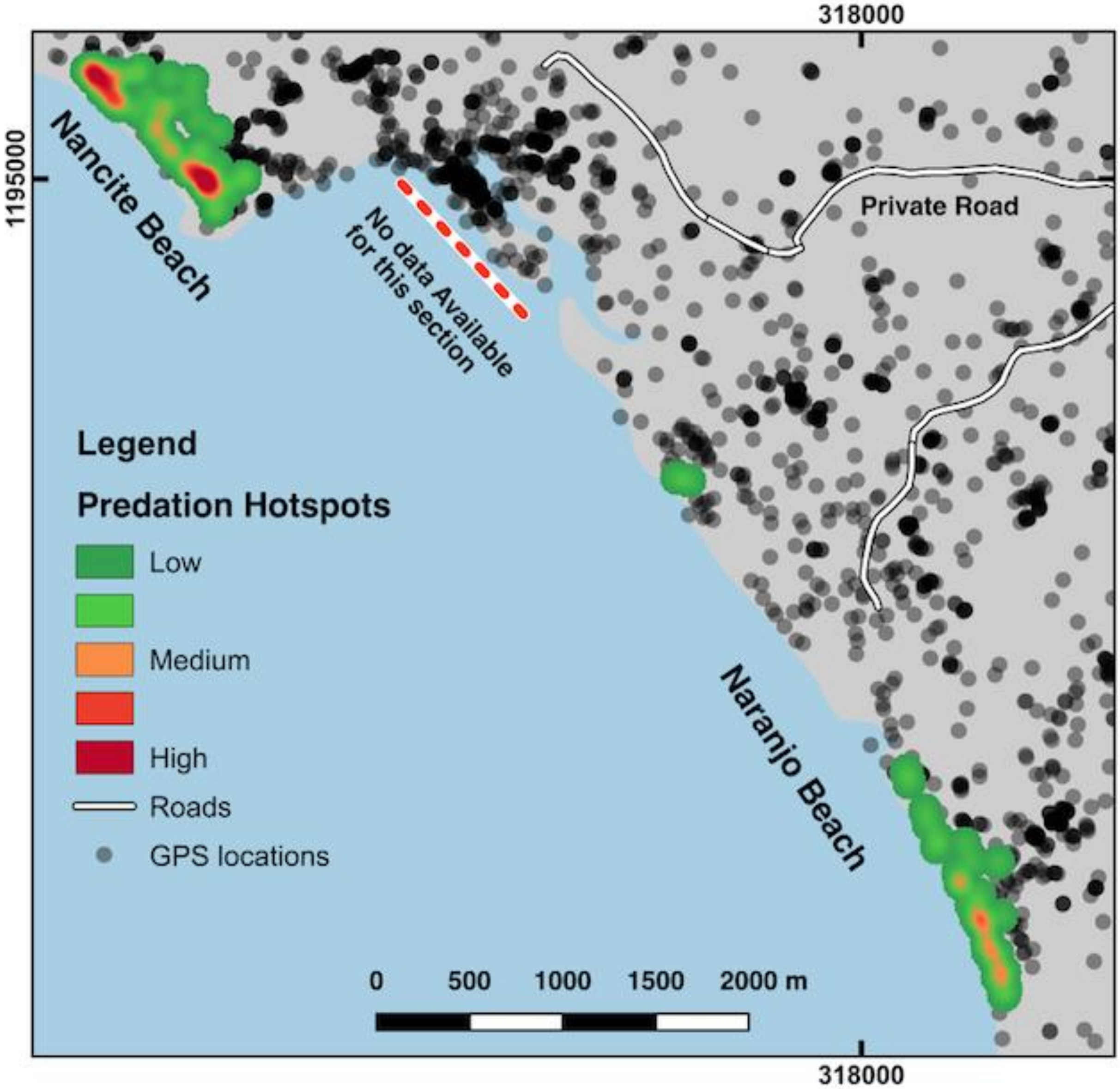

Figure 3.5 Locations of jaguar-predated turtle carcasses ("Predation hotspots"; cf. Escobar-Lasso et al. 2017) and a GPS-collared jaguar at Nancite and Naranjo beaches in Santa Rosa Nacional Park in northwestern Costa Rica.

CHAPTER 4

CAMERA TRAP SITE PLACEMENT EFFECT ON DRY FOREST WILDLIFE PHOTO RATES IN NORTHWESTERN COSTA RICA: FURTHER IMPLICATIONS FOR JAGUAR (*Panthera onca*) CAMERA TRAP STUDIES

Abstract

The use of camera trap methods has come with pitfalls and inconsistencies, including ignoring factors and interactions that may influence species photo rates. The majority of jaguar (*Panthera onca*) camera trap studies placed cameras at sites where jaguar detection could be improved, but did not account for potential bias. This study evaluated methodological implications of a paired camera trap design at trail and off-trail locations, and seasonality, on jaguar and non-target species photo rates. From June 2016 to June 2017, camera traps were deployed at 58 different sites in a hexagon grid array of 3-km^2 each in the Santa Rosa Sector (SSR) of Guanacaste National Park in Costa Rica. Half of the cameras were located at a trail location that jaguars were likely to use, and the other half at an off-trail location closest to each hexagon centroid. We estimated a photographic relative abundance index (RAI: no. of independent photos/100 trap nights) and used Generalized Lineal Models (GLM) to assess statistical evidence. With a total effort of 19,408 trap nights, we recorded 12,678 independent photo events of 64 species of amphibians, reptiles, birds and mammals. Most average RAIs were higher at trail locations, whereas eastern-spotted skunk (*Spilogale putorious*), tayra (*Eira Barbara*), coati (*Nasua narica*), agouti (*Dasyprocta punctata*), nine-banded armadillo (*Dasypus novemcinctus*) and thicket tinamou (*Crypturellus cinnamomeus*) had lower RAI and some seasonal effects. For jaguars, sex ratio data showed a lower male proportion at off-trail locations. Analysis of competitor and prey interaction data indicated temporal avoidance at trail locations. Further jaguar camera trap studies might highlight camera placement as important source of

bias that might influence results; hence conservationists must be warned of this in order to avoid wrong decision making.

Introduction

Camera trapping is a widely popular, non-invasive method to assess wildlife over long periods of time (Rovero and Zimmermann 2016) due to low maintenance and the high volumes of information collected. Thus, large-scale wildlife ecological studies have implemented this method with a variety of variations (O’Connor et al. 2017) and analytical applications (e.g., capture/recapture, occupancy, photo indexes). This extensive use of camera traps also has come with pitfalls and inconsistencies across most studies, ignoring habitat heterogeneity (Cusack et al. 2015), and how particular species distribution and interactions may influence photo rates of other species. Therefore, species interactions mechanisms of competition or avoidance could be assessed by comparing occupied vs. unoccupied site differences (Gause 1932) through camera-trap metrics (Harmsen et al. 2010; Sollmann et al. 2012; Booker 2013).

For jaguars (*Panthera onca*) and non-target species, most habitat studies show a variety of ecological responses depending on local environmental factors (Morato et al. 2016; Rovero and Zimmermann 2016; Rabelo et al. 2019). These studies use different assessment techniques (Novak et al. 2005; Morato et al. 2016; De la Torre et al. 2017; Gutierrez-Gonzáles and López- Gonzáles 2017), but camera trapping is used the most for jaguar and medium-size sympatric species (O’Connell et al. 2011). Nevertheless, the majority of jaguar camera trap studies mostly place cameras in sites where jaguar detection can be improved so to maximize photos for density estimates (Cusack et al. 2015; O’Connor et al. 2017); however, not accounting for this might lead to a biased inference (O’Connor et al. 2017). A common practice is to use the same design to associate non-target multiple species at same camera sampling site (Blake and Mosquera 2014), i.e., using the same camera placement to infer prey and predator relationships with environmental variables. However, it may be that prey avoid places frequented by predators in the first place (Valeux et al. 2011), and therefore confusing these interactions' effect on photo rates. Also, several studies have argued the use of non-random camera trap placement (Cusack et al. 2015; O'Connor et al. 2017), due to the violation of randomization, limiting the proportion of environmental variation embraced, as well as the sampling bias resulting from differences in the presence or relative abundance of multiple species at other kinds of sites (Kolowski and Forrester 2017).

Given the previous sources of bias already reported in camera trap studies, and that methodological variants are rarely compared against ecological results, we aim to evaluate the methodological implications of a paired camera trap design at trail and off-trail locations, while taking into account seasonality, and the effect on jaguar and non-target species photo rates. We also assess whether interpretation of jaguar-specific camera trap ecological study data (sex ratio, competitor relationships, activity patterns, abundance, and prey interactions) are influenced by camera placement.

Materials and Methods

Study area

This study was conducted in Sector Santa Rosa (SSR), within the Área de Conservación Guancaste (ACG) located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza, 1992). SSR encompasses 387 km^2 and is dominated by the few remaining tropical dry forests in Central America (Janzen 1988; Gillespie et al. 2000). Due the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980's involving protected area status, the recovery of abandoned pastures by active fire suppression

(Klemens et al. 2011), protection from many human activities, and also the recovering of large vertebrate populations. In the area, average annual rainfall of 1,600 mm is highly seasonal (monthly averages from 0 mm to 1040 mm); the wet season usually spans from May to November, and the dry season (with almost no rain and temperatures over 37°C) is December to April (Fig. 4.1). Nevertheless, due to high climate variation during the last decades (Campos 2018) seasonality was defined from SRS historic precipitation records (Fig. 4.1). For such data we aggregated the weekly accumulated precipitation in order determine whether the weekly precipitation sum was higher or lower in comparison with annual precipitation week average (μ=10 mm). Thus, a week with $\geq$ 10 mm was classified as a wet week, whereas a week with $\leq$ 10 mm was a dry week.

Data collection

From June 2016 to June 2017 automatic trail cameras (Bushnell®, Trophy Cam models 119436, 119446, 119456) were deployed at 58 different sites in a hexagon grid array of 3 km^2 each at SSR (Fig. 4.2). Half of the cameras were located at a trail location that jaguars were likely to use, and the other half at an off trail location closest to each hexagon centroid (Fig. 4.2). Each camera was affixed to a tree at a height of approximately 40 cm and set to be active for 24 h/day in photo mode with the minimum delay (1 sec) between consecutive triggers. Once deployed, cameras were checked on average every month to replace batteries and change SD memory cards, if necessary. For each camera deployment, we recorded the location, camera operation dates (and therefore, number of trap nights), and the number of independent photo events for each species. Photos were considered an independent photo of a species if they were: (1) taken at least 30 minutes apart (e.g., a series of 3 photos of the same species taken in consecutive seconds = 1 photo event); (2) consecutive photos of the same species could be identified as different individuals (spots, scars, horns/antlers, sex) and not part of the same group (e.g., 15 minutes apart, going in opposite directions = 2 photo events); or (3) photos of the same species separated by photos of a different species (e.g., species 1, followed 2 minutes later by a species 2, followed five minutes later by species 1 = 1 species with 2 photo events and 1 species with 1 photo event).

Statistical analysis

To examine and identify potential data issues (e.g., normality, overdispersion, outliers) and fulfill model assumptions, we followed the data exploration protocol suggested by Zuur et al. (2010). The number of independent photos of species at a site were analyzed using generalized linear models (GLM; Zuur et al. 2009) with a log link function, as is customary for count data, implemented using the statistical software R.4.0.0 (R Core Team 2020) with the package lme4 1.1 (Bates et al. 2015). Due to overdispersion in the counts, we assumed a negative binomial error distribution (Zuur et al. 2009), and to account for variation in effort, we used the log of the number of trap nights as an offset to standardize the counts.

In order to assess the effect location (Loc) and seasonality (Seas) on photographic relative abundance index (RAI: no. of independent photos/100 trap nights*)*, five *a priori* models were developed for each species. One model included the intercept, one only singular predictor, one the additive effect of the two predictors, and one the first order interactions for the two predictors (Table 4.1).

The empirical supports of these five candidate models were evaluated using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002), and throughout the model comparison for each species we determined the most plausible models due the highest Akaike weight (*W;* range = 0 to 1; Anderson 2007). Based on the *W* we assessed the evidence from one model over another (Burnham and Anderson 2002). Because we were particularly interested in those models showing interactions and the additive effects of Season (Seas) and Location (Loc) on photo rates, we included in the confidence set of models, based on the *W* value, those for species where the interaction and the additive effect of Seas and Loc differed by <10% from the top model (Thompson and Lee 2000).

Specifically, for jaguar photo rates at trail and off-trail locations, we contrasted additional ecological information gathered from camera traps. Sex ratio statistical differences at off-trail/trail locations were assessed through Welch t-test (Shahbaba 2011). Competitor relationships and prey interactions at off-trail/trail locations were contrasted with linear regression analysis using RAI of each species (Zuur et al. 2007). To quantify activity patterns we used Ridout and Linkie's (2009) approach with the package Activity 1.3 (Rowcliffe 2019), using Walt test to contrast temporal distribution aggregation differences for circular data, smoothed with 10,000 bootstrap resamples to calculate confidence intervals (Rovero and Zimmermann 2016).

Results

We mounted a total effort of 19,408 trap nights and recorded 12,678 independent photo events of 64 species of amphibians, reptiles, birds and mammals. We included in our analysis 10 bird species and 19 mammal species with >10 independent photo records (Table 4.2). Most averaged RAI registered were higher at trail locations, whereas easter-spotted skunk (*Spilogale putorious*), tayra (*Eira Barbara*), coati (*Nasua narica*), agouti (*Dasyprocta punctata*), nine-banded armadillo (*Dasypus novemcinctus*) and thicket tinamou (*Crypturellus cinnamomeus*) report the highest RAI at off trail locations (Table 4.2).

Model selection based on *W* (Table 4.3) showed the intercept model was the most plausible for pauraque (0.54), tamandua (*Tamandua mexicana*; 0.39), variegated squirrel (*Sciurus variegatoides*; 0.46), agouti (0.46), coati (0.31), tayra (0.48), eastern-spotted skunk (0.41), striped hog-nosed skunk (*Conepatus semistriatus*; 0.32), ocelot (*Leopardus pardalis*; 0.43), tapir (*Tapirus bairdii*; 0.45) and white-tailed deer (*Odocoileus virginianus;* 0.54), whereas roadside hawk (*Rupornis magnirostris*; 0.48), common black hawk (*Buteogallus anthracinus*; 0.65), double-striped thick-knee (*Burhinus bistriatus*; 0.54), crested guan (*Penelope purpurascens;* 0.36), nined-banded armadillo (0.43), white-faced capuchin monkey (*Cebus imitator;* 0.37), coyote (*Canis latrans*; 0.36), gray fox (*Urocyon cinereoargenteus*; 0.59), raccoon (*Procyon lotor*; 0.42), jaguar (*Panthera onca* ; 0.67) and collared peccary (*Pecari tajacu*; 0.38), location (Loc) had the most influence (Table 4.3). With regard to great curasao (*Crax rubra*; 0.46), and common opossum (*Didelphis marsupialis*; 0.44*),* the additive effect of Loc and Seas were fitted as top model, and white-winged dove (*Zenaida asiatica*; 0.55) and puma (*Puma concolor*; 0.39) included the interaction of these two predictors as the most plausible (Table 4.3).

Overall, jaguar recorded the most empirical support for Loc effect on RAI (*W*= 0.67). Further sex ratio analysis at off-trail/trail locations showed lower male proportion at off trail locations (mean = 0.25), in contrast to trail locations (mean = 0.62), indicated enough statistical evidence for these differences (t = -2.27, df = 14.00, p-value = 0.039), with no records of females with cubs at any location. Jaguar sex temporal aggregation showed temporal avoidance of males and females (Fig. 4.3; A, W= 10.01, p-value = 0.001), at off trial locations, whereas at trail locations overlap did not showed statistical evidence of temporal avoidance (Fig. 4.3; B, W= 0.375, p-value = 0.541).

Jaguar and puma RAI regression coefficients at off-trail and trail locations showed poor correlation, and no differences between species (Fig. 4.4; $R^2 = 0.003$, p-value =0.125); nevertheless, temporal aggregation analysis indicated avoidance between jaguar and puma at trails (Fig. 4.5; A, W= 6.92, p-value = 0.01) but not at off trail locations (Fig. 4.5; B, W= 1.828, p-value = 0.17 Off-trail), though temporal patterns at both locations were the same. For jaguar and white-tailed deer, RAI regression coefficients showed no pattern (Fig. 4.6; $R^2 = 0.04$, p-value =0.058) between species, but temporal activity suggested at both trail and off trail sites jaguars are more nocturnal and white-tailed deer are more diurnal (Fig. 4.7). Statistical evidence of temporal avoidance between jaguars and white-tailed deer were found at off-trail locations (Fig. 4.7; A,W = 4.27, p-value = 0.038) but not at trail locations (Fig. 4.7; B, W = 0.001, p-value = 0.97), though both locations depicted the same pattern. Collared peccary and jaguar RAI regression coefficients indicated no pattern (Fig. 4.8; $R^2 = 0.003$, p-value = 0.125); nevertheless, temporal activity suggested avoidance patterns (where peccaries tend to increase diurnal activity during jaguar's lowest activity peak), and statistical evidence of avoidance was found at off-trail locations (Fig. 4.9; A, W = 6.41, p-value = 0.011); at trail locations the activity pattern followed the same trend with no statistical significance (Fig. 4.9; B, W = 0.375, p-value = 0.541).

Discussion

An entirely randomized designs is a theoretical common requirement on biological field studies (Quinn and Keough 2002). Nevertheless, few field base camera-trap studies fulfil this assumption due logistic or budget constraints (Cusack et al. 2015). Though our study didn't completely achieve 100% randomness, our off-trail camera trap placement attempted to reach the closest random placement to compared photo rates with trail locations (Fig.4.2). RAI of 10 bird species and 19 mammals at trail and off-trail camera location indicated placement and seasonality are both important methodological placement strategies that might lead to different results regarding the species. For bird species we found statistical evidence of location effects for roadside hawk, double-striped thick-knee and crested guan, being more frequently registered at trail placements. Great curasao and thicket tinamou showed additive-effects evidence of seasonality and location, whereas white-winged doves were the only bird species showing evidence of interacting effect of location and seasonality. These observations suggest trail in comparison to off-trail locations provide easy access and detection of foraging facilities for generalists and grown dwelling bird species (Stiles et al. 2007); also, most detected species at trail locations weighed >500 gr, maybe suggesting improved camera sensor detection due to body size in contrast with <500-gr bird species (Cloyed et al. 2018) and that this might lead to biased results (Braczkowski et al. 2016, O'Connor el al. 2017). Additional seasonal RAI responses for Great curasao, thicket tinamou, and white-winged dove may be related to the fact that an important proportion of these species diet depend on seeds, waisted grain, and fruits that seasonally growth in the dry forest. (Stiles et al. 2007).

Statistical evidence of location effect on mammal RAI were identify for nine-banded armadillo, white-faced capuchin monkey, coyote, gray fox, raccoon, collared peccary, and jaguar. These mammal species showed location effect on RAI, mostly were generalists, and a carnivore (jaguar; Carrillo et al. 2000); therefore, this trail use preference could be a foraging strategy (Pianka 1966) to maximize energy reward due moving across open pathways that would increase resource allocation, also improving predator detection or vice versa for the jaguar. Weckel et al. (2006) and Harmsen et al. (2009) reported similar findings in the tropical rainforest where some species had high photographic rates at human-made trails instead of other type of pathways, suggesting trails photo rates are biased toward large carnivores such as puma and jaguar. Additive effect of location and seasonality on mammals RAI was only registered for the common opossum, a generalist species (Carrillo et al. 2000), likely to use mostly trails due the weak sense of smell, due more open areas spread and keep the odors longer, allowing common opossum to easily identify potential resource items during scarcity periods at man-made trails (Morgan et al. 1995). Puma were found more frequent at trails, but the statistical evidence suggested the interaction of location and seasonality also would affect places puma use the most. Perhaps factors as competition with top predators such jaguar, and prey availability would marginalize puma, affecting the places puma visit (Gutiérrez-González and López-González 2017). Statistical evidence for tamandua, variegated squirrel, agouti, coati, tayra, eastern spotted skunk, striped hog-nosed skunk, ocelot, tapir and white-tailed deer suggested these species RAI disregard of seasonal and location effect, though some species were more common frequent at off trail locations. This lack of evidence mostly related few records or like tapir and white-tailed deer both abundant species widely spread at trail and off trail locations, similar to Blake and Mosquera (2014).

Camera trap ecological studies mostly described five usages of camera trap method (O'Connell et al. 2011; Trolliet et al. 2014; Rovero and Zimmermann 2016); sex interactions, competition, prey-predator relationships, abundance, and temporal interactions. Hence, we tested some camera placement effect on jaguars. Sex interactions showed statistical evidence suggesting females temporally and spatially used the most off-trail locations compared with males. This behavior of sex avoidance has been already reported in other locations (Sunquist and Sunquist 2002; Silver et al. 2004; Salom et al. 2007; Astete et al. 2017) where most researchers speculated jaguar males could commit infanticide, and so owing to this it is likely females could use the most off-trail pathways to avoid infanticide (though during our study we did not record females with cubs). Jaguar competition with pumas did not shows spatial differences due camera placement; nevertheless, we found both frequent same places but temporally avoiding each other. This spatial pattern observed has been previously described in the rainforest ecosystem where due prey overlap both species frequent the same places (Emmons 1987; Foster et al. 2010; Gutiérrez-González and López-González 2017), observing temporal segregation where pumas become more diurnal during jaguar's nocturnal activity peaks (Harmsen et al. 2009; Herrera et al. 2018). No statistical evidence was found for jaguar prey interaction differences (white-tailed deer, collared peccary) due site placement effect, though we previously hypothesize predator-prey camera trap studies may be biased since places predator-frequented would repel prey due the high-risk foraging activity involved (Valeix 2011). However, this hypothesis may be partially supported, observing that white-tailed deer and collared peccary were active the most during the lowest peaks of jaguar activity, but collared peccaries were more frequent at off-trail locations, which were less frequented by jaguars, suggesting predator-prey place avoidance for collared peccary.

Our study suggests camera location placement and seasonality is a methodological constraint likely to influence inferences depending on target animal species in the dry forest of SSR. Roadside hawk, double-striped thick-knee, crested guan, nine-banded armadillo, white-faced capuchin monkey, coyote, gray fox, raccoon, collared peccary and jaguar were the most influence by camera location placement, using trails for movement, as well as to access resources. Detailed jaguar analysis show females used the most off trail locations, and jaguar co-specific and prey interaction indicated temporal avoidance mostly at trail locations. Owing to this, further jaguar camera trap ecological studies might take into account camera placement as important methodological source of biased that might influence distribution, abundance, or multiple species interaction results, hence conservationists as researchers must be warn of this in order to avoid wrong decision making or misleading conclusions.

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Table 4.1 Description of five priori candidate models describing the effect of location (Loc: Trail/ Off-trail) and seasonality (Seas: Dry/Wet) on relative abundance Index (RAI: no. independent photos per 100 trap nights in Santa Rosa Sector, Guanacaste Conservation Area, Northwestern Costa Rica.

Model	Description
1) RAI = log (Trap nights)	Intercept only
2) RAI = log (Trap nights) + Seas	RAI vary by Seas
3) RAI = log (Trap nights) + Loc	RAI vary by Loc
4) RAI = log (Trap nights) + Seas + Loc	RAI vary by Seas and Loc in an additive way
5) RAI = log (Trap nights) + Seas * Loc	RAI vary differently by Seas and Loc

Table 4.2 Relative abundance Index (RAI: no. independent photos per 100 trap nights; nu. of trap nights in parenthesis) for 10 bird species and 19 mammal species, seasonally at trail and off-trail locations in Santa Rosa Sector, Guanacaste Conservation Area, Northwestern Costa Rica (2016-2017).

		Dry season		Wet season	
		Trail	Off-trail	Trial	Off-trial
Species	Common name	(3291)	(3056)	(7337)	(5724)
Birds					
Nyctidromus albicollis	Pauraque	0.21	0.39	0.42	0.26
Zenaida asiatica	White-winged dove	2.85	0.00	2.90	0.72
Leptotila verreauxi	White-tipped dove	0.08	0.13	0.38	0.25
Rupornis magnirostris	Roadside hawk	0.34	0.00	0.18	0.02
Buteogallus anthracinus	Common black hawk	0.27	0.00	0.25	0.02
Burhinus bistriatus	Double- striped thick-knee	0.26	0.03	0.31	0.03
Crax rubra	Great Curasao	8.51	2.72	11.70	6.71
Penelope purpurascens	Crested guan	0.71	0.50	0.76	0.25

Crypturellus cinnamomeus	Thicket tinamou	0.06	0.10	0.57	0.56
Mammals					
Didelphis marsupialis	Common opossum`	0.43	0.12	0.12	0.05
Tamandua mexicana	Tamandua	0.03	0.07	0.10	0.04
Dasypus novemcinctus	Nine-banded armadillo	0.00	0.13	0.06	0.18
Cebus imitator	White-faced capuchin monkey	2.28	0.03	2.28	0.03
Sciurus variegatoides	Variegated Squirrel	0.00	0.03	0.03	0.03
Dasyprocta punctata	Agouti	3.96	5.45	4.46	9.06
Canis latrans	Coyote	0.20	0.00	0.09	0.02
Urocyon cinereoargenteus	Gray Fox	1.28	0.10	2.30	0.19
Procyon lotor	Raccoon	0.26	0.07	0.18	0.02
Nasua narica	Coati	0.11	0.43	0.23	0.25
Eira Barbara	Tayra	0.25	0.36	0.22	0.30
Spilogale putorious	Eastern spotted skunk	0.05	0.31	0.19	0.28
Conepatus semistriatus	Striped hog-nosed skunk	0.23	0.10	0.11	0.06
Leopardus pardalis	Ocelot	0.90	0.47	0.69	0.62

Puma concolor	Puma	1.33	0.33	0.96	0.79
Panthera onca	Jaguar	2.24	0.37	3.15	0.34
Tapirus bairdii	Tapir	1.76	1.63	1.48	1.08
Pecari tajacu	Collared peccary	0.51	2.42	0.41	1.07
Odocoileus virginianus	White- tailed deer	25.13	25.28	23.38	25.76

Table 4.3 Model importance weights for 10 bird species and 19 mammal species, describing the effect of seasonality (Seas) and Location (Loc: Trail/Off-trail) on Relative abundance Index (RAI) in Santa Rosa Sector, Guanacaste Conservation Area, Northwestern Costa Rica.

		Model description and AIC weights (*W*)				
Species	Common name	Intercept	Loc	Seas	Loc + Seas	Loc x Seas
Birds						
Nyctidromus albicollis	Pauraque	**0.54**	0.18	0.19	0.06	0.03
Zenaida asiatica	White-winged dove	0.09	0.19	0.03	0.14	**0.55**
Leptotila verreauxi	White-tipped dove	0.31	0.1	**0.4**	0.14	0.05
Rupornis magnirostris	Roadside hawk	0.11	**0.48**	0.07	0.19	0.15
Buteogallus anthracinus	Common black hawk	0	**0.65**	0.01	0.23	0.11
Burhinus bistriatus	Double- striped thick-knee	0.16	**0.54**	0.06	0.18	0.06
Crax rubra	Great Curasao	0.04	0.2	0.04	**0.46**	0.26
Penelope purpurascens	Crested guan	0.32	**0.36**	0.12	0.14	0.06
Crypturellus cinnamomeus	Thicket tinamou	0.02	0	0.6	**0.28**	0.1

Mammals						
Didelphis marsupialis	Common oposum	0.06	0.18	0.16	**0.44**	0.16
Tamandua mexicana	Tamandua	**0.39**	0.23	0.18	0.1	0.1
Dasypus novemcinctus	Nined-banded armadillo	0.08	**0.43**	0.04	0.25	0.2
Cebus imitator	White-faced capuchin monkey	0.15	**0.37**	0.14	0.24	0.1
Sciurus variegatoides	Variegated Squirrel	**0.46**	0.16	0.24	0.09	0.05
Dasyprocta punctata	Agouti	**0.46**	0.24	0.18	0.09	0.03
Canis latrans	Coyote	0.01	**0.36**	0.01	0.35	0.27
Urocyon cinereoargenteus	Gray Fox	0.02	**0.59**	0.01	0.28	0.1
Procyon lotor	Raccoon	0.23	**0.42**	0.09	0.19	0.07
Nasua narica	Coati	**0.31**	0.31	0.12	0.11	0.15
Eira Barbara	Tayra	**0.48**	0.23	0.18	0.08	0.03
Spilogale putorious	Eastern spotted skunk	**0.41**	0.27	0.15	0.1	0.07
Conepatus semistriatus	Striped hog-nosed skunk	**0.32**	0.27	0.2	0.16	0.05
Leopardus pardalis	Ocelot	**0.43**	0.28	0.15	0.09	0.05
Puma concolor	Puma	0.1	0.34	0.04	0.13	**0.39**

Panthera onca	Jaguar	0	**0.67**	0	0.24	0.09
Tapirus bairdii	Tapir	**0.45**	0.19	0.23	0.1	0.03
Pecari tajacu	Collared peccary	0.26	**0.38**	0.13	0.17	0.06
Odocoileus virginianus	White- tailed deer	**0.54**	0.19	0.19	0.06	0.02

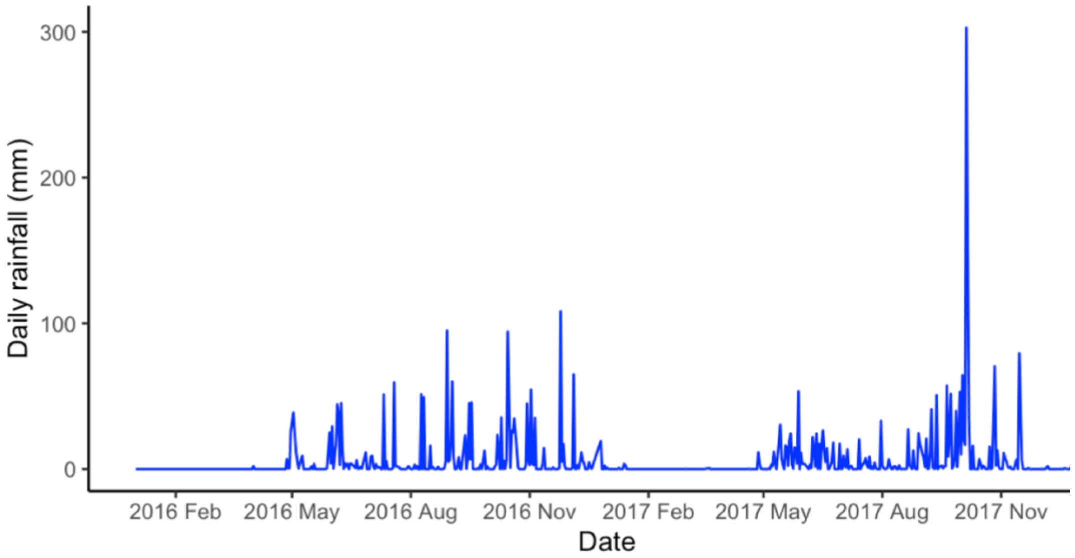

Figure 4.1 Daily rainfall in Sector Santa Rosa period 2016-2017. Guanacaste Conservation Area, Northwestern Costa Rica.

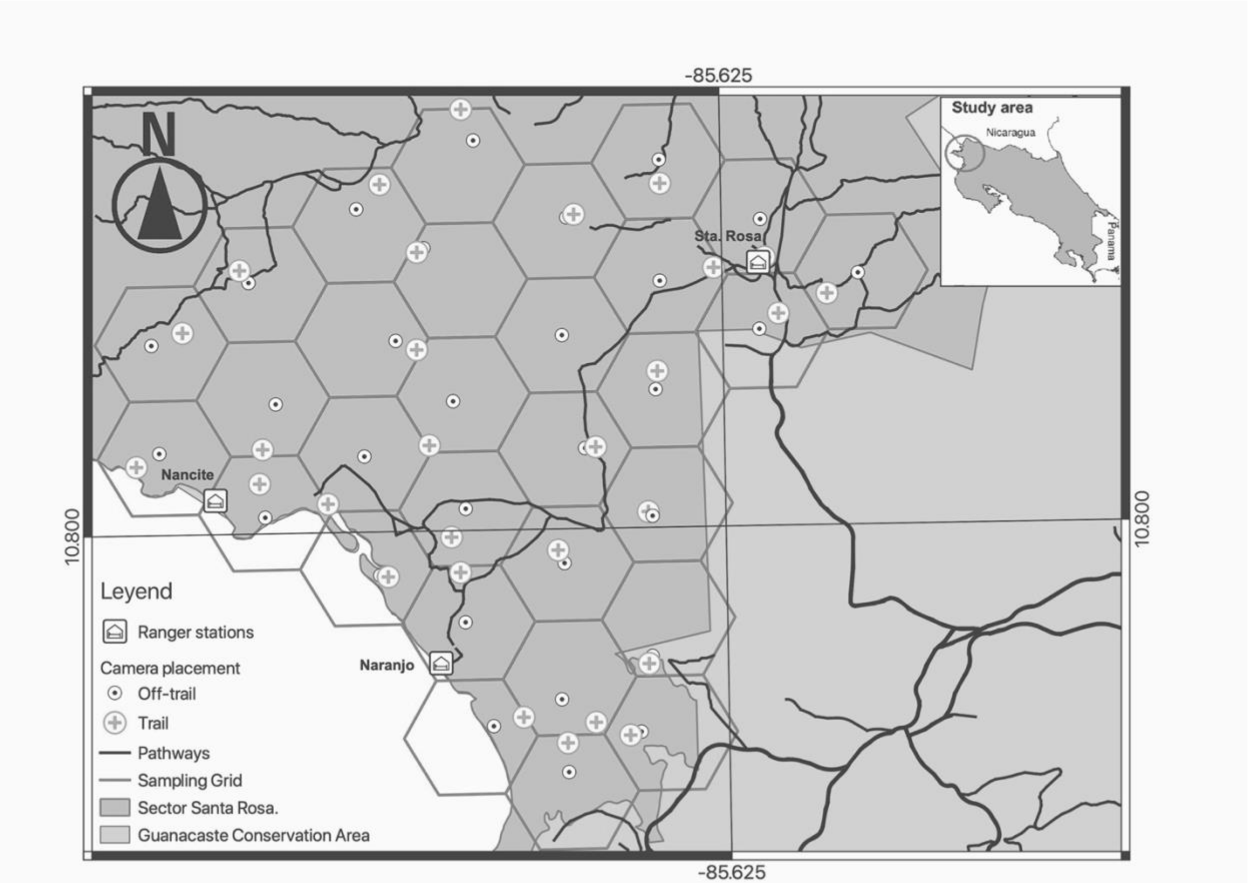

Figure 4.2 Camera trap deployment array at off-trail (n=28) and trial (n=28) locations in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

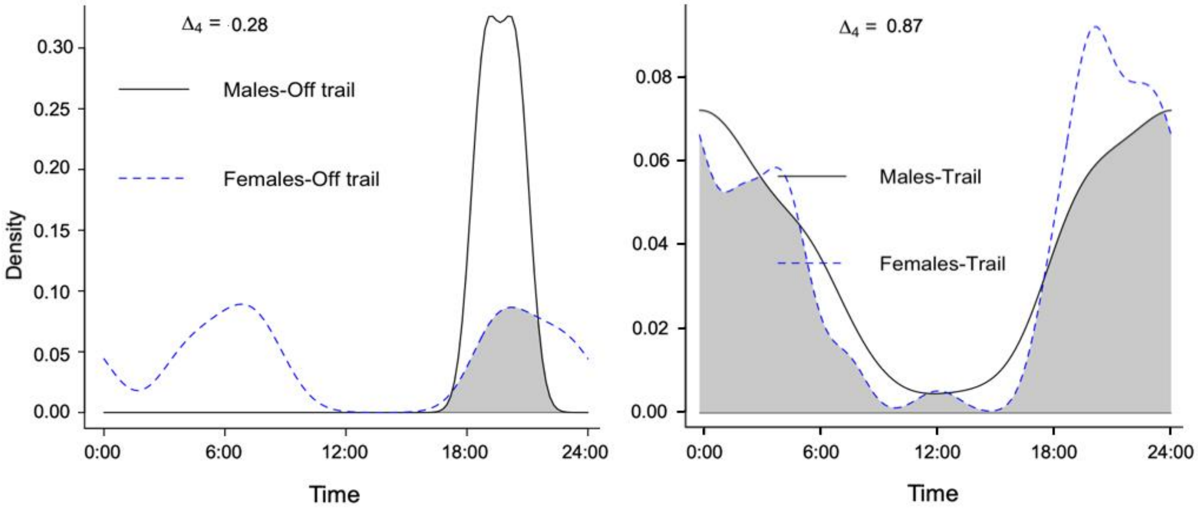

Figure 4.3 A) Jaguar (*P. onca*) males and females activity overlap at off-trail camera locations. B) Jaguar (*P. onca*) males and females activity overlap at trail camera locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica

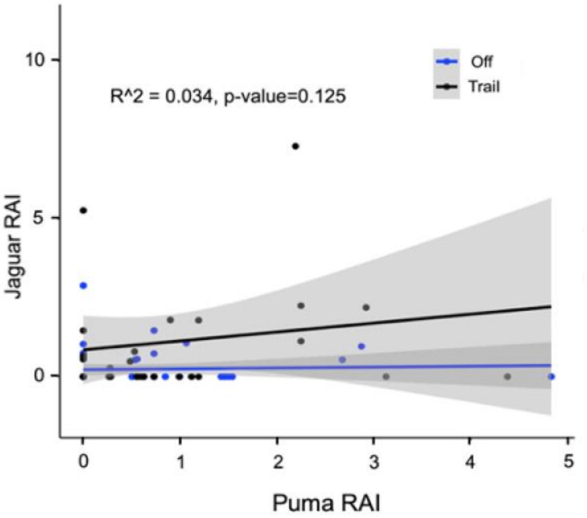

Figure 4.4 A) Jaguar (*P. onca*) and puma (*P. concolor*) relative abundance index (RAI) correlation at off-trail/trail camera trap locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

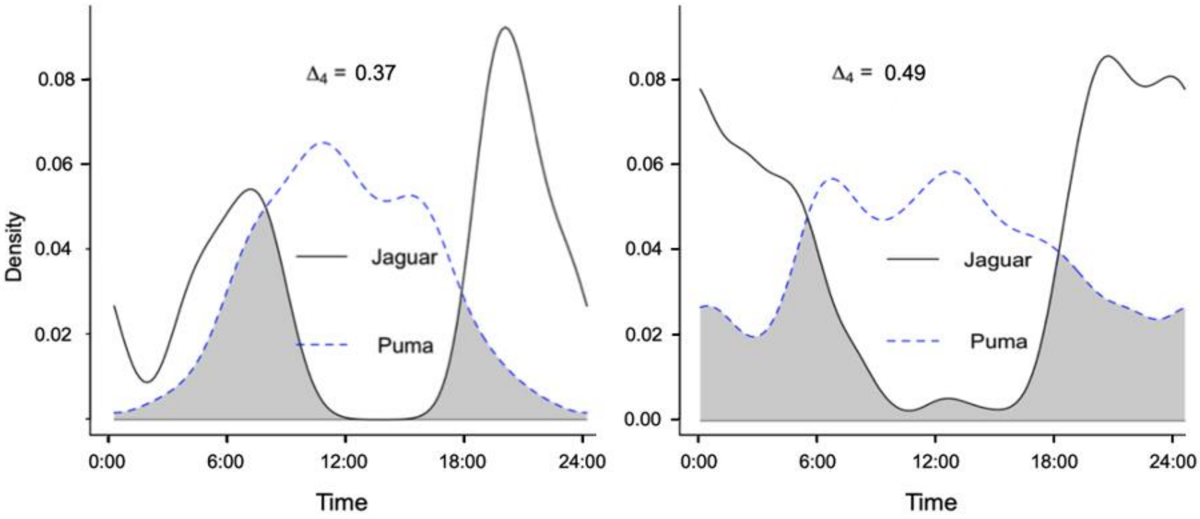

Figure 4.5 A) Jaguar (*P. onca*) and puma (*P. concolor*) activity overlap at off-trail camera locations. B) Jaguar (*P. onca*) and puma (*P. concolor)* activity overlap at trail camera locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

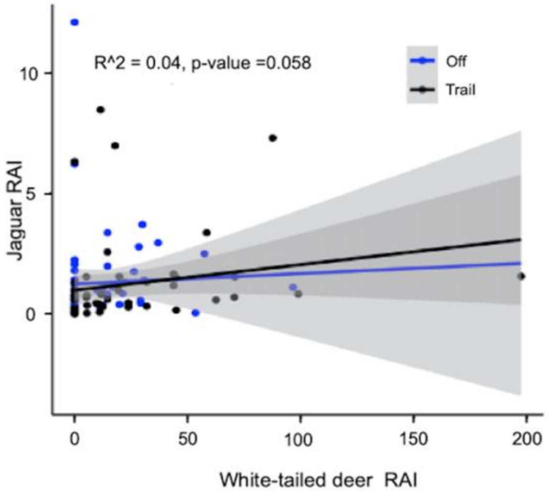

Figure 4.6 A) Jaguar (*P. onca*) and white-tailed deer (*O. virginianus*) relative abundance index (RAI) correlation at off-trail/trail camera trap locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

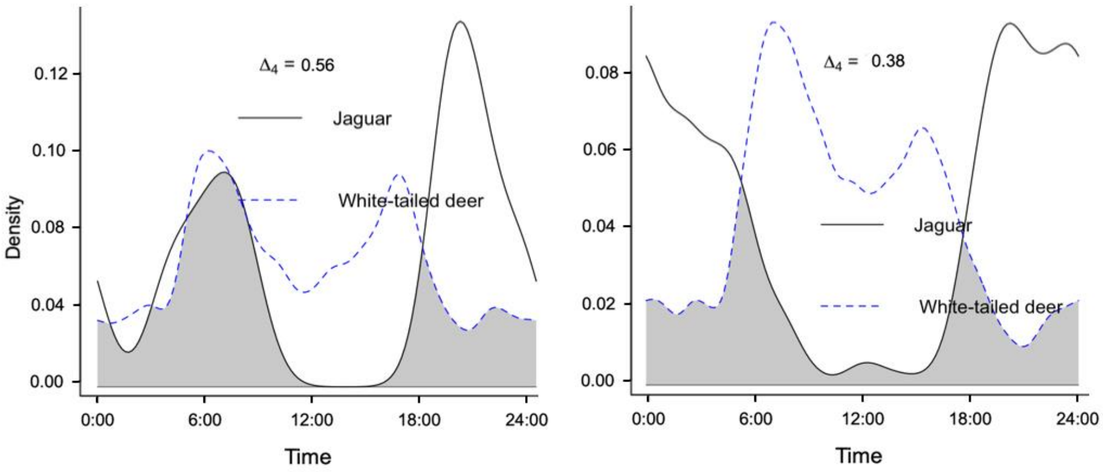

Figure 4.7 A) Jaguar (*P. onca*) and white-tailed deer (*O. virginianus*) activity overlap at off-trail camera locations. B) Jaguar (*P. onca*) and white-tailed deer (*O. virginianus*) activity overlap at trail camera locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

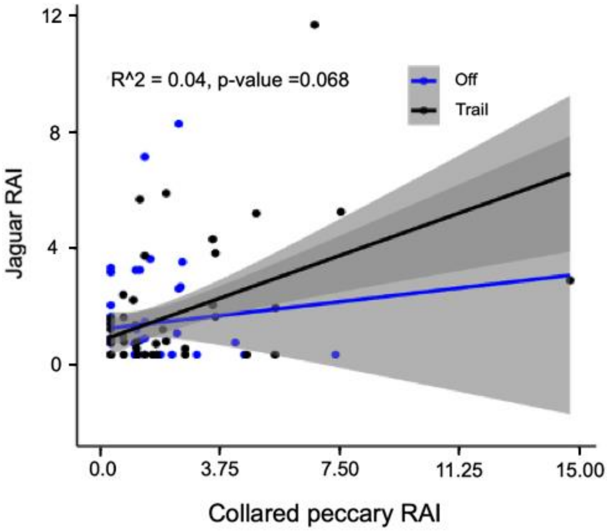

Figure 4.8 Jaguar (*P. onca*) and collared peccary (*P.tajacu*) relative abundance index (RAI) correlation at off-trail/trail camera trap locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

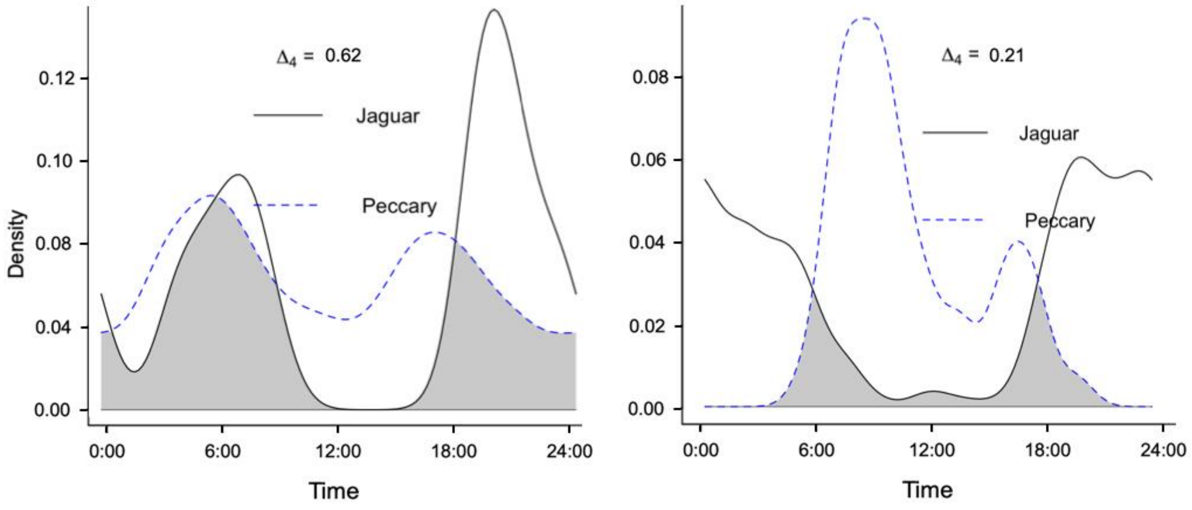

Figure 4.9 A) Jaguar (*P. onca*) and collared peccary (*P.tajacu*) activity overlap at off-trail camera locations. B) Jaguar (*P. onca*) and collared peccary (*P.tajacu*) activity overlap at trail camera locations. Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

CHAPTER 5

THE USE OF CAMERA TRAP AND SATELLITE TELEMETRY TECHNIQUE TO ESTIMATE JAGUAR (*Panthera onca*) POPULATION STRUCTURE IN NORTHWESTERN COSTA RICA

Abstract

Due to the elusiveness and rarity of jaguar (*Panthera onca*), conducting field studies on their ecology and behavior are difficult due to logistical constraints. Nevertheless, regular evaluations of a local jaguar population's status is an important part of conservation decision-making. Currently, camera trapping has become a standard method commonly used to elucidate jaguar abundance and demographic parameters, though evidence have shown sex ratio biases and density overestimates. In this study, we used camera trap location placement on and off trials to estimate jaguar population structure, combined with satellite telemetry data from one female jaguar, in Santa Rosa Sector to improve further jaguar population studies. We analyzed camera trap data from four season surveys conducted from June 2016 – June 2017 in order to apply spatial capture-recapture density estimates for jaguar. A total of 19 individual jaguars were detected (11 males; 8 females) with a resulting estimated population density of 2.6/100 km^2 (95% [CI] 1.7 – 4.0) jaguar females, and 5.0/100 km^2 jaguar males (95% [CI] 3.4 – 7.4). Based on telemetry and camera trap data, camera placement might bias individual detections by sex and thus density estimates. We recommend population assessments be made at several consecutive 3-month intervals, that intra-camera distance be increased to cover larger areas (so as not to restrict surveys to one or two individual home ranges, as in our case), and to carry out long-term camera monitoring programs instead of short-term studies to better support jaguar conservation strategies.

Introduction

Most carnivores over the world are elusive and solitary species (Sunquist and Sunquist 2002), thus monitoring such difficult-to-detect species is a challenge to answering ecological questions. The estimation of population parameters of endangered species is crucial to understand their ecology and distribution (Balme et al. 2009; O'Connell et al 2011), thus appropriate conservation strategies required accurate and trustworthy information (Tobler et al. 2013; Horn et al. 2020). Several non-invasive methods such as DNA analysis of scats or hair, camera trapping, and acoustic assessments, allow "capturing" individuals with minimal or no handling stress (Silver et al. 2004; Borchers et al. 2014; Royle et al. 2014); this compared to other techniques that involve physical capturing; e.g., telemetry and other animal tagging (Rabinowitz and Nottingham 1986; Morato et al. 2016). Jaguars (*Panthera onca*) are the largest felid in the Neotropics (Seymour 1989) and also a near threatened species (IUCN 2020) roughly inhabiting 50% of their original historic range distribution (Sanderson et al. 2002). Though jaguars play a key role in the ecosystem dynamics by balancing ecosystem services and ecological processes (Sunquist and Sunquist 2002; Estes et al. 2011), their local populations are threatened and vulnerable than one might expected (De la Torre et al. 2017). Therefore, regular evaluations of local jaguar populations' status are an important part of conservation decision-making.

Due to the elusiveness and rarity of jaguars, conduct of field studies on their ecology and behavior are difficult (Rabinowitz and Nottingham 1986; Salom et al. 2007). Often, camera traps are recommended to study elusive mammals like tigers (*Panthera tigris*) and jaguars (Karrant et al. 1995; Silver et al. 2004; O'Connell et al 2011; Rovero and Zimmermann 2016). Currently camera traps have become a standard method commonly used to elucidate jaguar abundance and demographic parameters (Silver et al. 2004; O'Connell et al. 2011; Royle et al. 2014) using their distinctive and unique rosette patterns (Silver et al. 2004; Borchers et al. 2014) with capture-recapture methods (Otis et al. 1978; Royle et al. 2014; Jędrzejewski et al. 2017). Although simultaneous comparison and adjustments of jaguar population estimates with satellite telemetry are limited (Soisalo and Cavancanti 2006; Nuñez-Perez 2011), evidence has shown sex ratio biases and density overestimates derived from camera trap data (Conde et al. 2010). Also, scale bias due the use of camera traps in small areas (Balme et al. 2009; <100 km^2) hinders accurate density estimation. Previous capture-recapture (CR) jaguar density estimates indicated the overestimation of jaguar density by 70% when contrasting simultaneous satellite-telemetry tracking and camera trapping (Soisalo and Cavancanti 2006); other studies showed discrepancies (Nuñez-Perez 2011).

Here, we describe jaguar populations in the Santa Rosa Sector of Guanacaste National Park in the dry forest of northwestern Costa Rica using camera traps and spatial capture-recapture methods (SCR; Sutherland et al. 2019), along with satellite telemetry data from one female jaguar. We examined the relationship of trail and off-trail camera placement on population density estimates, as well as how the sex-bias incurred by camera placement might affect detection rates of individuals and thus estimates of population structure. We compare camera traps estimates of density with those derived from satellite telemetry data, and make conservation and methodological recommendations to improve future jaguar population estimates.

Materials and Methods

Study area

This study was conducted in the Santa Rosa sector of the Guanacaste Conservation Area located in northwest Costa Rica (10°53′01″N 85°46′30″W; Boza, 1992). Santa Rosa encompasses 387 km^2 and is dominated by some of the last remaining tropical dry forests in Central America (Janzen 1988; Gillespie et al. 2000). Average annual rainfall is 1,600 mm that is highly seasonal (monthly averages from 0 mm to 1040 mm). The wet season (months with $\geq$ 40mm of rain) is May to November, and the dry season (with almost no rain and temperatures over 37°C) is December to April. Due the rarity of dry forest ecosystems, a large-scale restoration effort was initiated in the 1980's involving protected area status, the recovery of abandoned pastures by active fire suppression (Klemens et al. 2011), protection from many human activities, and also the recovering of large vertebrate populations. In Santa Rosa there are two important sea turtle nesting beaches: Playa Nancite (length = 1.05 km) where massive numbers of turtles come ashore during the wet season (Fonseca et al. 2009); Playa Naranjo (length = 5.64 km) where turtle nesting occurs year-round, but increases during the wet months (Drake et al. 2003). As important prey item, turtle nesting peaks influence the movement and behavior of jaguars in the area (Montalvo et al. 2020).

Data collection

From 15 June 2016 to 13 June 2017, we conducted a constant camera trap effort (trap nights) in Santa Rosa. Fifty-eight automatic trail cameras (Bushnell®, Trophy Cam models 119436, 119446, 119456) were deployed in 29 hexagons in a grid array of 3 km^2 each (Fig. 5.1). Half of the cameras were located in a trail location that jaguars were likely to use and the other half at an off-trail location (one camera per site) within 200 m of each hexagon centroid (Fig. 5.1). The total camera array covered an area of 105 km^2.

Each camera was affixed to a tree at a height of ~40 cm and set to be active for 24 h/day in photo mode with a minimum delay of 1 sec between consecutive triggers. Once deployed, cameras were checked on average every month to replace batteries and change SD memory cards, if necessary. For each camera deployment, we recorded the location and camera operation dates.

We identified jaguars based on individual spot patterns (Silver et al. 2004), classifying sex (male, female, unknown), age (cub, young, adult), and whether individuals were collared or not collared. Adults were sexed by presence/absence of testicles and nipples (Jędrzejewski et al. 2017) and aged by their size and physical appearance to categories of cubs (<12 m), young (12-24 m), and adults (>24 months; Jędrzejewski et al. 2017).

Density estimation

For adult jaguar density estimates we used the package oSCR version 0.42 (Sutherland et al. 2019) in R version 3.3.2 (R core team 2016). The oSCR package is based on spatial capture models of *N* individuals associated to specific location patterns that represent the center of activity, as well as the specific probability of observing one individual relating to the distance from other individuals center of activity (Sutherland et al. 2019). Also allowing to build models with class sex population information (Royle et al. 2015) and multiple- seasons in the model's structure (Sutherland et al. 2019). In this study we used season, sex structure, and camera placement (trail/off-trail) to investigate their effects on population density (*D*), the baseline encounter rate (*p*), and space use (*sigma*) (Table 5.1). The area within the distribution of individual activity centers assumed to be randomly distributed is known as state space (*S*) and was created using a buffer area three times *sigma* (6,000 m) around the camera array, with 0.5 x 0.5 km resolution (Sutherland et al. 2019). Candidate models that represented hypothesis analyzed were evaluated using the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002), and throughout model comparison we determined the most plausible models due AICc differences (ΔAICc) and weights (*W*). If a model included single effect that do not reduce the AICc value compared with a null model (model response ~ 1) were not considered as supportive effect.

Satellite telemetry and camera trap data

In order to identify potential sources of bias between satellite telemetry and camera trap data that potentially affects population estimates, we used a previous dataset (N = 5,924 locations) of a collared jaguar female in the same study area (Montalvo et al. 2020). Additionally, descriptive statistics from camera trap and telemetry data within this array were used to depict the population structure and whether camera traps inside the *S* area effectively detected this collared female.

Results

Camera trapping and individual detection

A total effort of 18,170 continuous trap nights yielded 948 identifiable jaguar photos, resulting in 188 independent identifiable jaguar photo captures, and 19 different jaguar individuals (females = 8, males = 11). Camera trap efforts were constant across sampling seasons (Table 5.1), recording average 1.2 independent jaguar photo captures/100 trap nights. The total number of jaguar captures registered was frequently high (91%) at trail locations (Table 5.2) compared to off trail locations (9%), detecting both jaguar females (Figure 5.2) and males (Fig. 5.3) mostly near (<1 km) the coast line. The accumulated number of different jaguar individuals across sampling days reported more jaguar individuals at trail camera locations; however, male numbers were high (Fig. 5.4) compared to female individuals, and for such off-trail locations jaguar individuals were registered less often than at trail camera locations; nevertheless, female individuals there were recorded more frequently than males (Appendix 1.1). Monthly records of jaguar individuals were relatively constant during the sampling effort ($\bar{x} = 6$) except for in June (Fig. 5.5).

Density estimation

Model selection based on AIC (Table 5.3) showed as top model the one assuming constant density (D), encounter rates (p) that varied sex, and camera location, as well as specific sex and session on space use (*Sigma*)(AIC:2526, *w*: 0.98). Maximum likelihood parameter estimates of top model on real scale showed a density of 7.7 (95% [CI] 5.1 – 11.5) jaguars per 100 km^2, segregated in 2.6 (95% [CI] 1.7 – 4.0) female jaguars per 100 km^2 and 5.0 male jaguars (95% [CI] 3.4 – 7.4) per 100 km^2 (Fig. 5.6), and additional probability of being a male (Ψ Prob) of 0.656 (Table 5.4).

Variation in baseline detection rates showed male jaguars at off trail locations ($p = 0.0003$; 95%CI = 0.0001 – 0.001) were significantly lower than females ($p = 0.002$; 95%CI = 0.002 – 0.005). Overall, jaguar baseline detection rates were significantly higher at trail locations than off trail locations (Fig. 5.7); nonetheless, female jaguars (0.0247; 95%CI = 0.009 – 0.0681) and male jaguars (0.004; 95% CI = 0.0007 – 0.0018) detection rates were not statistically different at either location type. Estimated average spatial scale parameter (*sigma*) was 2,102 m (95%CI = 1691.2– 2617.6) and showed unequal space use; male jaguars use was greater than that of female jaguars, with some variation across sessions (Fig. 5.8).

Camera trap and satellite telemetry data consistency

Our camera trap array embraced almost 95% of the home range of the collared female jaguar; nevertheless, her image was recorded at only 13 camera locations (Fig. 5.9), mostly near the coast line. The capture ratio of the collared female jaguar to other jaguar individuals was similar each month (1:1.0-3.0; mean = 1.58), except for December (1:14); this means that, on average, there were about 2.6 jaguar “units” within the female’s 89-km^2 range, and thus a density of only 2.9 individuals/100 km^2 in any months (vs. a camera-trap estimate of 7.6/100km^2). In each month, photos of at least 1 other female and 1 or more males were recorded within the collared female’s range. Comparison of satellite telemetry locations within multiple nested buffer distancing ratios around cameras deployed at trail and off trail locations showed the high number of cumulated locations at trail camera deployments (Fig. 5.11), though the monitored female spent most time at off trail locations based on telemetry data.

Discussion

This study provides a fine scale robust jaguar population structure estimate, taking into account the methodological constraints of site placement and sex biased, by contrasting camera trap results with data from one collared female jaguar in the tropical dry forest ecosystem.

Jaguar population estimates that address the effect of detectability and sample size are numerous (Maffei et al. 2011); however, few density studies delve further in bias linked to detection as result of individual sex or camera location. For example, Harmsen et al. (2010) found male jaguars are associated with wide trails as easily accessible travel routes, whereas female jaguars use both trails and dense forest areas the same, hypothesizing that dense forest provides alternative travel routes to avoid cub infanticide by dominant males. For tigers (*Panthera tigris*) in India, a similar pattern was identified in density studies; depending on sex and age, photo rates decreased or increased, assuming old well-established tigers moved freely and submissive individuals avoid encountering them (Karranth et al. 2011; Chimbioputo et al. 2018). Our findings indicated high numbers of male jaguars at trails, opposite to that of females who used off trail locations more often; this is the same pattern observed in Venezuela in a year-round jaguar density study where females with cubs avoided places highly frequented by unrelated individuals (Jędrzejewski et al. 2017). In our study we did not registered female jaguars with offspring, but previous sampling efforts showed some females without cubs frequently photographed on trails, and feeding their cubs at sea turtle prey sites many times during the same month.

Jaguar density estimates did not fluctuate significantly across four seasons during the sample year; therefore, we report an average density estimated of ~7.7 jaguars/ 100 km^2. Previous jaguar estimates in Santa Rosa reported ~2.23 jaguars/100 km^2, using non-spatially-explicit methods (Alfaro 2006), whereas other studies did not register enough individual records to perform CR models (Montalvo et al. [2015] recorded only two juvenile males and two females). Compared with prior efforts, current jaguar population numbers at Santa Rosa showed a relative high density, presumably because of the recovery of prey populations, as well as the availability of sea turtles at most Santa Rosa beaches (Janzen 1988; Alfaro et al. 2016), where sea turtles are significant low-cost reward (MacArthur and Pianka 1966; Montalvo et al. 2020).

With regard sex-specific jaguar density, we found differences for males ($\bar{x}$ = 5.0 jaguars/ 100 km^2) and females ($\bar{x}$ =2.6 jaguars/ 100 km^2), a pattern previously reported in high density areas in South America (Maffei et al. 2011; Tobler et al. 2013). The baseline encounter rates for jaguar males and females at trail and off trail locations showed that, though female jaguars were the less abundant, they more likely to be photographed at both camera placements. Jędrzejewski et al. (2017) found jaguar females without offspring are less shy and likely to visit same places as males. Additionally, the findings observed in this study are consistent with other taxa where camera location placement influenced photo rates results, as well as species detection (Cusack et al. 2015; Cloyed et al. 2018), highlighting strong methodological constraints as result of ignored behavior patterns. Jaguar males seems to walk longer distances than jaguar females based on camera trap data, similar to what Morato et al. (2016) found for regional data movement analysis; jaguar males tend use larger areas than do females.

Telemetry home range data of a collared female identified intense space use that almost fit our camera array area. Despite this, the female used trail locations the most, and thus camera placement at trail locations could increase significantly the detections chances of this collared female. Though camera site placement at trail locations might shade patterns of distribution or intra specific interactions, the use of camera placement at trail locations could improve detection of individuals as CR field arrays (Karanth 1995; Silver 2004). Additional home range of collared female showed a constant number of individuals ($\bar{x} = 3$) detected in our camera array that did not vary monthly, suggesting different sex individuals occasionally overlap home ranges during the year, potentially affecting the detection of individuals for population estimates as a fact of sampling extent due some individuals temporally use or avoid specific areas as long as territorial individuals are present (Soisalo and Cavancanti 2006; Nuñes-Péres 2011).

These findings suggest that camera location arrangement might influence final results in highly seasonal ecosystems, especially for estimates that do not accounting for sex and camera placement as covariates, resulting in biased estimates. Though most camera trap studies ignore the effects of camera placement on estimates (abundance, population index and richness), animal distribution and movements follow non-random patterns, therefore, standardizing and classifying placements sites regardless the ecosystem is important, thus these finding can be extrapolated to other ecosystems using camera trapping in conservation studies.

Our results also recommend the use of SCR as a robust method to estimate jaguar populations as long as the frequency of occurrence of jaguar individuals is high enough to allow use of the modeling tools. The jaguar population estimates at Santa Rosa suggests that the jaguar population might have increased in recent years, identifying it as an important jaguar conservation hotspot in the Costa Rica. Based on our detection rates, further jaguar population estimates at Santa Rosa should occur in time periods >3 months, and camera coverage of larger areas that do not restrict the study to one or two individual home ranges.

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Table 5.1 Sampling effort for a jaguar camera trap density study in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

Session	Period	Trap array (Km^2)	State space (Km^2)	No. of camera stations			Trap nights	No. of occasions	No. of ind.	Average cap.	Spatial cap.
				Trail	Off-trail	Sum					
1	15-Jun--14 Sep 2016	105	160	29	29	58	4394	92	16	3.69	1.75
2	15 Sep--14 Dec 2016	105	160	29	27	56	4954	91	13	4	2.08
3	15 Dec--14 Mar 2017	105	160	28	27	55	4857	90	10	3.7	1.8
4	15 Mar--13 Jun 2017	105	160	28	27	55	3965	91	11	3.45	1.73

Table 5.2 Jaguar individual captures registered at different camera placement locations (trail/off-trail) in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

ID Individual	Sex	Camera placement loc.	
		Trail	Off-trail
Jaguar01	F	59	11
Jaguar02	F	28	1
Jaguar04	F	8	---
Jaguar11	F	3	---
Jaguar13	F	2	---
Jaguar16	F	2	---
Jaguar08	F	1	---
Jaguar19	F	---	1
Jaguar03	M	29	---
Jaguar12	M	12	---
Jaguar10	M	7	---
Jaguar15	M	5	1
Jaguar09	M	4	---
Jaguar14	M	3	---
Jaguar18	M	---	3
Jaguar17	M	2	---
Jaguar05	M	2	---

Jaguar06	M	2	---
Jaguar07	M	2	---

Table 5.3 Model selection results for 11 candidate models analyzed including: session effects (session), male/female sex effect(sex), trail/off trail camera location (loc) and constant effect (~1), in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

Density	Detection	Space use	K	AIC	Delta AIC	Weight	Cum. weight
D (~1)	***p(~sex + loc)***	***sig(~session + sex)***	***10***	***2556***	***0***	***0.98***	***0.98***
D (~session)	p(~sex + loc)	sig(~session)	12	2564	7.7	0.19	0.99
D (~1)	p(~sex + loc)	sig(~1)	6	2567	11.2	0.001	1
D (~session)	p(~loc)	sig(~sex)	9	2614	57.6	<0.001	1
D (~1)	p(~sex)	sig(~session)	8	2693	137.1	<0.001	1
D (~1)	p(~sex+ session)	sig(~session)	11	2695	139.3	<0.001	1
D (~1)	p(~sex+ session)	sig(~1)	8	2704	148.1	<0.001	1
D (~1)	p(~session)	sig(~session)	10	2739	183.1	<0.001	1
D (~1)	p(~1)	sig(~session)	7	2742	185.9	<0.001	1
D (~1)	p(~1)	sig(~1)	4	2747	190.6	<0.001	1
D (~1)	p(~session)	sig(~1)	7	2752	196.2	<0.001	1

Table 5.4 Maximum likelihood parameters estimates from the top model of jaguar density, that included constant density D (~1), based line detection varied according to sex (sex) and trail/ off trail camera location (loc), sex- and session-specific space use: sig (~ session+ sex), and sex ratio Ψ, in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

Parameter	**Coefficient**	**SE**
p (intercept: female, off trail)	-5.94	0.286
p (male)	-1.898	0.284
p (trail)	2.265	0.255
sig (intercept: female, session 1)	7.656	0.077
sig (session 2)	-0.024	0.099
sig (session 3)	-0.353	0.118
sig (session 4)	-0.212	0.103
sig (male)	0.248	0.125
Density	-2.565	0.15
Ψ Prob	0.646	0.297

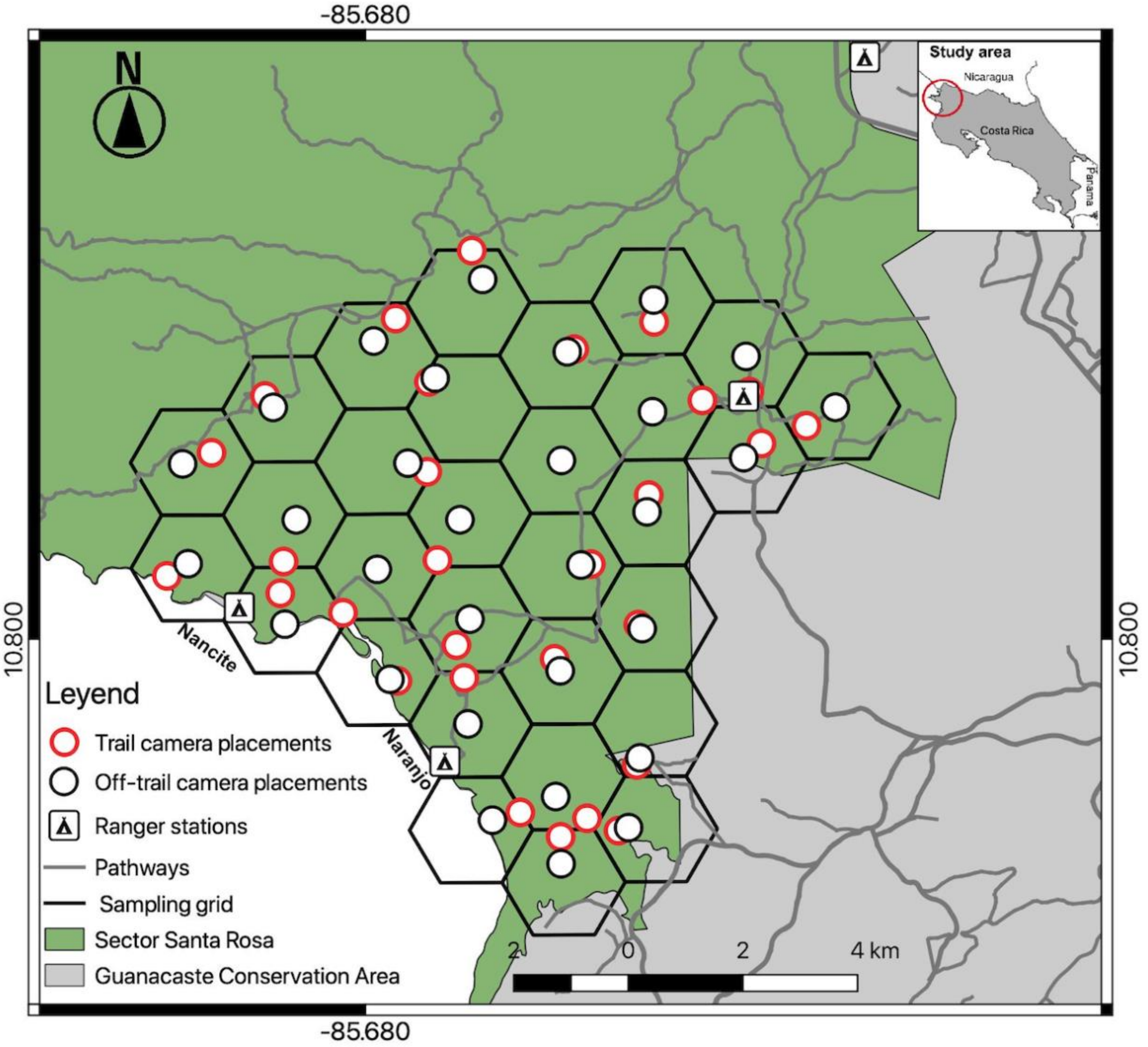

Figure 5.1 Camera trap deployment array at off-trail (n=29) and trial (n=29) locations in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

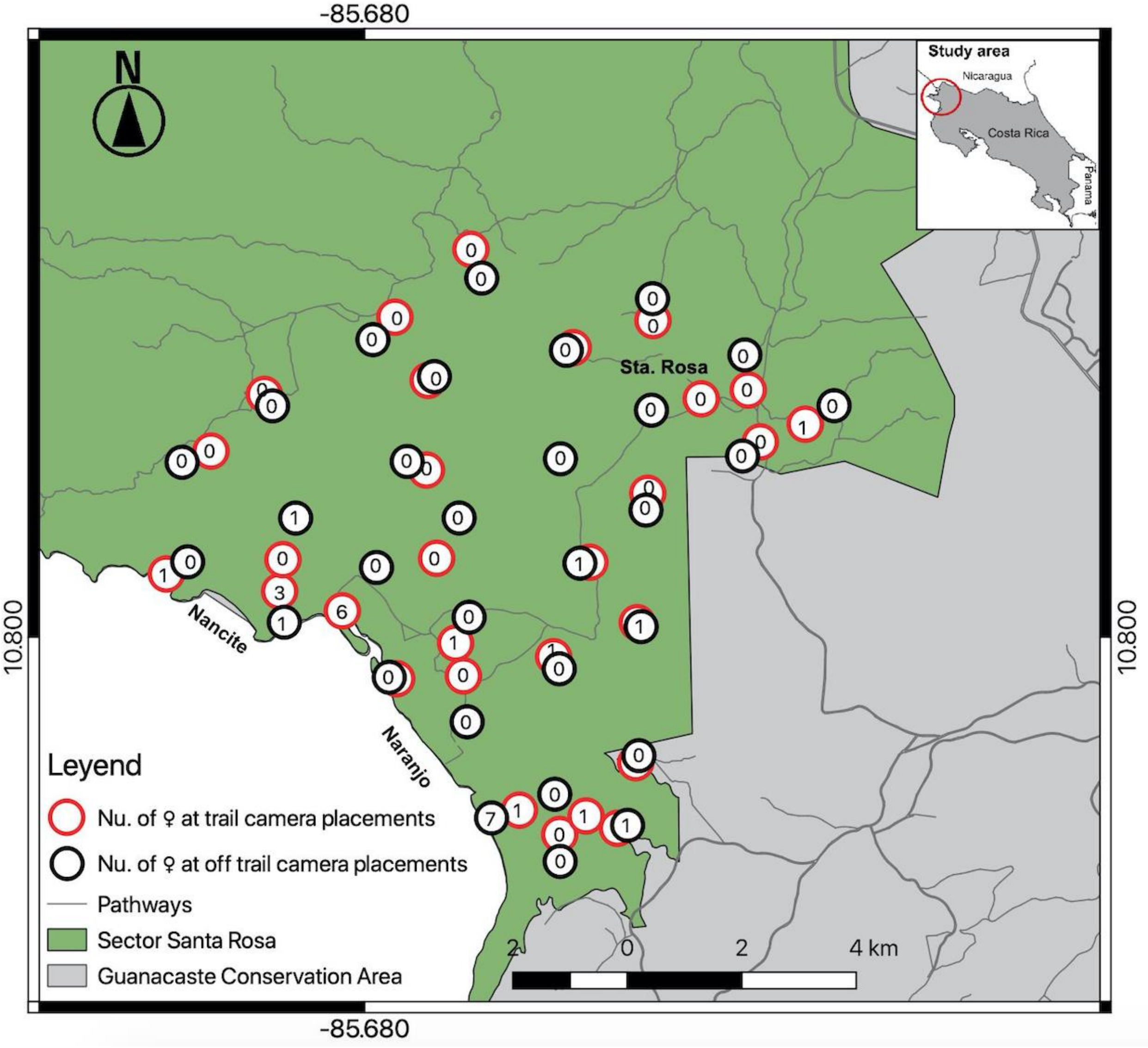

Figure 5.2. Spatial detections of different jaguar (♀) individuals at trail/off trial camera placement locations in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

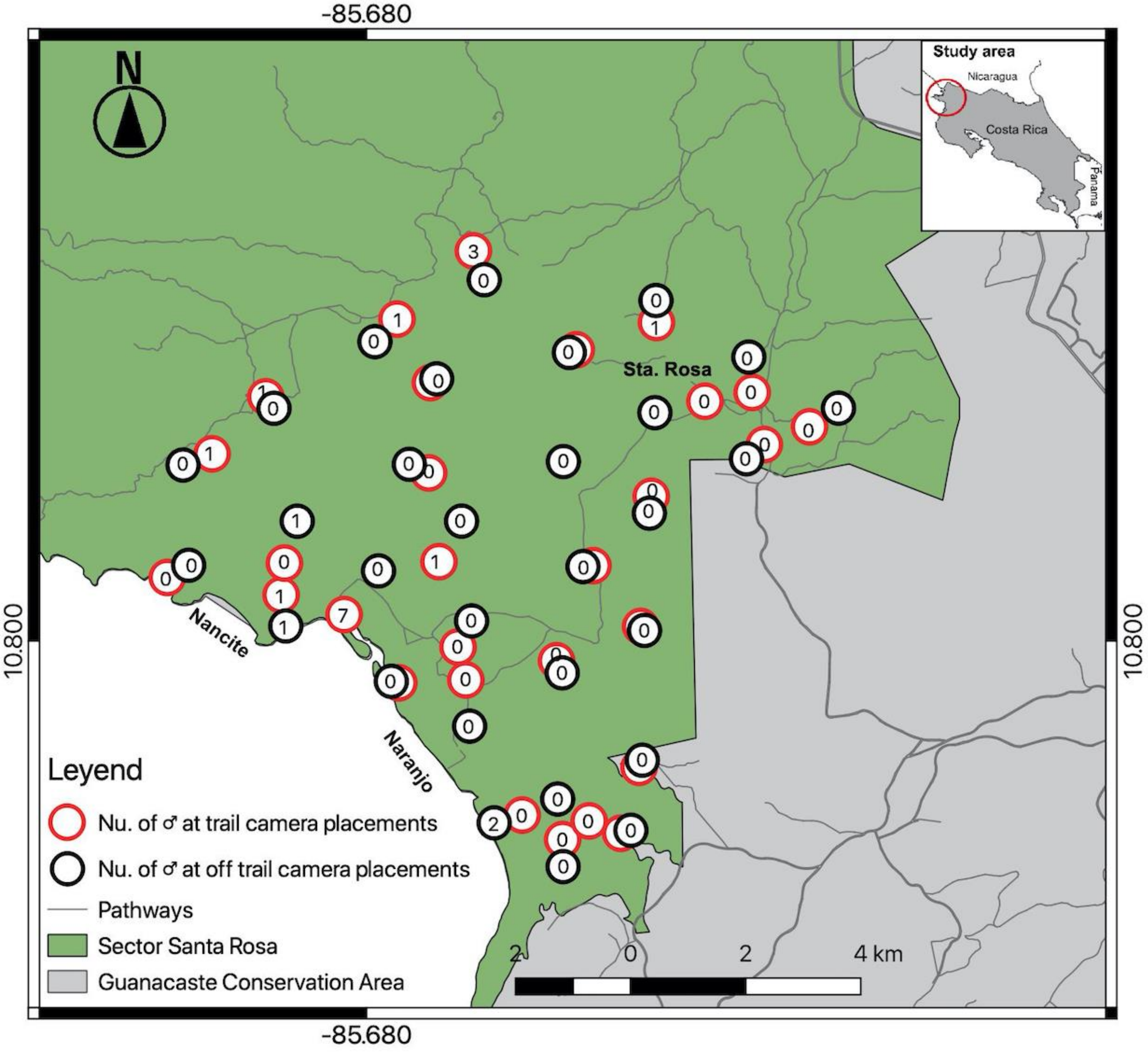

Figure 5.3 Spatial detections of different jaguar (♂) individuals at trail/off trial camera placement locations in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

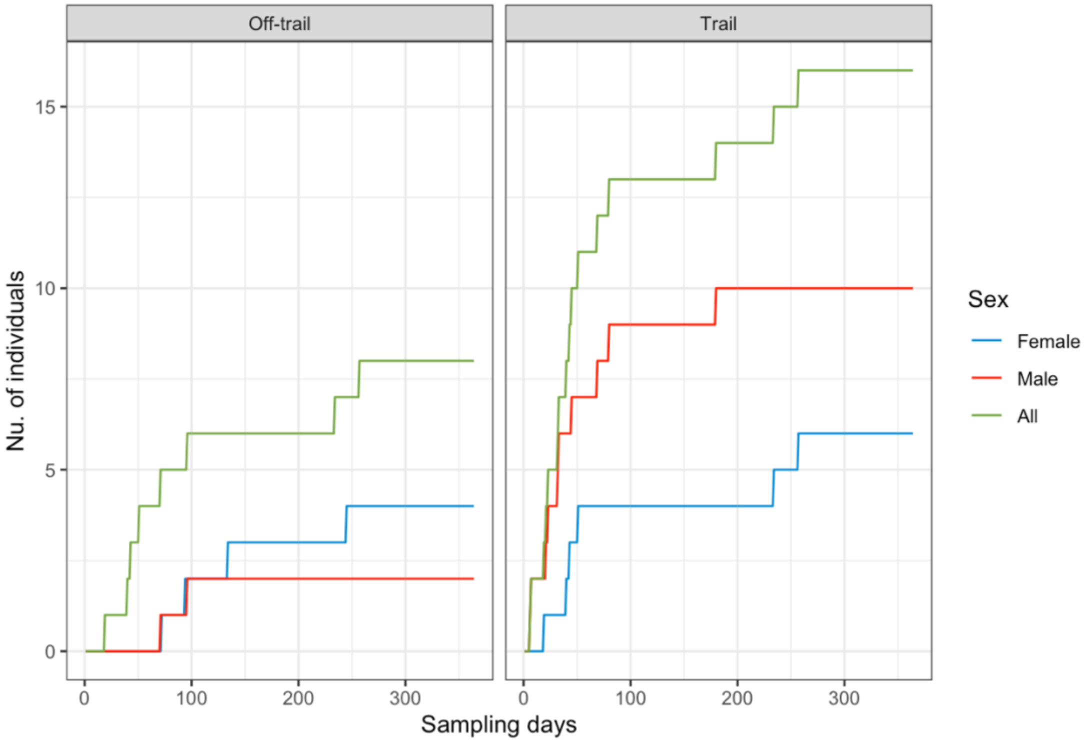

Figure 5.4 Accumulated number of jaguar individuals by sex at trail/off trail camera placement locations across sampling days for a jaguar camera trap density study in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

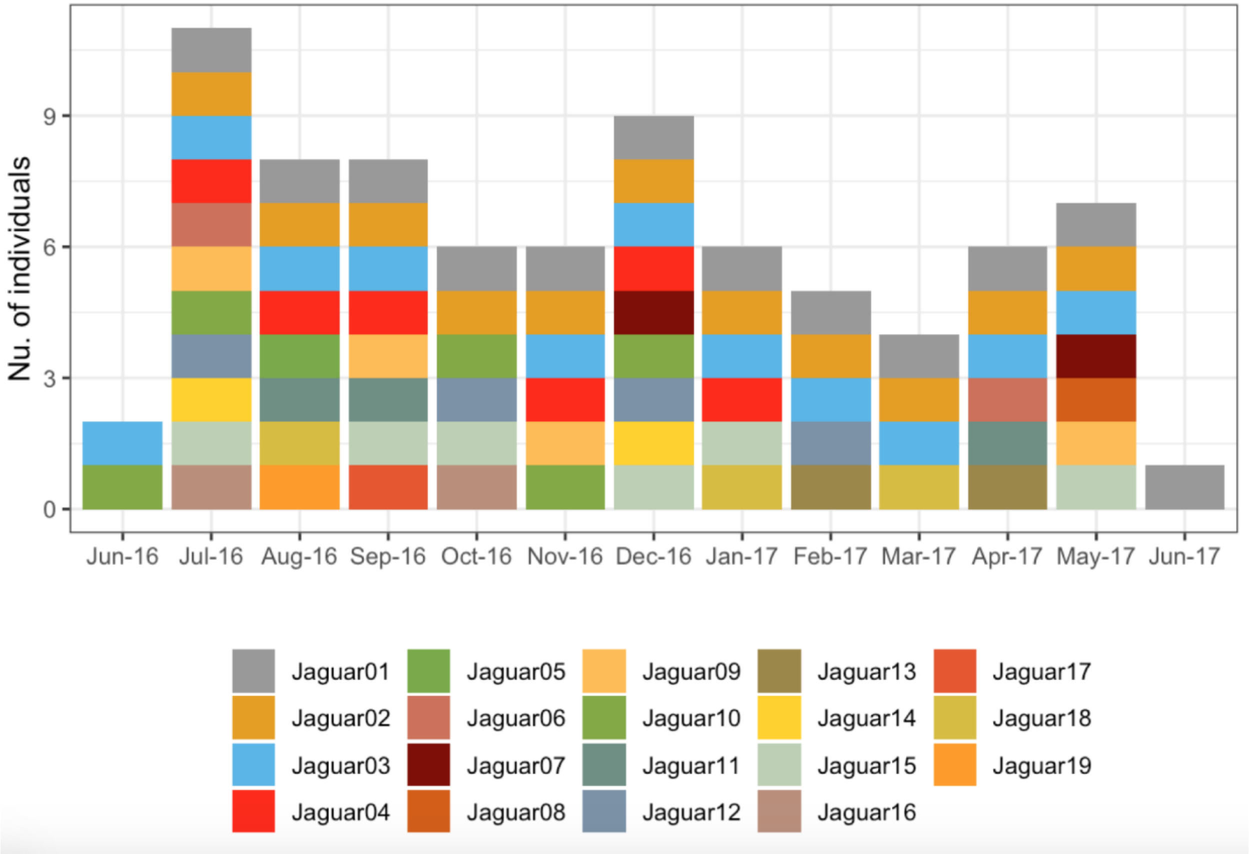

Figure 5.5 Monthly number of jaguar individuals registered in a camera trap density study in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

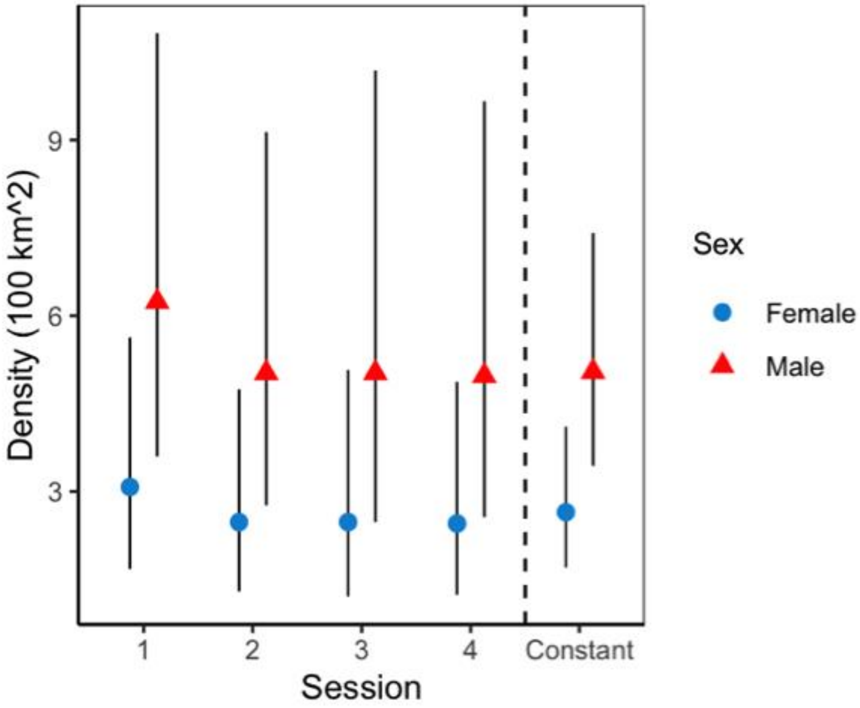

Figure 5.6. Sex/ session specific jaguar density, from top model structure in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica. The black line represents 95% confidence intervals.

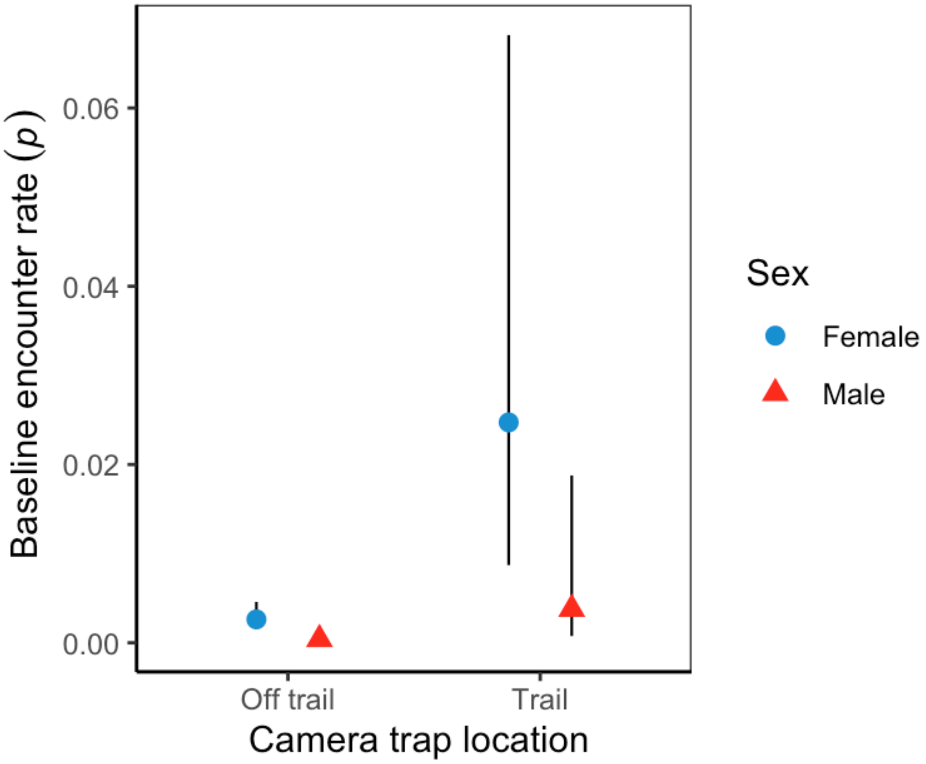

Figure 5.7. Sex/camera trap location-specific effect on jaguar baseline encounter rates, from top model structure in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica. The black line represents 95% confidence intervals.

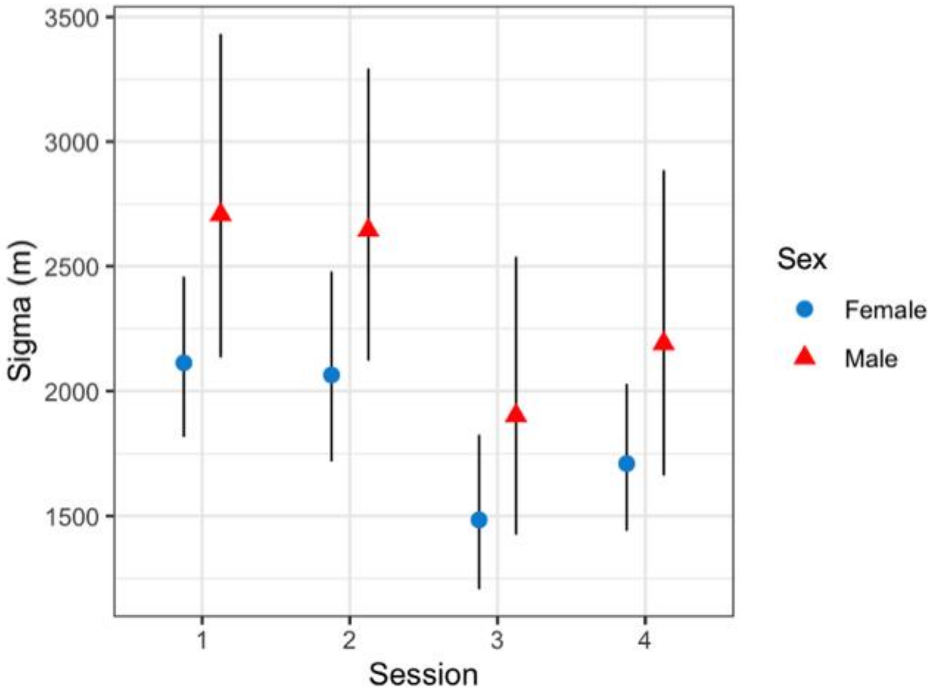

Figure 5.8. Sex/ season specific effect on jaguar sigma (m) from top model structure in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica. The black line represents 95% confidence intervals.

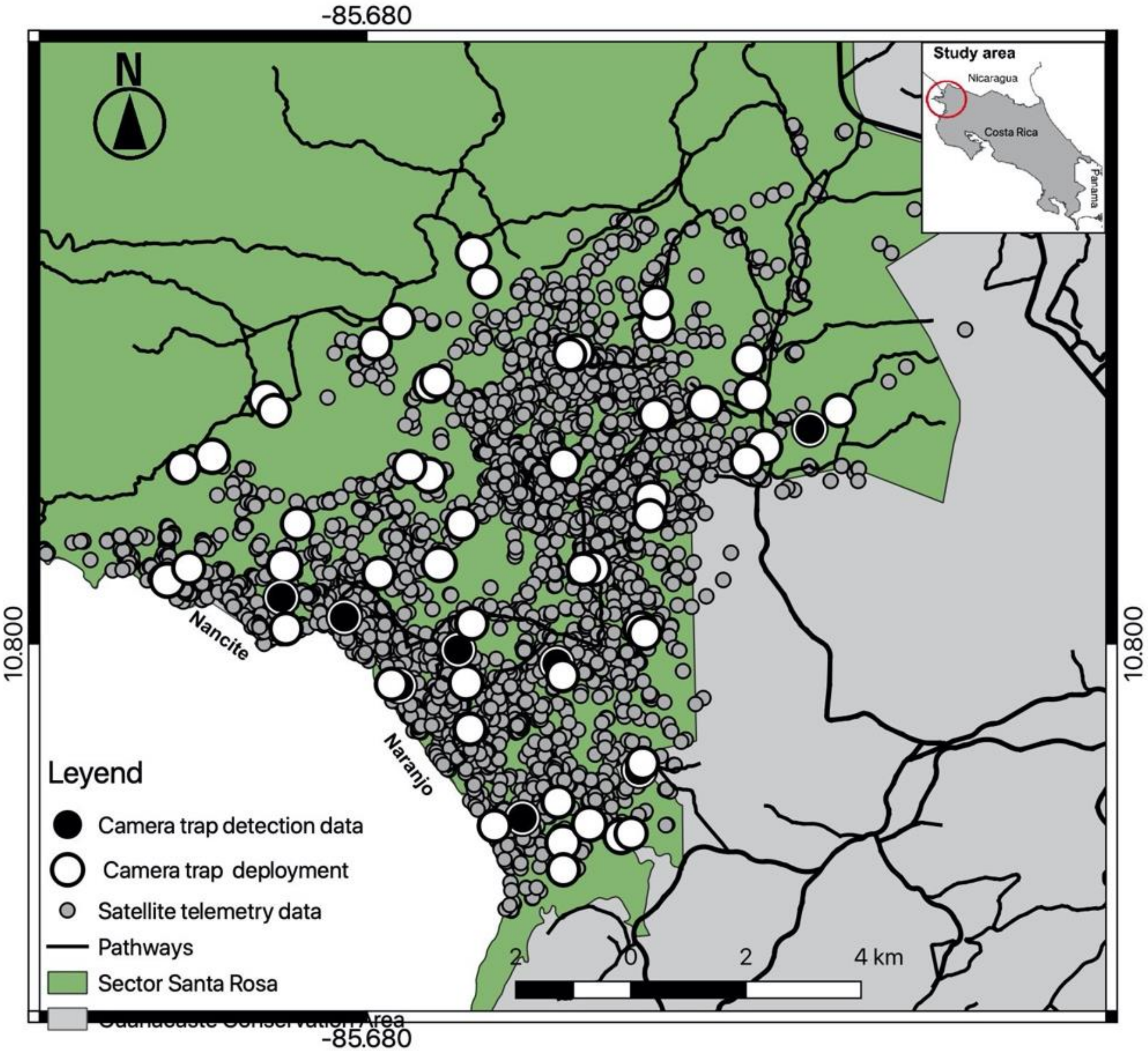

Figure 5.9. Spatial detections of collared female jaguar within camera trap density study, overlaid with satellite telemetry data for the same individual in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

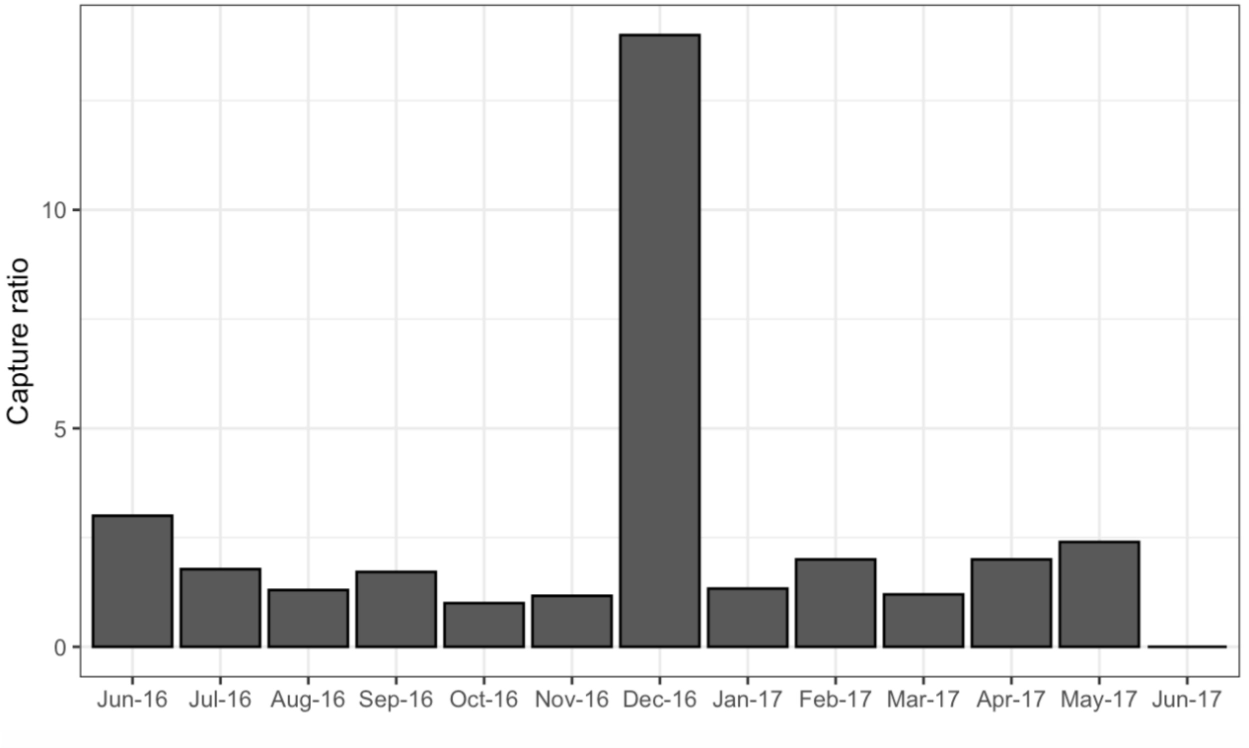

Figure 5.10 Monthly capture ratio of collared female jaguar captures related to the number of other jaguar individuals photo captured during the same month for a density study in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

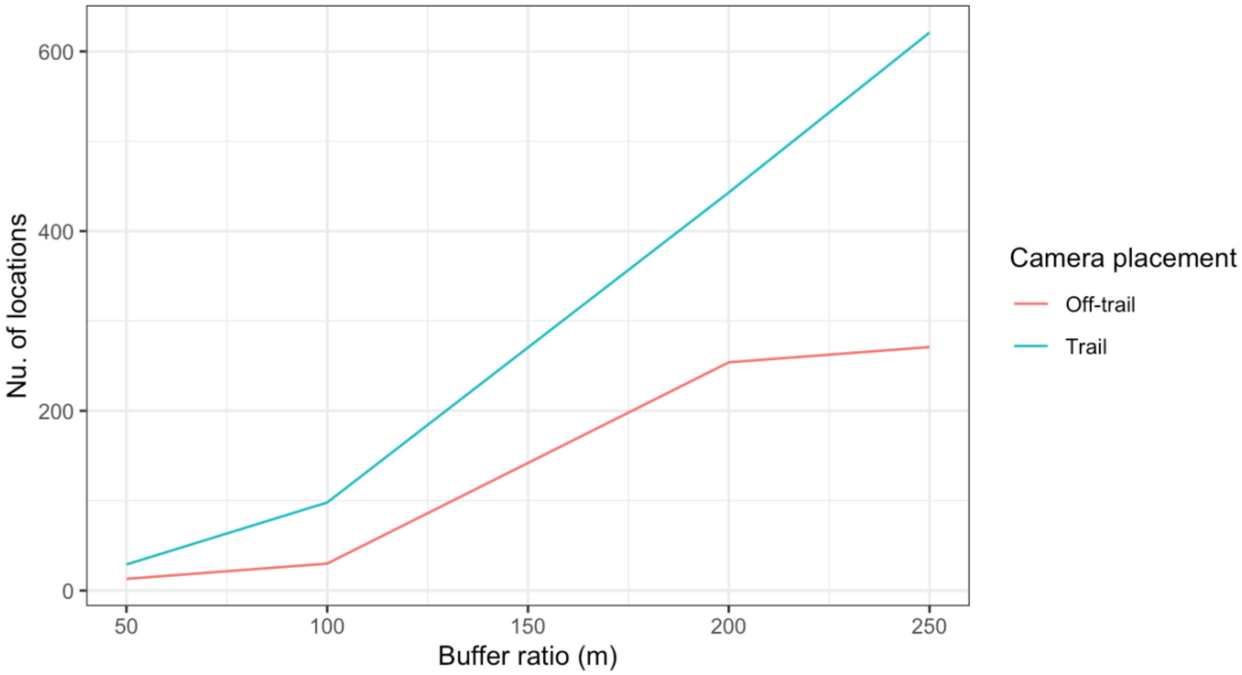

Figure 5.11 Number of satellite telemetry locations of a collared female jaguar, located within multiple buffer ratio distances around camera location placements (trail/off trail) in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

Tropical dry forest ecosystems in Costa Rica are endangered and rare. Therefore, protecting and restoring the few outstanding remnants of dry forest ecosystems are critical to maintain the longevity of ecological processes at all the trophic levels. For such a case, large vertebrates such as the jaguar and other interacting species need long term information to support previous and further conservation decision making. Though Guanacaste Conservation Area is ahead in conservation efforts in the country, there is still a lack information on large vertebrate population. This dissertation provided valuable ecological information, as well as some of the common shortcomings wildlife conservationist and managers must take into account to improve conservation of key species like jaguar.

This study showed modeling is a common and useful technique to elucidate jaguar distribution, and in the last decade the number of jaguar modeling distribution studies increased. Most of these studies within the jaguar distribution range indicated that numerous studies used variables suggested by previous studies citation and were limited by data availability (common layers from Geographic Information Systems), ignoring whether specific group of variables are significant. According to our literature review important variables inclukded hunting pressure, human activities, precipitation, temperature, vegetation type, conspecifics, prey, and distance to water. Jaguar modelers should avoid using non-significant variables to produce better models in the future and make better predictions in areas without quantitative jaguar data.

Our study also showed that in dry forest ecosystems water is a crucial resource, influencing large vertebrate behavior and habitat use. As a consequence of these pattern species photo rates from camera trap data at waterholes and pathways during the dry/wet season indicated capuchin monkeys (*Cebus capucinus*), tiger herons (*Trigrisoma mexicanum*), white-tailed deer (*Odocoileus virginianus*), and tapirs (*Tapirus bairdii*) were the most influenced by waterholes during the dry season. Detailed ecological understanding of the linkage between water regimes and the distribution of these four species would help to understand the effect of climate change on large vertebrate behavior in the dry forest ecosystem.

Data from single female jaguar equipped with a satellite telemetry unit, combined with sea turtle track count surveys, showed a combination of olive ridley and green turtle nesting abundance, moon phase and sea surface temperature determined the frequency of jaguar predation activity and movements. Across Playa Naranjo and Playa Nancite, we found places where this collared female spends most of the time was related to sea turtle nesting concentrations. Observing some costal fidelity during the sea turtle nesting peak season. Though this study did not address the field array to the effect of tourism on jaguar-sea turtle interactions, we believe that intense tourism activity at Playa Naranjo would negatively affect predator-prey interactions at unique nesting beaches in the area. Hence, tourism intensity during the sea turtle nesting peaks should be more restricted.

With regard to the use of camera trap placement at trail/ off-trail location and seasonality, most average RAI were higher at trail locations, jaguar sex ratio at trail/off-trail locations differed with male proportions were lower at off trail locations, and competitor and prey interactions indicated temporal avoidance at trail locations. We observed a similar pattern at trail/off-trail locations for jaguar density estimates, observing how placement could biased sex ratios or sex-individual detection. AGuanacaste Conservation Area is reported to have one of the highest jaguar population densities in Costa Rica, and we attribute this to the ecosystem restoration processes that have been developed, combined with law enforcement and biodevelopment of this conservation unit. Finally we emphasize that extended long-term camera monitoring programs would better support jaguar conservation strategies instead of short-term studies.

Based on the data collected in this study, long-term studies of jaguar populations might give more realistic and useful insights to conservation if researchers paid more attention to species' behavior and interactions that could be biasing our results. Thus, it is important to continuously rethink the "what?" and "how?" of the things we are doing in conservation science to effectively understand ecological processes. Additional observation from this study suggests some large herbivores are more sensitive to changes of climate than other species; therefore, further jaguar studies should continue to tackle the effects of climate variability on prey species and its relationship with large predator ecology in a unique ecosystem such the tropical dry forest.

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APPENDIX

Appendix 1.1 References for various types of modeling approaches used to assess jaguar distribution.

Model method	Nu. of Documents	References
Telemetry	14	Schaller & Crashaw 1980; Rabinowitz & Nottingham 1986; Cacelli de Azevedo & Murray 2007; Cavalcanti 2008; Colchero et al. 2010; Conde et al. 2010; Cullen et al. 2013; Gonzalez-Borrajo et al. 2016; Morato et al. 2016; De la Torre et al. 2017; McBride & Thompson 2017; Gese et al. 2018; Morato et al. 2018; De la Torre & Rivero 2019.
Camera trap	33	Weckel et al. 2006; Harmsen et al. 2009 ; Bitetti et al. 2010; Foster et al. 2010; Sollmann 2010; Davis et al. 2011; Harmsen et al. 2011; Negrões et al. 2011; Sollmann et al. 2012; Arroyo et al. 2014;Oliveira, G. 2014; Borrego 2015; Guilder et al. 2015; Michalski et al. 2015; Watkins et al. 2015; Fort 2016; Jordan et al. 2016; Astete et al. 2017a; Astete et al. 2017b; Dobbins et al. 2017; Gutiérrez-Gonzàlez & López-González 2017; Jędrzejewski et al. 2017; Luja et al. 2017; Roopsind et al. 2017; Rowe 2017; Souza et al. 2017; Souza et al. 2017; Silva et al. 2018; Araujo 2018; Blake & Loiselle 2018; Espinosa et al. 2018;Hidalgo-Mihart et al. 2018; Ávila-Nájera et al. 2019.
Genetics	2	Haag et al. 2010; Mae-White 2017

Historic records	21	Hatten et al. 2003; Boydston & Gonzàles 2005; Torres et al. 2008; Gomez 2011; Rodriguez-Soto et al. 2011; Sandoval et al. 2011; Cuervo-Robayo & 2012; Ferraz et al. 2012; Paschoaletto et al. 2012; Torres et al. 2012; De Angelo et al. 2013; Morato et al. 2014; Zeilhofer et al. 2014; Bernal-Escobar et al. 2015; Carvalho et al. 2015; Dueñas-Lopez et al. 2015; Cuykens et al. 2017; DeMatteo et al. 2017; Romero-Muñoz et al. 2018; Zárrate-Charry et al. 2018; Portugal et al. 2019
Sign counts	2	De Angelo et al. 2011; Booker 2016
Interviews	3	Petracca 2010; Zeller et al. 2011 ;Petracca et al. 2013
GIS	9	Sanderson et al. 2002; Rabinowitz & Zeller 2010; Zeller & Rabinowitz 2011; Silveira et al. 2014; Olsoy et al. 2016; Pardo et al. 2017; Thornton et al. 2016; Thompson & Velilla 2017;De la Torre et al. 2018

Appendix 1.2 Candidate predictive variables used to evaluate jaguar density (# individuals/ 100 km^2) and jaguar relative abundance index (RAI: # Jaguar records/ 100 trap nights) records/ 100 trap nights) correlations with surrogate environmental and anthropogenic, reported as the most significant in peer review documents.

No	**Variable abbreviation**	**Classification**	**Data description**	**Source**	**Reference #**
1	Prec	Environmental	Mean annual precipitation(mm), from 1950-2000	www.worldclim.org/bioclim	[1]
3	Temp	Environmental	Mean annual temperature (ºC), from 1950-2000	www.worldclim.org/bioclim	[1]
4	Urban_dev	Anthropogenic	Development Threat Index 2015	https://sedac.ciesin.columbia.edu/data/set/lulc-development-threat-index	[2]
5	Freshwater_	Environmental	Trends in Global Freshwater Availability from the Gravity Recovery and Climate Experiment (GRACE), from 2002-2016	https://sedac.ciesin.columbia.edu/data/set/sdei-trends-freshwater-availability-grace	[3]

6	Footprint	Anthropogenic	Global Human footprint, 1995-2004	https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-ighp	[4]
7	Veg	Environmental	Global percentage of tree cover 2008	https://globalmaps.github.io/ptc.html#summary	[5]
8	Protect	Anthropogenic	Natural resource protection from 2010-2015	https://sedac.ciesin.columbia.edu/data/set/nrmi-natural-resource-protection-child-health-indicators-2016	[6]

Reference #

[**1**] Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol.2005; 25: 1965-1978. doi:10.1002/joc.1276. Accessed 18/02/2020.

[**2**] Oakleaf, J. R., C. M. Kennedy, S. Baruch-Mordo, P. C. West, J. S. Gerber, L. Jarvis, and J. Kiesecker. 2019. Development Threat Index. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/61jv-th84. Accessed 18/02/2020.

[**3**] Rodell, M., J. S. Famiglietti, D. N. Wiese, J. T. Reager, H. K. Beaudoing, F. W. Landerer, and M.-H. Lo. 2019. Trends in Global Freshwater Availability from the Gravity Recovery and Climate Experiment (GRACE). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4TT4P2C. Accessed 18/02/2020.

[**4**] Wildlife Conservation Society - WCS, and Center for International Earth Science Information Network - CIESIN - Columbia University. 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (IGHP). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4GF0RFQ. Accessed 18/02/2020.

[**5**] Vegetation (Percent Tree Cover) - Global version - Version 1 © Geospatial Information Authority of Japan, Chiba University and Collaborating Organizations. Accessed 18/02/2020.

[**6**] Center for International Earth Science Information Network - CIESIN - Columbia University. 2016. Natural Resource Protection and Child Health Indicators, 2016 Release. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H48913TX. Accessed 18/02/2020.

Appendix 1.3 Jaguar density (# individuals/ 100 km^2) and jaguar relative abundance index (RAI: # Jaguar records/100 trap nights) records/ 100 trap nights) extracted from peer review documents.

Country	Survey	Stations	Average operation days per camera	RAI	Density	Reference
Argentina	Iguazu 2004	39	45	0.5	1.07	(Paviolo et al. 2008)
Argentina	Iguazu 2006	47	45	1.4	1.46	(Paviolo et al. 2008)
Argentina	Urugua-i	34	45	0.134	0.3	(Paviolo et al. 2008)
Argentina	Yaboti	42	45	1.6	0.2	(Paviolo et al. 2008)
Belize	Cockcomb basin	20	59	1.65	8.8	(Silver et al. 2004)
Belize	Chiquibul	15	27	3.5	7.48	(Silver et al. 2004)
Belize	Fireburn	16	63	1.2	5.3	(Miller 2006)
Belize	Gallon Jug Estate 2004	28	62	3.3	11.28	(Miller 2005)
Belize	Gallon Jug Estate 2005	24	62	4.7	8.8	(Miller 2005)
Belize	Mountain Pine Ridge	--	80	3.3	2.32	M. Kelly unpubl. data, in (Maffei et al. 2011)
Belize	Mountain Pine Ridge	--	64	7.1	5.35	M. Kelly unpubl. data, in (Maffei et al. 2011)

Bolivia	Cerro Cortado I Kaa-Iya	38	60	0.96	5.11	(Silver et al. 2004)
Bolivia	Cerro Cortado II Kaa-Iya	28	60	0.405	5.37	(Maffei et al. 2004)
Bolivia	El Encanto	20	60	0.4	5.66	(Arispe et al. 2007)
Bolivia	Estacion Isoso I, Kaa-Iya 2005	22	56	2.2	3.16	(Maffei et al. 2006)
Bolivia	Estacion Isoso II, Kaa-Iya 2006	20	64	2.4	3.93	(Romero-Muñoz et al. 2007)
Bolivia	Guanaco, Kaa-Iya I	16	60	1.1	2.05	(Cuéllar et al. 2004a)
Bolivia	Guanaco, Kaa-Iya II	18	60	2.9	2.09	(Cuéllar et al. 2004b)
Bolivia	Palmar I, Kaa-Iya 2006	23	61	2.4	1.32	(Romero-Muñoz et al. 2006)
Bolivia	Palmar II, Kaa-Iya	--	--	2.4	1.13	(Montaño et al. 2007)
Bolivia	Ravelo I, Kaa-Iya	36	60	0.1	2.27	(Maffei et al. 2004)
Bolivia	Ravelo II, Kaa-Iya	--	--	0.15	1.57	(Cuéllar et al. 2003)
Bolivia	Rios Tuichi and Hondo, Madidi	66	28	0.86	2.84	(Silver et al. 2004)
Bolivia	Rios Tuichi and Hondo, Madidi	32	29	0.267	1.68	(Wallace et al. 2003)
Bolivia	Tucavaca I, Kaa-Iya	32	60	2.03	2.57	(Silver et al. 2004)
Bolivia	Tucavaca II, Kaa-Iya	16	60	1.25	3.1	(Maffei et al. 2004)
Brazil	Emas National Park	--	62	4.6	2	(Silveira 2004)
Brazil	Fazenda Santa Fe	--	--	4.02	2.59	L. Silveira and N.M. Negrões, in (Maffei et al. 2011)
Brazil	Fazenda Sete 2003	16	20	13.6	10.3	(Soisalo and Cavalcanti 2006)

Brazil	Fazenda Sete 2004	16	60	16.35	11.7	(Soisalo and Cavalcanti 2006)
Brazil	Moro do Diablo	73	20	3	2.47	(Cullen 2006)
Brazil	Serra da Capivara	20	84	6.5	2.67	(Silveira et al. 2010)
Colombia	Amacayacu	--	--	0.56	4.2	(Payan 2009)
Costa Rica	Corcovado	11	30	1.9	6.98	(Salom-Perez et al. 2007)
Costa Rica	San Cristobal	15	43	1.1	6.7	(Rojas 2006)
Costa Rica	Talamanca ZPLT (Coton)	10	60	3.17	5.42	(Gonzáles-Maya 2007)
Ecuador	Yasuni ITT	32	64	0.3	2.2	(Araguillin et al. 2010)
Guatemala	La Gloria-Lechugal	33	46	1.5	1.54	(Moreira et al. 2007)
Guatemala	Dos Lagunas Rio Azul	25	47	0.85	11.1	(Moreira et al. 2008b)
Guatemala	Tikal	15	34	5.9	6.63	(Garciaa et al. 2006)
Guatemala	Laguna del Tigre	24	49	4.34	6.32	(Moreira et al. 2009)
Mexico	San Luis Potosi 2008	27	31	5.03	3.2	(Avila Nájera 2009)
Panama	Darian	23	35	0.8	1.9	(Moreno 2006)
Panama	Darian	22	50	0.8	4.38	(Moreno 2006)
Peru	Los Amigos 2005	24	62	1	10.1	(Tobler et al. submitted)
Peru	Los Amigos 2006	40	62	1.48	7.13	(Tobler et al. submitted)
Peru	Los Amigos 2007	40	62	1.95	12.2	(Tobler et al. submitted)

Peru	Bahuaja Sonene, Tambopata	43	62	0.5	8.1	(Tobler et al. submitted)
Peru	Espinoza	38	122	3.01	6.9	(Tobler et al. submitted)

Appendix 1.4 Peccary relative abundance index (RAI: # Jaguar records/ 100 trap nights) records/ 100 trap nights) extracted from peer review documents.

Country	Survey	RAI (# Peccary records/ 100 trap nights)	Reference
Argentina	Iguazu 2004	0.48	Bitetti et al. 2014
Argentina	Iguazu 2006	0.48	Bitetti et al. 2014
Belize	Cockcomb basin	1.925	Weckel et al. 2006
Bolivia	Cerro Cortado I Kaa-Iya	9.74	Gomez et al. 2012
Bolivia	Cerro Cortado II Kaa-Iya	9.74	Gomez et al. 2012
Brazil	Emas National Park	1.5	Foster et al. 2013
Brazil	Fazenda Santa Fe	1.38	Negrões et al. 2011
Brazil	Fazenda Sete 2003	8	Foster et al. 2013
Brazil	Fazenda Sete 2004	33	Foster et al. 2013
Brazil	Moro do Diablo	0.86	Michalski et al. 2015
Colombia	Amacayacu	0.9	Pardo et al. 2008
Costa Rica	Corcovado	6.22	Wong et al. Unpublish data

Costa Rica	Talamanca ZPLT (Coton)	8	Gonzales-Maya 2007
Ecuador	Yasuni ITT	2.4	Torres& Gavilanez 2019
Guatemala	Dos Lagunas Rio Azul	6.29	Moreira et al. 2009
Mexico	San Luis Potosi 2008	0.88	Avila Nájera 2009
Panama	Darian	5.68	Fort 2016
Peru	Los Amigos 2005	66	Tobler et al. 2009
Peru	Los Amigos 2006	35	Tobler et al. 2009
Peru	Los Amigos 2007	82	Tobler et al. 2009
Peru	Bahuaja Sonene, Tambopata	42	Tobler et al. 2009

Appendix 1.5 Number of jaguar individual captures registered at different capture locations by sex and camera placement locations (trail/off-trail) in Sector Santa Rosa, Guanacaste Conservation Area, Northwestern Costa Rica.

ID Individual	Sex	Nu. captures	Nu. Capture locations	Camera placement loc.	
				Trail	Off-trail
Jaguar01	**F**	**70**	**13**	**J4,J6,J7,J8,J9,J12,J20,J24,J30**	**C18,C19,C26,C35**
Jaguar02	F	29	4	J12, J19, J20	C29
Jaguar04	F	8	2	J12,J19	---
Jaguar11	F	3	1	J12	---
Jaguar13	F	2	1	J12	---
Jaguar16	F	2	2	J12, J21	---
Jaguar08	F	1	1	J20	---
Jaguar19	F	1	1	---	C33
Jaguar03	**M**	**29**	**7**	**J3,J6,J12,J13,J15,J18,J19**	**---**
Jaguar12	M	12	6	J3,J6,J_palo_seco,J12,J21,J22	---
Jaguar10	M	7	3	J6,J7,J12	---
Jaguar15	M	6	4	J14,J15,J17	C29

Jaguar09	M	4	2	J12,J15	---
Jaguar14	M	3	2	J6,J21	---
Jaguar18	M	3	2	---	C26,C35
Jaguar05	M	2	2	J7,J19	---
Jaguar06	M	2	2	J12,J20	---
Jaguar07	M	2	1	J7	---
Jaguar17	M	2	1	J12	---