

ECOLOGY OF A CARNIVORE COMMUNITY IN AN AGRICULTURAL LANDSCAPE IN
NORTHEAST BRAZIL

By

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ABSTRACT

ECOLOGY OF A CARNIVORE COMMUNITY IN AN AGRICULTURAL LANDSCAPE IN NORTHEAST BRAZIL

By

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Understanding the factors that affect the presence and distribution of carnivores in human-dominated landscapes is one of the principal goals of conservation ecology. My research sought to determine those factors in a carnivore community inhabiting an agricultural landscape in Bahia, Brazil. To reach this goal I used camera traps and conducted semi-structured interviews in human communities in my study area. The carnivore community studied included eight species of the cat, weasel, raccoon and dog families (puma (*Puma concolor*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), tayra (*Eira barbara*), South American coati (*Nasua nasua*), crab-eating raccoon (*Procyon cancrivorus*), crab-eating fox (*Cerdocyon thous*), and domestic dog (*Canis familiaris*). Results indicated that habitat is a key factor determining the distribution of some species in the carnivore community. Some species, such as the crab-eating fox, had a high probability of using rubber crops and a low probability of using forested areas, whereas others, such as the South American Coati, had a low probability of using rubber crops and a high probability of using forested areas. Analysis at a larger scale indicated that in the case of the crab-eating foxes and the South American coatis landscape-related variables were the best predictors of the animals' frequency of site use. The frequency of site use by tayras was best predicted by resource-related variables, and for the wildcats (*Leopardus* spp.) by human-related variables. Results from interviews with stakeholders showed that, the carnivore with the highest frequency of reported negative impacts was the puma due to the fear related to its presence. I also found that the factors that best explained tolerance for pumas were related to personal evaluative attitudes

(likability) and perceived benefits. These findings elucidate the complexity of the actions required to propose more appropriate management strategies for carnivore conservation in tropical agricultural systems. The results make an important contribution to our knowledge of why carnivores adapt or fail to adapt to agricultural landscapes with applications for sustainable agriculture within and beyond the Northeast of Brazil.

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To my loved ones

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Finally, I wish to express my thanks to my parents for their unmeasurable love, for teaching me the love for nature, for supporting my passion for what I love, and for being so patient and understanding during this eight-year process. To my mom for always giving me strength in the difficult moments. To my beloved Bernardo for his love, support, patience and help.

PREFACE

“The destruction of these forests is irreversible, within any sort of human time scale. What is lost when a tropical forest is destroyed is not only greater in variety, complexity and originality than other ecosystems, it is incalculable. For although cataloguing of the boreal forest is conceivable- and well advanced, in fact- cataloguing of a tropical forest is well beyond our resources, now or in the imaginable future. The disappearance of a tropical forest is therefore a tragedy vast beyond human knowing or conceiving” Warren Dean, 1995 (With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest).

It was in 2006 when I visited Brazil for the first time and what was left of the Atlantic Forest. I was intrigued by the persistence of many species after centuries of disturbances of all kinds. This, added to the little information available on many of the carnivore species, drove my desire to pursue my PhD and to study carnivore ecology in human-modified landscapes. Given that ecology is the study of the interactions between organisms and their environment, one of the main challenges I faced when I decided to study this topic was on how to integrate the complexity of such interactions into a PhD thesis. Therefore, in order to study the carnivore interactions in an agricultural landscape in Northeast Brazil, I have included in my dissertation three chapters. The first chapter focuses on determining the habitat use by carnivores in a rubber/forest landscape. The second chapter focuses on determining the effects that different factors, related to landscape, human presence and resource availability, have on the frequency of site use by carnivores. Finally, the third and last chapter, explores the human dimensions of the human-carnivore co-occurrence, and includes a study case on the predictability of tolerance for pumas.

It is my hope that this dissertation contributes to the knowledge on how and why carnivore species persist in agricultural landscapes and that this knowledge may contribute to the implementation of more biodiversity friendly agricultural practices in tropical areas. This dissertation also represents a lifelong commitment to continue working to support biodiversity conservation.

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CHAPTER 1. DETERMINING HABITAT USE BY CARNIVORES IN A RUBBER/FOREST LANDSCAPE IN BRAZIL USING MULTISPECIES OCCUPANCY MODELS¹.

ABSTRACT

Understanding the factors that influence the distribution of wildlife in human-dominated agricultural landscapes is one of the main challenges for devising strategies for biodiversity conservation, especially in landscapes where setting aside large protected areas is not feasible. My research sought to determine the effect that different habitats have on the distribution of a mammalian carnivore community inhabiting a 4,400-ha rubber plantation/forest landscape in Bahia, Brazil. I used a multispecies occupancy model to determine the probabilities of habitat use by each species. I found that there was a significant difference in habitat use probabilities between domestic dogs (*Canis familiaris*), crab-eating foxes (*Cerdocyon thous*) and coatis (*Nasua nasua*), with domestic dogs and foxes having higher probabilities of using rubber groves and coatis preferring forest. The low detection probability (<0.2) of tayras (*Eira barbara*) and wildcats (*Leopardus* spp.) precluded a reliable estimation of habitat use probabilities using occupancy models. The results show the long-term potential of rubber/forest landscapes in the conservation of carnivore communities in the Atlantic forest.

Keywords: Mammalian carnivores, rubber agroforestry, occupancy models, Atlantic forest, Bahia.

¹ This chapter will be submitted for review as a research paper

INTRODUCTION

Determining how carnivores respond to landscape modifications is a principal goal of conservation ecology. Due to the ongoing large scale modification of natural areas throughout the world, it is becoming increasingly urgent to understand how these changes affect carnivore species in order to devise land management strategies that help mitigate the negative effects of forest fragmentation and the replacement of forest with agricultural lands. The responses of carnivores to agricultural lands vary, depending not only on the type of cultivar in the matrix and the amount and configuration of native vegetation remaining, but also on the ecology of the species (Mudappa et al. 2007; Lyra-Jorge et al. 2008; Caruso et al. 2016), and even characteristics like gender (Stewart et al. 2013) and the specific behavior of individual animals (Linnell et al. 1999). Therefore, devising management strategies for carnivores requires detailed studies on the variations of the effects of habitat modification on the different species.

Most carnivore studies to date have focused on large species which is justifiable for several reasons: they are charismatic and thus evoke the sympathy of the general public; they have a strong direct and indirect effect on human communities where they share the landscape; their populations are declining over large geographical areas; and they have a significant role in structuring ecosystems (Ripple et al. 2014). Mesocarnivores on the other hand have received less attention, even though this group is more species-rich and, like their larger counterparts, play important roles in structuring ecosystems (Roemer et al. 2009). In an increasing number of human-dominated landscapes large carnivores are being extirpated, making mesopredators the apex predators (Roemer et al. 2009), and yet how they adapt to these landscapes is poorly known. Also, in the

case of mesopredator species that are non-obligate meat eaters, they act as seed dispersers and thus may have an important role in maintaining the long-term viability of plant populations in fragmented landscapes (Jordano et al. 2007; Rosalino et al. 2010).

Tropical rainforests are among the most species rich and threatened ecosystems on the planet, with vast areas being converted to agricultural lands each year (FAO & JRC 2012). The demand for natural rubber (*Hevea brasiliensis*) is one of the principal drivers of forest conversion in some of the most species-rich rainforests, with more than 2 million ha planted during the past decade and an additional 4.3-8.5 million ha expected to be planted by 2024 (Warren-Thomas et al. 2015). Given this situation, it is essential to determine how rubber plantation landscapes affect carnivore communities so that land management strategies can be devised to ameliorate the negative impacts of rubber agroforestry on biodiversity.

Nowadays, the majority of the natural rubber is produced in Southeast Asia, but rubber is also grown in West Africa and throughout the tropical rainforests of Central and South America. Although the rubber tree is native to Brazil, the prevalence of South American leaf blight caused by the endemic fungus (*Microcyclus ulei*), makes it difficult for this country to produce sufficient rubber to meet its needs. Nonetheless, the federal government of Brazil has the goal of making the nation self-sufficient in natural rubber by increasing the area under rubber cultivation (Ministry of Agriculture of Brazil 2011). The majority of the internal production of rubber is located in the Atlantic forest (Ministry of Agriculture of Brazil 2011), a biodiversity hotspot of which, after 500 years of intensive human exploitation, less than 16% remains, mostly in fragments <50 ha (Ribeiro et al. 2009). Some of the first rubber plantations in the Atlantic forest were planted in the state of

Bahia in the 1950s in areas at the time covered with extensive tracts of lowland rainforest. After seven decades, these plantations, which consist of mosaics of forest and rubber groves, offer an opportunity to study the capacity of these landscapes to sustain biodiversity in the long-run and to provide insights on how to design rubber plantations in a biodiversity friendly manner in the Atlantic forests and in other parts of the tropics where rubber expansion is underway. The aim of this study was to determine how a carnivore community in one of the oldest rubber plantations in Bahia has responded to the resulting landscape mosaic, using occupancy models to test for habitat use of the various species. The results provide insights to help guide managers of old and new plantations throughout the tropics to adapt plantation design to accommodate wildlife and make rubber a biodiversity friendly crop.

METHODS

Study site

The 4,400-ha study site consisted of the 3,386 ha of the Reserva Ecológica Michelin (REM) and adjacent properties in the municipalities of Ituberá and Igrapiúna, Bahia, Brazil (39°10'W 13°47'S to 39°13'W 13°54'S) (Figure 1.1). The natural vegetation is composed of lowland evergreen rainforest, with an average yearly precipitation of 2000 mm and average temperatures of 21- 28°C (Flesher & Laufer 2013). The study area consists of 1,800 ha of forest divided into four main blocks (one of them is part of a 13,000-ha forest block that extends beyond the study area), riparian forest corridors (30-50 m wide and up to 12 km long), cattail wetlands, streams, small rivers, abandoned old rubber groves mixed with pioneer tree species in a secondary forest-like assemblage, and approximated 1,000 ha of actively cultivated rubber groves. Although all of the forests were exploited for timber, firewood collecting, and *Euterpe edulis* palm extraction prior to

the creation of the reserve (2005) and some forest patches are manioc fallows, the flora is still highly diverse (Rocha-Santos & Talora 2012). The small forest fragments and riparian forests are dominated by pioneer trees (principally, *Cecropia*, *Schefflera*, *Vismia*, *Albizia*, *Byrsonima*, *Miconia*, *Henrietta*, *Tibouchina*, *Tapirira*, *Senna*, *Kielmeyera*, *Himatanthus*, *Inga*, *Stryphnodendron*, *Bauhinia*), Rubiaceae, Melastomataceae, and Piperaceae shrubs/bushes, thin vines, and *Cyperus* grasses. Rubber trees in the area reach up to 15m height and are planted in rows with a spacing of approximately 8m (between rows) x 3m (between trees in the same row). This allows a density of approximately 500trees/ha with well-developed pioneer vegetation in the inter-rows. The floristic composition of the pioneer vegetation in the inter-rows is similar to the composition mentioned previously for the riparian forests. Rubber collection or tapping involves a superficial diagonal cut in the bark, then the latex that starts dripping down the trunk is led into a spout and in turn into a cup that is attached to the tree by a wire. Tappers in the area start working early in the morning and finish around midday. Workers tap the trees on average every 4 days and rubber trees can be tapped for decades by shifting the cuttings around the trunk and thus allowing recent cuts to heal over (Flesher 2006). The average distance between riparian corridors is ≤ 400 m and the maximum distance between forest blocks is 1 km.

The study fauna

The study fauna included all of the terrestrial and scansorial mammalian carnivores extant in the region: puma (*Puma concolor*), jaguarundi (*Puma yagouaroundi*), ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), oncilla (*Leopardus tigrinus*), tayra (*Eira barbara*), South American coati (*Nasua nasua*), crab-eating raccoon (*Procyon cancrivorus*), crab-eating fox (*Cerdocyon thous*), and domestic dog (*Canis familiaris*). Other carnivores found in the study landscape but not

included in the study were the southern river otter (*Lontra longicaudis*) due to their aquatic habit, and kinkajou (*Potos flavus*) due to their arboreal habit. The jaguar (*Panthera onca*) was extirpated in the 1950/60s (Flesher 2006). Long-term (1997-2015) monitoring through transect censusing shows that the relative abundance of the medium and large mammal fauna has increased by 117% since the creation of the REM (Flesher unpublished data) with the abundance of prey species reaching levels similar to well protected reserves elsewhere in the neotropics (Flesher & Laufer 2013).

Data collection

To study the carnivores, I set up a 90-site grid, with a spacing of approximately 600 m between sites. Of the 90 sites, 30 were located in the forests, 30 in riparian corridors and 30 in rubber groves (with medium to well-developed inter-rows, i.e. height > 3 m) (Figure 1.1). Each month I placed 30 cameras trap at 30 sites chosen randomly (10 in forest, 10 in riparian corridors and 10 in rubber groves), with a subsequent rotation to another 30 sites the next month and so on until I had sampled all 90 sites before repeating any in a trimestral random rotation. Each camera was in place for an average of 22 days/month. In this way I sampled each of the 90 sites four times between February 2013 and January 2014 (i.e. once in a three-month sampling period). The objective of the rotation was to maximize the area sampled, to reduce bait habituation by maximizing the time between bait placement, and to reduce spatial autocorrelation by maximizing the distance between sites sampled at one time.

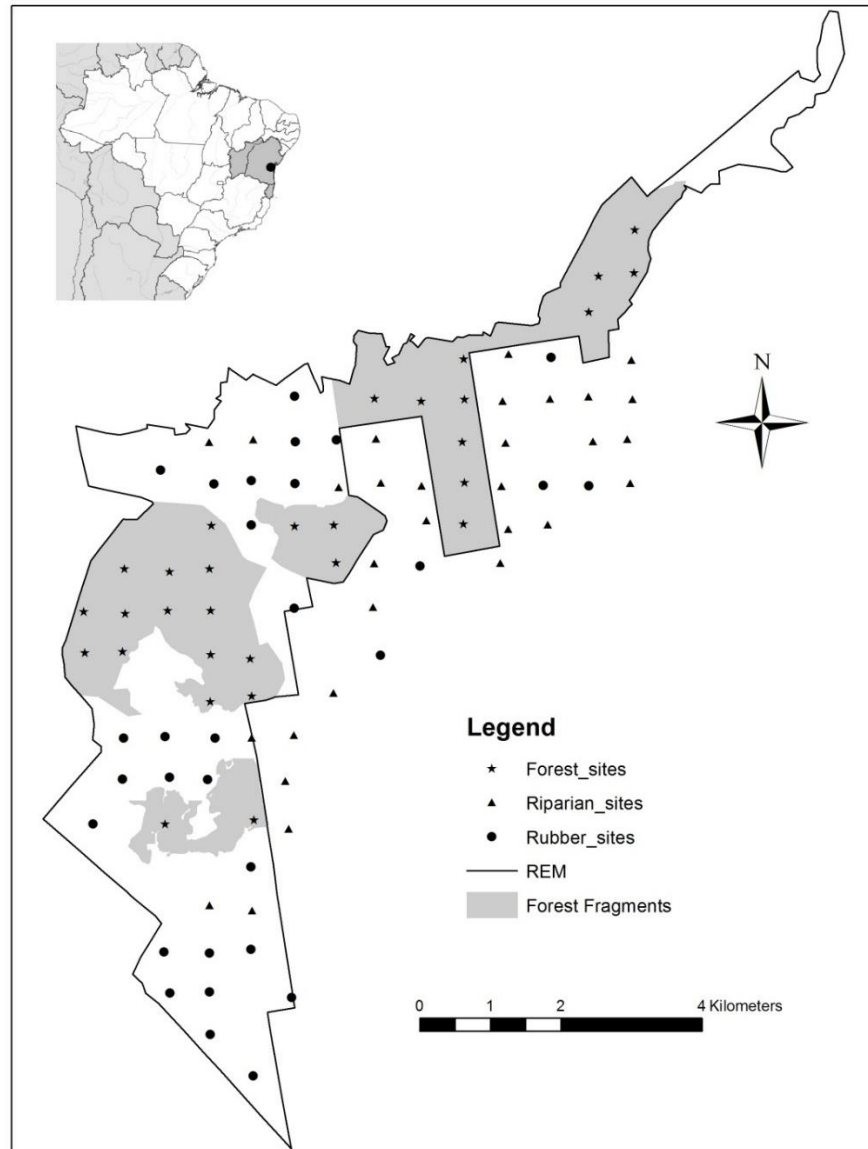


Figure 1.1. Study area and location of the sampling sites, Igrapiúna, Bahia, Brazil, 2013-2014.

Sampling design

I used two types of cameras, Bushnell (Trophy Cam - Bushnell Corporation) and Tigrinus (Digital 6 - Tigrinus Equipamentos para Pesquisa Ltda). All cameras were set up to work 24 hours/day and with equivalent settings in order to reduce the chances of missing animals. The cameras were

randomly assigned to each site while guaranteeing that all sites received both brands over the sampling year. Given that the grid was laid out without reference to previous information on carnivore movements/presence and with the aim that the animals would pass in front of the cameras, I placed lures one time at the beginning of the month at each one of the 30 sites to be sampled. The lure consisted of 500 gr of smashed sardines in oil placed on the ground, 5 ml of banana oil applied on top of a stick placed on one side of the sardines, and 10 ml of a mix of lures (Raccoon Lure No. 1 by Russ Carman, Magna Gland Lure by Russ Carman, Mega Musk Lure by Russ Carman and Ausable Brand Catnip Oil Pint) applied on top of another stick placed on the other side of the sardines.

Statistical analysis

Occupancy has been defined as the proportion of area, patches, or sample units that is occupied or where a species is present (MacKenzie et al. 2006). I used a Bayesian approach and a multispecies occupancy model (Dorazio & Royle 2005; Zipkin et al. 2009) to determine the habitat used by each species of carnivore. Occupancy models can be described as a hierarchical, coupled logistic regression, with one regression describing the true occurrence (referred also as the state or ecological process) and the other describing the detection probability (referred also as the observation process), given that the species occurs (Kéry & Schaub 2012). The effects of ignoring the imperfect detection (i.e. assuming that a non-detection is equivalent to an absence) have been broadly discussed (MacKenzie et al. 2002) and occupancy models represent a step forward by estimating occupancy while accounting for imperfect detection (i.e. <1) of the species.

By including the parameters at the species level as random effects governed by a common set of hyper-parameters or parameters at the community level (Appendix 1), multispecies occupancy models allow for the estimation of covariate effects at the species level and of the aggregated effects at the community level (with both levels being related to each other) (Zipkin et al. 2009). These models are extremely valuable given that they increase the precision in occupancy estimates for most species in the community by borrowing strength from the entire community (Russell et al. 2009). This allows for the inclusion of infrequently observed species, whose occupancy otherwise could not be estimated through single species occupancy models (Zipkin et al. 2009).

Camera data results were organized per species, in a 90 sites (rows) by 4 period (columns) matrix, containing binary data where 1 represented when a species was detected at a specific site during a specific sampling period and 0 when it was not detected. Thus, I used a binary state model in which true occurrence z_{ij} is a latent state variable, specified as $z_{ij} \sim \text{Bernoulli}(\psi_{i,j})$, where $\psi_{i,j}$ is the occurrence probability of species i at site j . The observation model was specified as $x_{ijk} \sim \text{Bernoulli}(\rho_{i,j,k} \cdot z_{ij})$, where x_{ijk} is the detection/non-detection data for species i at site j and for the period k , and $\rho_{i,j,k}$ is the detection probability for species i at site j and for the period k (Zipkin et al. 2009). I included the different types of habitat as covariates, and in the detection model, the different types of cameras used. In both models the covariates were included as indicators (i.e.0 or 1). The ecological process model was as follows:

$$\text{logit}(\psi_{i,j}) = \alpha_{0i} + \alpha_{1i}\text{forest}_j + \alpha_{2i}\text{riparian}_j$$

Where, $\psi_{i,j}$ is the probability that species i occurs at site j , α_{0i} is the occurrence probability for species i in rubber groves on a logit scale, α_{1i} is the difference (on a logit scale) in the occupancy

probability between rubber groves and forest areas for species i , and α_{2i} is the difference (on a logit scale) in the occupancy probability between rubber groves and riparian areas for species i .

The observation model was as follows:

$$\text{logit}(\rho_{i,j,k}) = \beta_{0i} + \beta_{1i} \text{camera}_{j,k}$$

Where: $\rho_{i,j,k}$ is the detection probability of species i at site j for the period k (if present, $z=1$), β_{0i} is the detection probability (on a logit scale) of species i when using Bushnell cameras, and β_{1i} is the difference in the detection probability (on a logit scale) between Bushnell and Tigrinus cameras for species i (See full code in appendix).

I assumed a closed community (i.e. absence of local extinctions or colonization during one year); however, in order to account for weak temporary emigration, and since it may be confounded with the detection probability, I refer to the occupancy probability as the probability of use sometime during the study period as suggested by Kéry and Schaub (2012).

I did all analyses using R (R Core Team 2016) and R2OpenBUGS (Sturtz et al. 2015), used non-informative priors, and ran three chains each for 55,000 iterations, burning 15,000 and thinning the model by 3. I assessed convergence of the model by looking at the R-hat values, with values <1.1 being considered acceptable (Gelman & Rubin 1992). Finally, I assessed model fit by estimating the Bayesian p-value (Zipkin et al. 2009), which is a measure of the discrepancy between the observed data and data simulated under the proposed model with values close to 0.50 indicating an adequate fit and values near 0 or 1 indicating a poor fit.

RESULTS

I registered 483 captures (a species detection/24 hrs.) in 7954 camera days (Bushnell=3203, Tigrinus=4751) (Forest=2849, Riparian Corridors=2370, Rubber Groves=2735). The only species inhabiting the landscape that was not registered by the cameras was jaguarundi. The species with highest number of captures were coati (n= 208), domestic dog (n =143) and fox (n =80) (Table 1.1). For the statistical analysis I merged the detections of ocelot, margay and the unidentified individuals of the genus *Leopardus* into one group (referred hereafter as wildcats *Leopardus* spp.). I excluded the registers from puma and raccoon from the analysis due to the low number of captures for these species.

Table 1.1. Total number of captures and sites where each species was detected per habitat in 7,954 camera days, Igrapiúna, Bahia, Brazil, 2013-2014.

Species	Common name	Forest		Riparian		Rubber		Total	
		Captures	Sites	Captures	Sites	Captures	Sites	Captures	Sites
<i>Canis familiaris</i>	Domestic dog	16	7	19	13	108	24	143	44
<i>Cerdocyon thous</i>	Crab-eating fox	2	2	19	14	59	21	80	37
<i>Eira barbara</i>	Tayra	8	6	12	10	6	5	26	21
<i>Leopardus pardalis</i>	Ocelot	1	1	0	0	4	2	5	3
<i>Leopardus wiedii</i>	Margay	2	2	4	4	4	2	10	8
<i>Leopardus spp.</i>	(unidentified)	5	4	2	2	0	0	7	6
<i>Nasua nasua</i>	South-American coati	156	28	48	20	4	3	208	51
<i>Procyon cancrivorus</i>	Crab-eating raccoon	0	0	2	1	0	0	2	1
<i>Puma concolor</i>	Puma	1	1	1	1	0	0	2	2
Total		191	51	107	65	185	57	483	173

Results from the multispecies occupancy model showed that although the average number of sites used at least once during the study period for most of species was similar (Table 1.2), there were large differences in terms of the habitats they used (Figure 1.2).

Table 1.2. Posterior estimations of carnivore occupancy and detection, Igrapiúna, Bahia, Brazil, 2013-2014. PI = Posterior intervals.

	# of sites occupied	Mean ψ	Mean ψ forest	Mean ψ riparian	Mean ψ rubber	Mean ρ	Mean ρ Bushnell	Mean ρ Tigrinus
Domestic dog (<i>Canis familiaris</i>)								
Mean	49.59	0.55	0.27	0.52	0.85	0.41	0.54	0.35
SD	2.97	0.06	0.09	0.11	0.08	0.04-0.00	0.07	0.05
95% PI	45-56	0.44-0.66	0.12-0.46	0.32-0.73	0.67-0.99	0.33-0.5	0.4-0.68	0.27-0.45
Crab-eating fox (<i>Cerdocyon thous</i>)								
Mean	55.96	0.62	0.12	0.82	0.91	0.23	0.37	0.15
SD	6.13	0.08	0.08	0.16	0.08	0.04	0.07	0.03
95% PI	44-66	0.46-0.74	0.02-0.31	0.49-1	0.71-1	0.16-0.31	0.25-0.52	0.09-0.22
Tayra (<i>Eira barbara</i>)								
Mean	73.63	0.82	0.80	0.90	0.75	0.09	0.18	0.04
SD	15.03	0.17	0.24	0.14	0.23	0.03	0.06	0.02
95% PI	38-90	0.42-1	0.25-1	0.5-1	0.27-1	0.05-0.17	0.1-0.35	0.02-0.08
Wildcats (<i>Leopardus</i> spp.)								
Mean	58.83	0.65	0.66	0.70	0.6	0.1	0.21	0.05
SD	23.42	0.26	0.31	0.28	0.29	0.06	0.11	0.03
95% PI	20-90	0.21-1	0.14-1	0.2-1	0.13-1	0.04-0.25	0.08-0.49	0.01-0.14
South American coati (<i>Nasua nasua</i>)								
Mean	55.21	0.62	0.98	0.71	0.17	0.42	0.67	0.29
SD	2.00	0.04	0.03	0.10	0.08	0.03	0.06	0.04
95% PI	52-60	0.54-0.7	0.88-1	0.52-0.9	0.05-0.34	0.35-0.49	0.56-0.78	0.22-0.37

Domestic dogs showed a higher probability of using rubber groves than forest sites, and to a lesser extent, than riparian corridors (Figure 1.2). The differences between the use of rubber groves and forest, and between rubber groves and riparian corridors were in both cases statistically significant, given that the 95% posterior interval of these parameters did not overlap zero ($\alpha_{1\text{dog}} = -3.06$, 95% posterior interval = -5.61 to -1.45, and, $\alpha_{2\text{dog}} = -1.94$, 95% posterior interval: -4.50 to -0.33, respectively).

Foxes showed a higher probability of using rubber groves than forest sites, and to a lesser extent than riparian corridors (Figure 1.2). The difference in the probabilities of use of rubber groves and

forest was significant, ($\alpha_{1fox} = -5.26$, 95% posterior interval = -10.17 to -2.58), while the difference between rubber groves and riparian corridors was not significant ($\alpha_{2fox} = -0.06$, 95% posterior interval: -4.05 to 6.94).

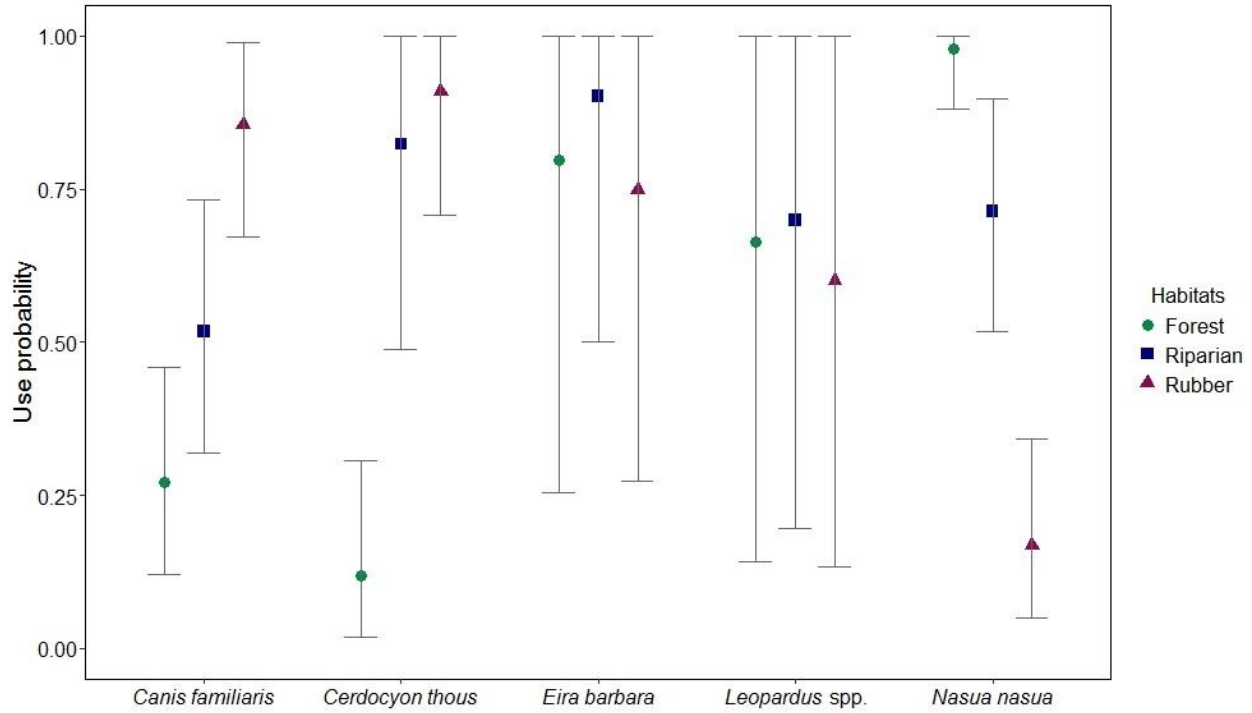


Figure 1.2. Probabilities of habitat use by each species, Igrapiúna, Bahia, Brazil, 2013-2014. The symbols indicate the posterior means and the bars indicate the 95% posterior intervals.

Tayras and wildcats showed no significant differences in the probability of habitat use and the broad posterior intervals reaching 1.00 in all cases indicated that the low detection probability (≤ 0.1) of these species (Table 1.2) impeded a reliable estimation of habitat use (Figure 1.2). Coatis, unlike the other species, showed a significantly higher probability of using forest than rubber groves ($\alpha_{1Coati} = 8.76$, 95% posterior interval: 3.41 to 25.64), and a significantly higher probability of using riparian corridors than rubber groves ($\alpha_{2Coati} = 2.69$, 95% posterior interval: 1.24 to 4.38) (Figure 1.2).

At the habitat level, riparian corridors seemed to act as a transitional habitat for all species (Figure 1.2). A further analysis, revealed the different patterns in variation of use probability, for all the species, along a continuum of native arboreal vegetation cover (i.e. forest and riparian vegetation) (Figure 1.3).

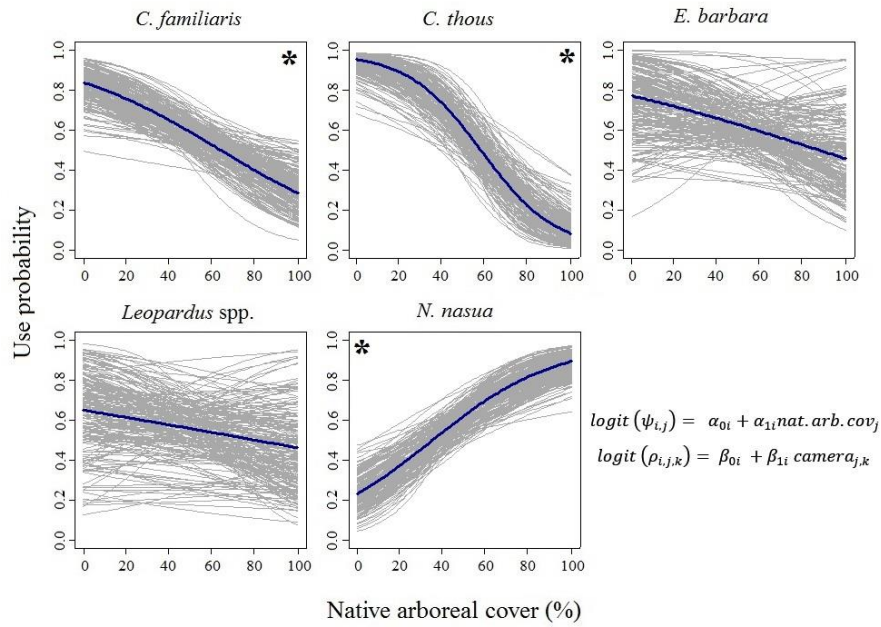


Figure 1.3. Use probability for each species at different percentages of native arboreal cover (i.e. forest and riparian vegetation). Igrapiúna, Bahia, Brazil, 2013-2014. The * indicate significance at 95% posterior interval. Dark lines represent the use probability. Gray lines are 200 Markov chain Monte Carlo draws randomly selected for visualization of uncertainty.

The results showed that there was a lower detection probability for all species when using Tigrinus as opposed to Bushnell cameras (Figure 1.4). The difference between the camera types had a significant effect on the detection probability of all species ($\beta_{1D0g} = -0.78$, 95% posterior interval: -1.40 to -0.12, $\beta_{1Fox} = -1.23$, 95% posterior interval: -1.80 to -0.65, $\beta_{1Tayra} = -1.69$, 95% posterior interval: -2.58 to -0.99, $\beta_{1Leop.} = -1.68$, 95% posterior interval: -2.65 to -0.93, $\beta_{1Coati} = -1.61$, 95% posterior interval: -2.21 to -1.08).

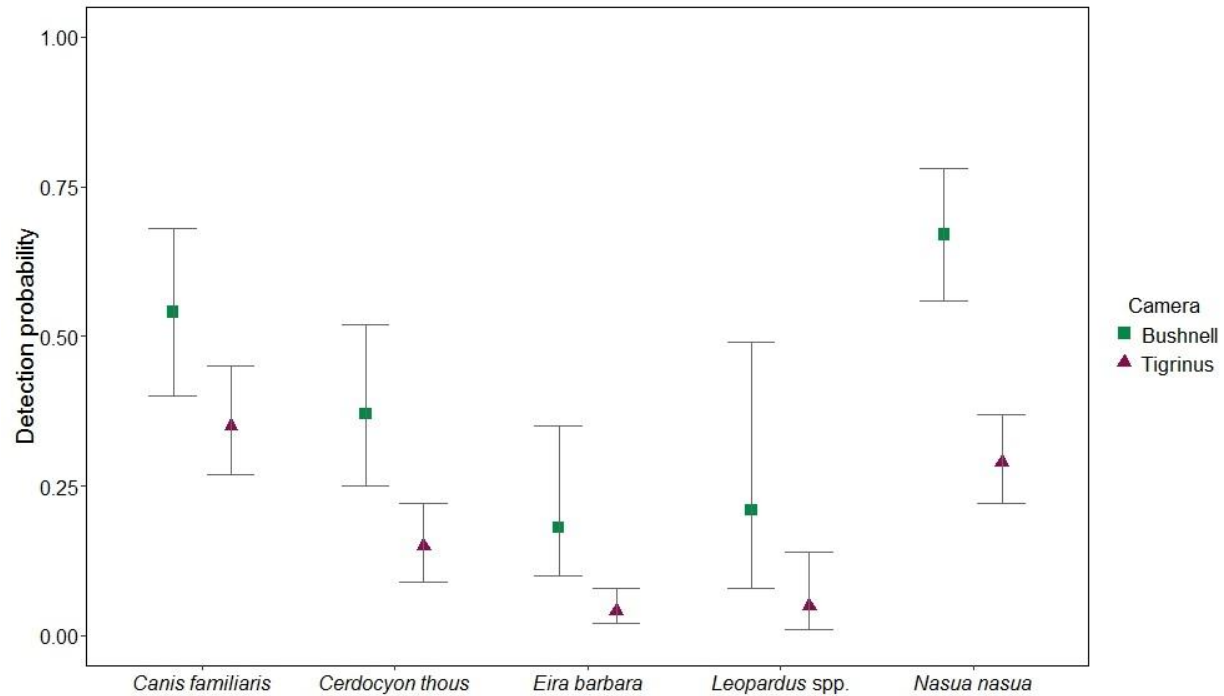


Figure 1.4. Detection probabilities for each species, Igrapiúna, Bahia, Brazil, 2013-2014. The symbols indicate the posterior means and the bars indicate the 95% posterior intervals.

The goodness of fit test for the model was 0.53, indicating a good fit (0.50 is a perfect fit between an ideal dataset i.e. a new dataset generated under my model, and my actual data set).

DISCUSSION

Ecological aspects at the species level

The rubber/forest landscape studied supports, after seven decades of extraction and in terms of species richness, an almost intact mammalian carnivore fauna. Distribution maps of the bush dog (*Speothos venaticus*), show that this species may have been present historically in the area (DeMatteo & Loiselle 2008) but further information on causes and approximate time of disappearance is unclear. The jaguar, which is the only confirmed carnivore species missing from

the community, was extirpated by hunters during the land conversion events. Although almost all of the species used all of the available habitats at some time or another during the study period, there was clear variation among species in their probability of use of each habitat. This shows that with the appropriate management actions (Flesher & Laufer 2013) and the preservation of forest and riparian corridors, rubber agroforestry plantations can contribute to the conservation of carnivore faunas and thus play an important role in biodiversity conservation. Understanding how each species uses the various habitats is a first step to understanding why they do so, and to inform biodiversity friendly management practices on rubber plantations.

Comparisons among camera trap studies are limited, due to the different known and unknown factors that may affect the detection probability of species (e.g. landscape structure, sampling logistics, habitat sampled, equipment used etc.), and even how the results of such studies are presented. However, I attempt here to compare the results from different studies in order to provide a better understanding of the reasons behind the difference in the habitat use probability of the studied species. I attempt such comparison by looking at the capture rates (i.e. captures over the sampling time) because these are the most frequently reported values in camera trap studies.

Domestic dogs are the only non-native carnivores in the area but are nonetheless an important part of the ecosystem, due to their abundance and use of all habitat types. Other studies in the Atlantic forest have shown that domestic dogs are becoming one of the most abundant species in this biome and their negative effect on wildlife (Lacerda et al. 2009; Paschoal et al. 2012; Frigeri et al. 2014). In the study landscape I found, that domestic dogs have significantly less probability of using forests (with a mean probability of 0.27) than riparian corridors and rubber crops, indicating that the former habitats may serve as partial refuges for wildlife from this non-native predator. The

preference of domestic dogs for the rubber groves is not surprising as they often accompany their owners on their rubber tapping rounds, returning to the villages when the work in the rubber groves is done. Dogs may enter the forest to accompany hunters throughout the study region and to pursue prey on their own, as it is common for farmers to starve their dogs in the belief that this will make them better hunters (Flesher pers. Comm.). However, the higher use probabilities of dogs for rubber areas and the frequent observation of rubber workers along the dog's captures indicate that, in my study area, dogs generally preferred to stay close to their owners in the rubber groves, rather than to wander in the forested habitats on their own.

Foxes' preference for rubber groves and riparian corridors, and low probability of using forest is consistent with the results from other studies in neotropical areas showing that foxes prefer open, forest edge and agricultural habitats to forest habitats in mosaic landscapes (Trolle 2003; Vieira & Port 2007; Lyra-Jorge et al. 2008; Cassano et al. 2012). Foxes showed the third highest capture rate at the landscape level (i.e. with all habitats aggregated), which is consistent with other studies using camera traps in mosaic landscapes where their capture rate is the second or third highest, after the crab-eating raccoon and/or the domestic dog (Trolle 2003; Cassano et al. 2012), but which was not the case in other regions in the Atlantic forest (Lyra-Jorge et al. 2008; Paschoal et al. 2012; Carvalho et al. 2013). I believe that the differences with the study of Lyra-Jorge et al. (2008) is the result of intra-guild predation and inter-specific killing, given that the species with the highest relative frequencies in their study area was the puma and the maned wolf (*Chrysocyon brachyurus*), both potential predators of foxes (Oliveira & Pereira 2013). In the case of the studies conducted by Paschoal et al. (2012) and Carvalho et al. (2013) the low number of records for the foxes may be due to the fact that in their studies only forest habitats were sampled. There was a

high spatial overlap in habitat use between dogs and foxes, however, they used the same parts of the landscape at different times of the day, with dogs captured 92% of the time during the day and foxes captured 73% of the time during the night. The preference of foxes for rubber areas and riparian corridors is likely due to their generalist and opportunist diet (Rocha et al. 2004; Rocha et al. 2008; Cazetta & Galetti 2009); also their nocturnal behavior allows them to explore these areas and reduce human encounters.

Although the low detection probability of tayras (0.09) impeded a reliable estimation of habitat use using occupancy models, the fact that the variation of the number of captures and number of sites occupied between habitats was equal to or less than a one-fold difference, may indicate that the tayra is a habitat generalist. This is consistent with other studies showing that tayras are common in a wide variety of agricultural/forest mosaics (Naughton-Treves & Salafsky 2004; Flesher 2006; Lyra-Jorge et al. 2008; Cassano et al. 2009; Michalski et al. 2011; Cove et al. 2014). Although Cassano et al. (2014) showed that management intensification in agroforestry systems and the presence of dogs affect tayras negatively, and Estrada et al. (1993) found that they have a strong preference for forest habitats; at the landscape level (i.e. with all captures per habitat aggregated and assuming an equal detection probability across studies/landscapes), tayras have higher capture rates in mosaic landscapes with forest and diverse agricultural systems (i.e. cacao *cabrukas*, pineapple and rubber plantations) (Cassano et al. 2012; Cove et al. 2013) than in less modified landscapes (Trolle 2003; Tobler et al. 2008). The ability of tayras to use all habitats in the studied rubber/forest landscape, even at daylight (96% of captures registered during the day), is likely due to their behavior. They are described by farmers in the region as fast, alert, fearless, and hard to kill with shot (Flesher 2006). Also, their opportunistic omnivorous diet allows them to

exploit not only food items from forest habitats, but direct and indirect (e.g. insects, small mammals, nesting birds) food items associated with agricultural lands (Soley 2012; Cove et al. 2014).

Like in the case of tayras, the low detection probabilities of the wildcats (0.1) preclude statistically based conclusions about habitat use probability using occupancy models. However, in the case of the margays, in terms of capture rates at the landscape level (assuming equal detection probabilities across studies/landscapes), their higher capture rates in landscapes with large tracts of remaining forests (Tobler et al. 2008; Hodge 2014) in comparison to those in mosaic agricultural landscapes (Lyra-Jorge et al. 2008; This study, Cove et al. 2013) may be indicators that, although they persist in agricultural systems, they are mostly a forest/tree dwelling species as mentioned by Bisbal (1993), Michalski et al. (2011) and Mondolfi (1986). When present in agroforestry systems, as in this case, and based on the captures per habitat, they use all the habitats in the area, consistent with results from other studies (Mondolfi 1986; Azevedo 1996; Vaughan 2011). The low number of captures registered in the forests fragments in this study may be due to the use of exclusively ground level camera traps, which may not be adequate for comparing habitat use probabilities of this scansorial species in mosaic landscapes given that, due to the continuous dense canopy in the forest, it may spend more time on the trees than in the less dense riparian corridors and the more open canopy rubber groves.

Although ocelots have been described as tolerant, to some degree, to habitat disturbance (Paviolo et al. 2016), many studies have shown that their distribution is associated with forest cover or areas with >75% woody canopy (Emmons 1988; Sunquist et al. 1989; Harveson et al. 2004; Haines et

al. 2006; Michalski et al. 2011; Massara et al. 2015; Jordan et al. 2016). Although the species persists in agroforestry systems, capture rates at the landscape level (assuming equal detection probabilities across studies/landscapes) are higher in landscapes with less human influence (Trolle 2003; Tobler et al. 2008) than in agricultural landscapes (This study, Cassano et al. 2012; Cove et al. 2013). Although registered with low capture rates, I found that in my area ocelots made use of the rubber crops, which is consistent with capture rates of this species in other productive systems such as eucalyptus (Lyra-Jorge et al. 2008). At the habitat level, the low capture number in forests and the absence of captures in riverine areas may be a product of the low detection probability, given that many studies have shown their usage of riparian areas (Mondolfi 1986; Sunquist 1992; Flesher 2006; Michalski et al. 2010). While I was not able to definitively identify oncillas due to the poor quality of some of the photographs, interviews conducted by Flesher (2006) in the region suggest that it is the most seen small cat in the greater regional landscape. In terms of activity patterns, I found that 96% of the captures of the wildcats were registered at night.

Coatis showed a significantly higher use probability of forests and riparian corridors in comparison to the rubber groves which is consistent with other studies in neotropical areas that describe the coatis as a forest species (Trolle 2003; Desbiez & Borges 2010; Trovati et al. 2010; Cassano et al. 2012). The preference for forest and riparian corridors may be because the dense canopies of these habitats offer resting areas and food resources (Beisiegel 2001; Desbiez & Borges 2010; Trovati et al. 2010), which the open rubber canopies do not provide or provide in less quantity. Also, given their mostly diurnal behavior (91% of captures registered during the day), using less the rubber crops reduces their chances of human encounters. However, coati capture rates vary greatly between studies using different sampling methods, for example this study and the study conducted

by Trolle (2003) in the Acurí forests of the Pantanal found coatis common, whereas Lyra-Jorge et al. (2008) found them rare in a semi-deciduous forest in a eucalyptus/sugar-cane mosaic. Even studies focusing exclusively on forest habitats have frequently recorded few coatis when compared to other species (Tobler et al. 2008; Paschoal et al. 2012; Carvalho et al. 2013), indicating that habitat may not be by itself an adequate explanation for understanding coati distributions. My results showed considerably higher capture rates in relationship with other members of the community, which may be the result of the fact that it was the only species that showed a consistently strong attraction towards the lures observable by the behavior displayed in the photographs, and of their likely concentration of foraging activities within forest areas, known to increase detection probabilities (Cove et al. 2013).

The low number of captures of crab-eating raccoons is surprising, as I found tracks of this animal along the roads throughout the area and they are seen occasionally along the roads at night. Other studies conducted in the state of Bahia also found raccoons to be common in other agroforestry systems (Cassano et al. 2009; Cassano et al. 2012). I believe that my results are a sampling artifact and further research is needed to elucidate the factors that affect the detectability of this species. On a larger regional scale raccoons are widely reported in all landscape types and track registers indicate that they are habitat specialists in that they are more common near wetland habitats, but generalists in terms of broader habitat classifications (i.e. they exploit wetland habitats wherever these occur in the regional landscape) (Flesher 2006).

I only captured pumas twice with the camera traps, one in a forest and one in a riparian area, but regularly found scats, tracks, and rakings in all forest habitats and sometimes in the rubber groves,

indicating that they used all the habitats in the study area. The small size of the study area relative to the home range of pumas suggests that there are few individuals inhabiting the area. The low number of captures may be related to the fact that pumas regularly use trails and unpaved roads (Foster et al. 2010), and thus the placement of the cameras independently of the trail network may have made my sampling design inadequate for determining the habitat use of this species.

There was one terrestrial carnivore in the community that was not captured by the camera traps: the jaguarundi. Although personnel from the reserve and I did see it several times in different habitats before, during and after the study period, interviews in the broader region conducted by Flesher (2006) indicate that the jaguarundi is rarely seen. These results are consistent with other studies in areas with different levels of human disturbance and where the species has not been recorded or has been recorded with very low capture rates (Tobler et al. 2008; Cassano et al. 2012; Cove et al. 2013).

In terms of future studies, it is clear that there is a necessity for accounting for the difference in detection probabilities as a result of the usage of different equipment. Many global databases are including results from different studies and in those cases results must be analyzed with care when obtained through different equipment. Future carnivore studies in the REM should be directed towards telemetry studies, given that the effect of factors that may affect the carnivore community at a larger scale (e.g. the 13,000-ha forest block that extends beyond the study area and that is connected to one of the sampled fragments) remains unclear. Therefore, telemetry based studies could provide valuable information on how individuals move around the larger landscape.

Finally, I call for caution when providing study-based conclusions about the ecological requirements associated with the conservation of carnivore species, as results obtained in these studies are always dependent on the methods used and on the detection probabilities of the species. I agree with Banks-Leite et al. (2014) that in tropical areas and for reasons such as the rarity of the species (or simply the complexity of the logistics), it can be difficult to implement models that adjust for imperfect detection. However, it is the ethical obligation of researchers to try to minimize the effect of covariates on the detection probability or to be conservative at providing conclusions as in many occasions there may be unknown factors affecting the detections of the species. Providing non-conservative conclusions about species with low samples sizes, low number of sampled sites, low sampling effort, low detection probabilities, or ignoring the fact that sometimes many species present higher detection probabilities in disturbed ecosystems, either because of concentrated foraging activities or because aspects related to visibility, may lead to wrong conclusions and therefore mislead conservation actions. In addition, although the assumption under which the sighting of an animal in a specific discrete habitat point, is an indicator of the suitability of that habitat for the long-term viability of the species seems (and maybe is) obvious, other factors affecting populations at different temporal and spatial scales, which are usually not considered in ecological studies (e.g. physical and reproductive health) must be considered.

On the sampling and statistical methods

The benefits of camera trapping are vast as well as the information that can be obtained through their usage; however, the limited information I collected on certain species such as raccoons and pumas, shows, not surprisingly, that the grid scheme as used in this study for all the carnivores' species may be limiting due to the fact that animals do not move randomly in the landscape. On

the other hand, although the experimental design depends completely on the study objectives, focusing specifically on one species biases the information that is obtained about others. The integration of methods, each one of them with its advantages and disadvantages, is essential in understanding the ecology of the carnivore species: line transects, interviews, GPS collaring and analyses from scats are other ways to collect information and that are complementary to mammal surveys using camera trapping.

In statistical terms, the wide posterior intervals for habitat use probability that reach 1.00 in all cases for tayras and wildcats, are due to their low detection probabilities (<0.15), which made it difficult for the model to distinguish between a site where the species is truly absent and a site where it was simply not detected, particularly when the number of sampling periods is < 7 (MacKenzie et al. 2002). This limitation seems to happen most where the species exhibit a moderate level of captures and a low detection probability (Figure 1.5); therefore, indicating that for the model a species that is moderately common but difficult to detect, as is the case for tayras and wildcats, could be or could not be anywhere.

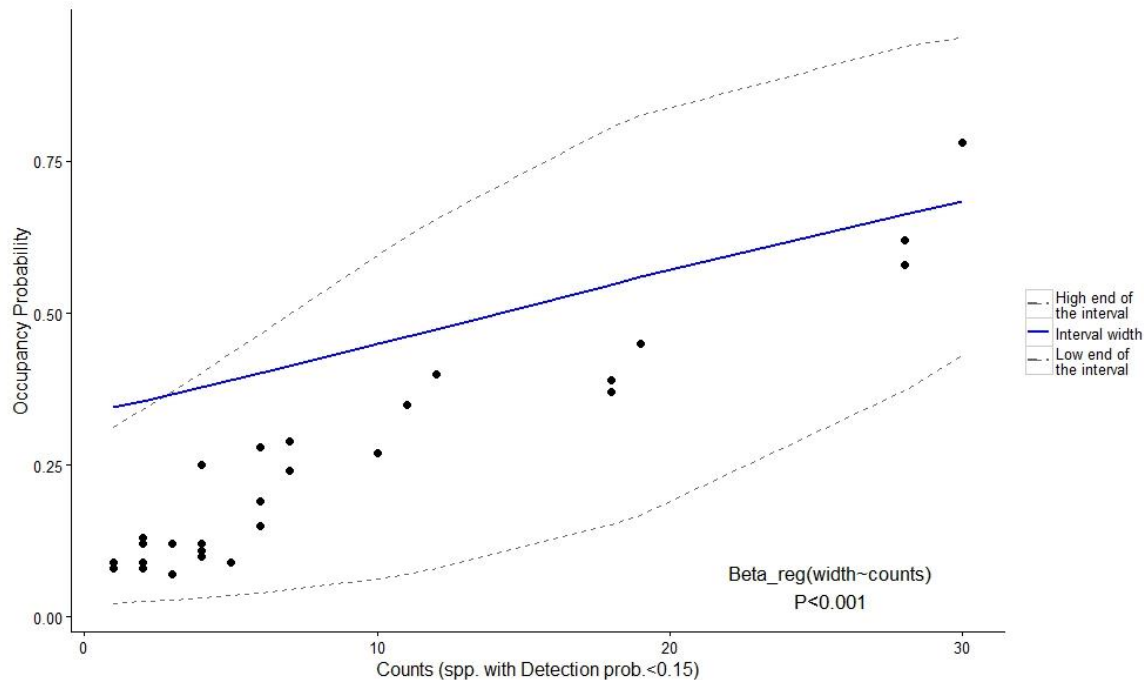


Figure 1.5. Relationship between the number of detections (counts or captures) and the predicted width of the interval (high end–low end) of the occupancy parameter for species with detection probability <0.15 in multispecies occupancy models. Data taken from Zipkin et al. 2009.

CONCLUSIONS AND RECOMMENDATIONS

Although conclusions on the specific minimum amount of forests and riparian areas that are necessary in agricultural systems to conserve carnivore populations in the long term is out of the scope of this research, it can be concluded from my results that rubber/forest landscapes may play a significant role in the conservation of carnivore communities in the Atlantic forest (See methods for a more detailed description on my area of study). Recommendations on how much area of native vegetation is required to sustain carnivore populations, not only require information beyond habitat use but deep analysis on why such habitats are being used by wildlife. Deeper analyses based on the natural history of the species, factors at a local scale (e.g. human interactions with the species of interest) and at a regional scale, as well as on multispecies interactions and long term

genetic viability, should be considered before providing specific guidelines for conservation. At hand, actions directed towards preserving the extant forested and riparian areas, and maintaining the well-developed inter-rows, would allow this crop, increasingly in demand, to be environmentally sustainable.

PERMITS – ETHICAL CONSIDERATIONS

I conducted this research with approval of the Animal Care and Used committee (IACUC) of Michigan State University under the AUF # 11/12-208-00. In addition, I collected the data with approval of the Brazilian government under the CNPq permit # 001308/2012-2.

APPENDIX

APPENDIX

OpenBUGS code for fitted model

```
model{

  #Create priors on the community level

  a0.mean ~ dunif(0,1)
  mu.a0 <- log(a0.mean)-log(1-a0.mean)
  tau.a0 ~ dgamma(0.01,0.01)

  a1.mean ~ dunif(0,1)
  mu.a1 <- log(a1.mean)-log(1-a1.mean)
  tau.a1 ~ dgamma(0.01,0.01)

  a2.mean ~ dunif(0,1)
  mu.a2 <- log(a2.mean)-log(1-a2.mean)
  tau.a2 ~ dgamma(0.01,0.01)

  b0.mean ~ dunif(0,1)
  mu.b0 <- log(b0.mean)-log(1-b0.mean)
  tau.b0 ~ dgamma(0.01,0.01)

  b1.mean ~ dunif(0,1)
  mu.b1 <- log(b1.mean)-log(1-b1.mean)
  tau.b1 ~ dgamma(0.01,0.01)

  #Create priors on the species specific level
  for (i in 1:N) {
    a0[i] ~ dnorm(mu.a0, tau.a0)
    a1[i] ~ dnorm(mu.a1, tau.a1)
    a2[i] ~ dnorm(mu.a2, tau.a2)
    b0[i] ~ dnorm(mu.b0, tau.b0)
    b1[i] ~ dnorm(mu.b1, tau.b1)

    # Estimate the occupancy probability (latent Z matrix) for each species i at each at site j.
    for (j in 1:J) {
      Z[j,i] ~dbin(psi[j,i],1) # True occurrence of species i at site j
      psi[j,i] <-1/(1+exp(-lpsi[j,i]))
      lpsi[j,i] <-min(999,max(-999, lpsi[j,i])) #stabilizing the logit
      lpsi[j,i] <-a0[i] + a1[i]*fore[j] + a2[i]*rip[j]
```

```

#Create a loop to estimate detection for species i at point j during sampling period k.
for (k in 1:K[j]) {
X[j,k,i] ~dbin(mu.p[j,k,i],1)
mu.p[j,k,i] <-Z[j,i]*p[j,k,i]
p[j,k,i] <-1/(1+exp(-lp.lim[j,k,i]))
lp.lim[j,k,i]<-min(999,max(-999, lp[j,k,i])) # Stabilizing logit
lp[j,k,i] <- b0[i] + b1[i]*cam[j,k]
Xnew[j,k,i] ~ dbin(mu.p[j,k,i],1)

#Create simulated dataset to calculate the Bayesian p-value
d[j,k,i]<- abs(X[j,k,i] - mu.p[j,k,i])
dnew[j,k,i]<- abs(Xnew[j,k,i] - mu.p[j,k,i])
d2[j,k,i]<- pow(d[j,k,i],2)
dnew2[j,k,i]<- pow(dnew[j,k,i],2)
}

dsum[j,i]<- sum(d2[j,1:K[j],i])
dnewsum[j,i]<- sum(dnew2[j,1:K[j],i])
} }

# Derived quantities - Calculate the discrepancy measure, defined as the mean (p.fit >p.fitnew)

p.fit<-sum(dsum[1:J,1:N])
p.fitnew<-sum(dnewsum[1:J,1:N])

for (i in 1:N) {

sites.z [i]<- sum(Z[1:90,i]) # Number of sites occupied

mean.psi[i]<-mean(psi[1:90,i]) # Avg occupancy prob. across all habitats

mean.psi.forest[i] <-exp(a0[i]+a1[i])/(1+exp(a0[i]+a1[i])) # Occ. in forest
mean.psi.riparian[i] <-exp(a0[i]+a2[i])/(1+exp(a0[i]+a2[i])) # Occ. in riparian
mean.psi.rubber[i] <-exp(a0[i])/(1+exp(a0[i])) # Occ. in rubber

mean.p[i]<-mean(p[1:90,1:4,i]) # avg.detection prob.

mean.p.bush[i] <- exp(b0[i])/(1 + exp(b0[i])) # Avg. detection for Bushnell
mean.p.tig[i] <-exp(b0[i]+b1[i])/(1+exp(b0[i]+b1[i])) # Avg. detect. for Tigrinus

} # Exclude from loop average all spp.

mean.p.bush.all<-exp(b0[1:5])/(1+exp(b0[1:5])) # Average p. Bushnell
mean.p.tig.all<-exp(b0[1:5]+b1[1:5])/(1+exp(b0[1:5]+b1[1:5])) # Average p Tigrinus
}

```

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REFERENCES

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CHAPTER 2. CARNIVORES IN AN AGRICULTURAL LANDSCAPE IN BRAZIL: IMPLICATIONS FOR CARNIVORE CONSERVATION IN TROPICAL AGRICULTURAL SYSTEMS².

ABSTRACT

Biodiversity conservation in agricultural landscapes is essential for the long-term preservation of carnivore communities and their roles in ecosystem functioning. However, proposing strategies to increase the contribution of these landscapes to the conservation of carnivores requires detailed understanding of the species-specific responses to the different factors associated with agricultural land use. My research aimed to assess the effect of landscape-related variables (distance to native arboreal vegetation and to roads), human-related variables (distance to human settlements and frequency of site use by domestic dogs *Canis familiaris*), and resource-related variables (distance to cocoa *Theobroma cacao* crops and frequency of site use by small mammals) on the frequency of site use of four carnivore species (crab-eating fox *Cerdocyon thous*, tayra *Eira barbara*, small and medium spotted cats *Leopardus* spp., and South American coati *Nasua nasua*). Results showed that the responses to these effects vary per species and in many occasions opposite effects were observed. I found that in the case of the crab-eating foxes and the South American coatis, their frequency of site use were best predicted by landscape-related variables. The frequency of site use by tayras was best predicted by resource-related variables. In the case of the small and medium spotted cats, the factors that best predicted their frequency of site use were associated with human-

² This chapter will be submitted for review as a research paper

related variables. These findings elucidate the complexity of the actions required to proposed more appropriate management strategies for carnivore conservation in tropical agricultural systems.

Key Words: Mammalian carnivores, Atlantic forest, Agricultural landscapes.

INTRODUCTION

The expansion of the agricultural frontier represents one of the main threats to tropical biodiversity conservation as the need for food and other agricultural-based products is constantly increasing under an already ongoing climate change scenario (Laurance et al. 2014). It is estimated that 48.6% of the terrestrial surface of the planet is under agricultural use (temporal and permanent crops and pastures) (The World Bank 2016). In addition, it is projected that by the end of the century the world population will reach 10.9 billion (3.7 billion more than in 2013) if the fertility rate remains constant at current levels, with most growth projected to occur in developing countries (United Nations 2013). Although the agricultural production (food products strictly) has been slowing down over the past decades, it will still need to increase globally by 70% by 2050, and in the case of the developing countries by 100%, in order to supply the population demand (Bruinsma 2009). Such expansion of the agricultural frontier is expected to occur at a higher rate in tropical areas due to its favorable climate for year round production and the generally lower price of its land when compared with temperate areas (Laurance et al. 2014). Therefore, it is clear that one of the main challenges in tropical biodiversity conservation is to seek strategies that promote conservation in agricultural systems.

Land transformation into agricultural systems may affect carnivore populations in several ways: 1) by habitat degradation (Crooks 2002; Crooks et al. 2011), 2) by altering the richness and abundance of food resources (i.e. fruit and prey)(Mortelliti & Boitani 2007), 3) by higher exposure to human activities (either due to edge effect and/or road establishment) (Basille et al. 2013), and 4) by facilitating the arrival of non-native competitors/predators (e.g. domestic dogs (*Canis familiaris*)) and their associated diseases (Vanak & Gompper 2010). However, the consequences of the aforementioned effects on carnivore populations depend not only on their directionality, magnitude and intensity but on the ecological requirement of the species involved (chapter 1, Caruso et al. 2016).

The case of the carnivore communities in the Atlantic forest of Brazil is particular due to the high diversity of this hotspot and its vast destruction, which is estimated to have left less than 16% of its original area in highly fragmented patches (Ribeiro et al. 2009). This hotspot holds today more than 100 million people, 3,000 cities and vast areas mostly dedicated either to urban or agricultural purposes (Ribeiro et al. 2011). In landscapes dominated by agricultural lands, actions such as the partial retention of native cover, the improvement of agricultural practices or technologies, as well as the implementation of more research-based governmental policies are necessary to mitigate the impact of agricultural activities, not only on carnivore species but on wildlife in general (chapter 1, Gibson et al. 2011; Ferreira et al. 2012; Laurance et al. 2014).

Understanding the effect of the factors related to farming on the frequency of site use by carnivore species is essential in proposing management strategies that support carnivore conservation in agricultural landscapes in the long term. The agricultural landscape here studied is characterized

by the predominance of rubber (*Hevea brasiliensis*) and cocoa crops (*Theobroma cacao*) (Flesher 2006). Although a previous study conducted in this area demonstrated the used of seventy years-old rubber areas by carnivores (Chapter 1), there are no reported animals in the area that feed on rubber seeds (Flesher 2006). The case of the cocoa is different as it is consumed by some species. In addition, the direct food resources offered by cocoa crops to wildlife increase when planted along with banana, as banana is consumed by most of the frugivorous/omnivorous wildlife (Flesher 2006). Here I assessed the effect of landscape-related variables (distance to native arboreal vegetation and to roads), human-related variables (distance to human settlements and frequency of site use by domestic dogs), and resource-related variables (distance to cocoa crops and frequency of site use by small mammals) on the frequency of site use of four carnivore species (crab-eating fox *Cerdocyon thous*, tayra *Eira barbara*, small and medium spotted cats *Leopardus* spp. (hereafter referred as wildcats), and South American coati *Nasua nasua*). These findings will contribute to build the scientific basis for the development of management strategies for carnivore conservation in tropical agricultural systems.

METHODS

Study Site

I conducted this study in the Brazilian state of Bahia, in a rural landscape between the municipalities of Ituberá and Igrapiúna. The study area has an extension of 4,400 ha and is composed mainly by forests (with different levels and types of disturbance), riparian areas, wetlands, rubber crops (of different ages) and cocoa crops (Figure 2.1). Most of the closest cocoa areas to my sampling sites were planted recently (maximum 8 years old), in areas that were

previously rubber monocultures (*Hevea brasiliensis*). The cocoa crops are shaded in their initial years with banana trees (*Musa* spp.) and in many cases mixed with rubber trees. After planting, cocoa crops start producing in 3 years, reaching full production in 7 years. Rubber trees start producing in 7-8 years (Flesher 2006). In the area, there is also an extensive network of unpaved roads used mainly for transporting people and goods to the nearest interstate highway.

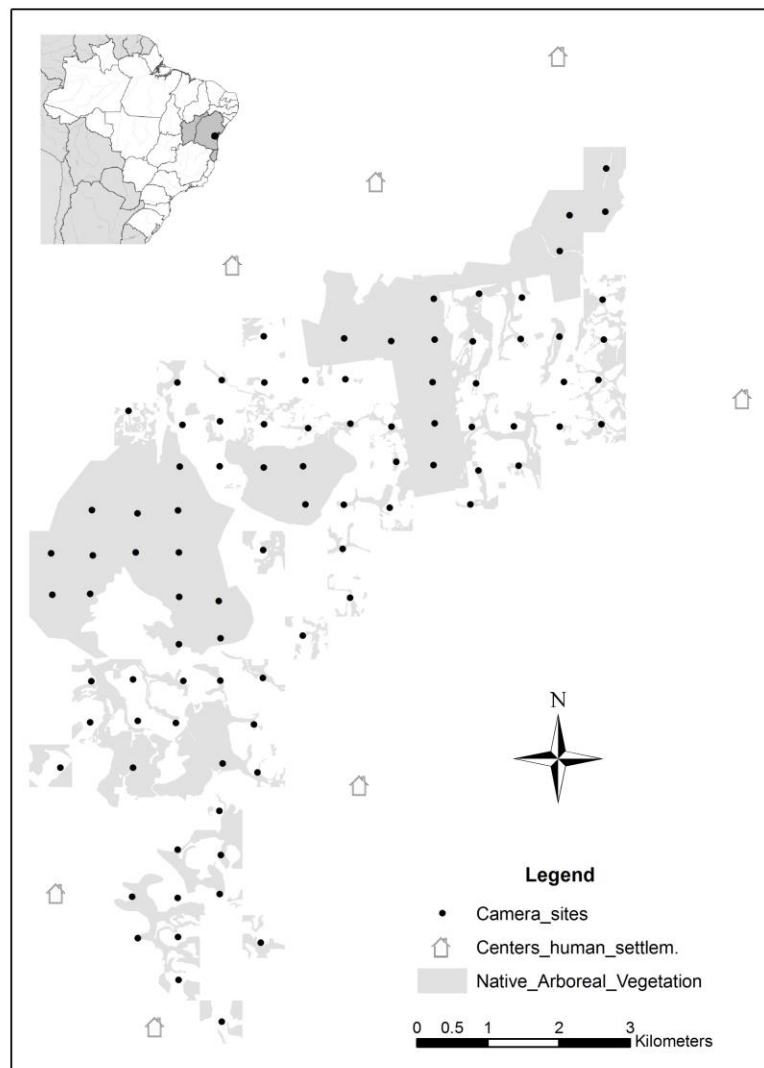


Figure 2.1. Study area and location of the sampling sites, native arboreal vegetation fragments (which includes forests and riparian areas) and closets human settlements (agglomeration centers). Igrapiúna, Bahia, Brazil, 2013-2014.

Data collection

Information on the frequency of site use per each one of the four carnivore species studied as well as of domestic dogs and small mammals, was obtained from 7954 camera days. Camera trap surveys followed a protocol previously described (chapter 1). The variable denominated small mammals included all species of opossums and rodents, except for those species registered to be heavier than 500 grs. in the literature (e.g. lowland paca *Cuniculus paca* and red-rumped agouti *Dasyprocta leporina*) (Emmons & Feer 1997). Frequency of site use per each species was defined as the number of captures per species per camera site (a species detection/24 hrs.). A total of 90 camera sites were analyzed. Thus, the dataset used comprised information for four species and 90 sites. The data set included 479 captures distributed in the following manner: coati (n=208), domestic dog (n=143), crab-eating fox (n=80), tayra (n=26), and wildcats (n=22) (Chapter 1).

The closest Euclidean distances (km) from each camera site to fragments of native arboreal cover (which includes riparian areas and forests of different successional stages), roads, human settlements, and cocoa crops were derived from a GeoEye high spatial resolution satellite image taken in the area in 2011 using ArcGIS 10.2. When necessary the information extracted from the geographical information system was validated against field-collected data. Given that some settlements' houses are scattered, I determined the center of agglomeration of each settlement by using the function kmeans in R (R Core Team 2016).

Statistical analysis

All statistical analyses were conducted in R (R Core Team 2016). Preliminary analyses showed that all correlations between the explanatory variables ranged between -0.32 and 0.43. Collinearity among the explanatory variables was tested by using the function `vif` in the package `usdm` (Naimi 2015), with all VIF values ≤ 1.36 , indicating lack of collinearity. Given that the sampling sites were located in specific habitats (see chapter 1 for specific description on the sampling protocol) and that crab-eating foxes and South American coatis showed a significant habitat use preference in the area (chapter 1), I included in the models for these two species their respective mean habitat use probability (chapter 1) as an offset to account for this known variability (Kéry 2010) (Table 2.1). By forcing the coefficient of habitat use probability to be 1, the offset is accounting for the additional variation resulting from locating the sampling sites in different habitats only for those species that have shown significant habitat preference. Next, I conducted a diagnosis for overdispersion of count data by visually inspecting the graphical posterior predictive checks, comparing the proportion of zeroes observed in my data with the proportion of zeroes generated under simulated Poisson models (Gabry & Goodrich 2016a). It was observable that the count data for South American coatis and crab-eating foxes were overdispersed, specifically zero-inflated (Figure 2.2), while the data for tayras and wildcats were not. Therefore, I analyzed the data for tayras and wildcats using Poisson models, and for South American coatis and crab-eating foxes using a negative binomial model, given the capability of this model to fit overdispersed count data (i.e. with variance larger than the mean) (Venables & Ripley 2002). All explanatory variables were standardized and centered in zero. I fit all models (Table 2.1) using Bayesian approach, with non-informative priors and through the package `rstanarm` (Gabry & Goodrich 2016b).

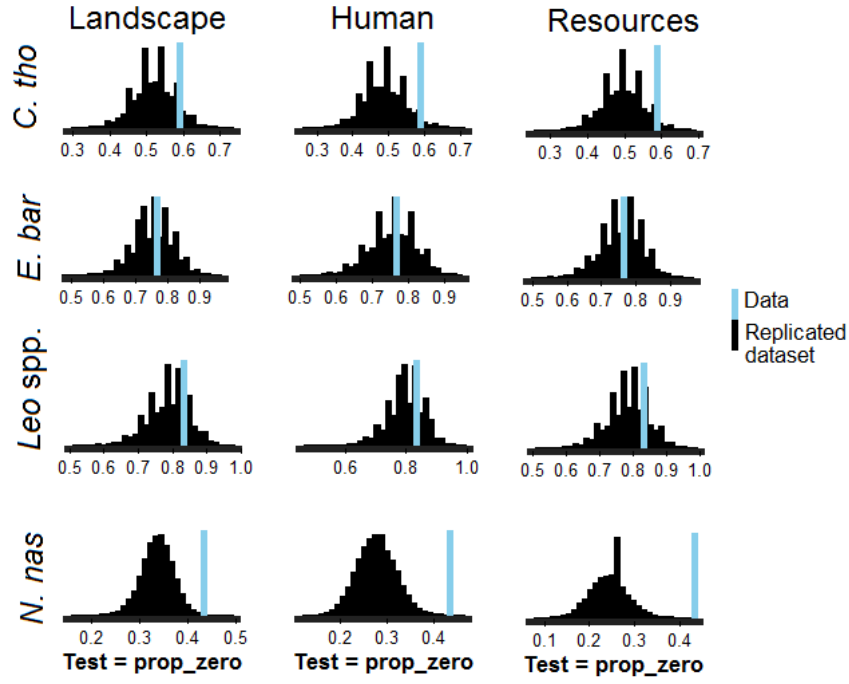


Figure 2.2. Graphical posterior predictive checks comparing the proportion of zeroes observed in my data (blue line) with the proportion of zeroes generated under simulated Poisson models (black lines). The Poisson models for crab-eating foxes *C. thous* and South American Coatis *N. nasua* include an offset to account for the differences in habitat use probability.

Table 2.1. Models specification where, λ_i is the mean or expected frequency of use of site i , $1 * \log(Hab_i)$ is the offset for habitat use probability per species given the habitat where site i is located, α_0 is the frequency of use of a site with average conditions (on a log scale and given that all explanatory variables have zero mean), and coefficients α_1 and α_2 are the effects (on a log scale) of the explanatory variables.

Category	Offset	Family	Model specification
Fox (<i>Cerdocyon thous</i>)			
Landscape	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(hab_i) + \alpha_0 + \alpha_1 disveg_i + \alpha_2 disroad_i$
Human	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(hab_i) + \alpha_0 + \alpha_1 dishuma_i + \alpha_2 dogs_i$
Resources	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(hab_i) + \alpha_0 + \alpha_1 discocoa_i + \alpha_2 SmMamls_i$
Tayra (<i>Eira barbara</i>)			
Landscape	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 disveg_i + \alpha_2 disroad_i$
Human	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 dishuma_i + \alpha_2 dogs_i$
Resources	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 discocoa_i + \alpha_2 SmMamls_i$
Wildcats (<i>Leopardus spp.</i>)			
Landscape	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 disveg_i + \alpha_2 disroad_i$
Human	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 dishuma_i + \alpha_2 dogs_i$

Table 2.1. (cont'd).

Resources	No	Poisson	$\log(\lambda_i) = \alpha_0 + \alpha_1 \text{discocoa}_i + \alpha_2 \text{SmMamls}_i$
Coati (<i>Nasua nasua</i>)			
Landscape	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(\text{hab}_i) + \alpha_0 + \alpha_1 \text{disveg}_i + \alpha_2 \text{disroad}_i$
Human	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(\text{hab}_i) + \alpha_0 + \alpha_1 \text{dishuma}_i + \alpha_2 \text{dogs}_i$
Resources	Yes	Neg.Bin	$\log(\lambda_i) = 1 * \log(\text{hab}_i) + \alpha_0 + \alpha_1 \text{discocoa}_i + \alpha_2 \text{SmMamls}_i$

I ran each model with 4 chains each for 10,000 iterations, half of which were automatically discarded after a warming up period. I assessed convergence of the model by looking at the R-hat values, with values <1.1 being considered acceptable (Gelman & Rubin 1992). I assessed model fit by measuring the discrepancy between the mean (fit.m) and the standard deviation (fit.sd) of the observed data and data generated under the proposed model through the estimation of the Bayesian posterior predictive p-values (ppp-value), with values close to 0.50 indicating a perfect fit and values near 0 or 1 indicating a poor fit (Carpenter et al. 2016). Finally, model selection was done by using the Watanabe-Akaike information criterion (WAIC) and leave-one-out cross-validation (LOO) values, which are fully Bayesian criteria for estimating pointwise out-of-sample prediction accuracy from a fitted model (Vehtari & Gelman 2014).

RESULTS

Results suggested that the factors that influence the frequency of site use of carnivores are different among species (Figure 2.3). All the models presented in here are statistically consistent as none of the Bayesian posterior predictive p-values registered values smaller than 0.05 or larger than 0.95 (Table 2.2). Therefore, although in terms of model comparison not all of them had equal predictive

ability, the fact that all of them exhibited in general a good fit allows me to discuss the effect of the different variables in the different models.

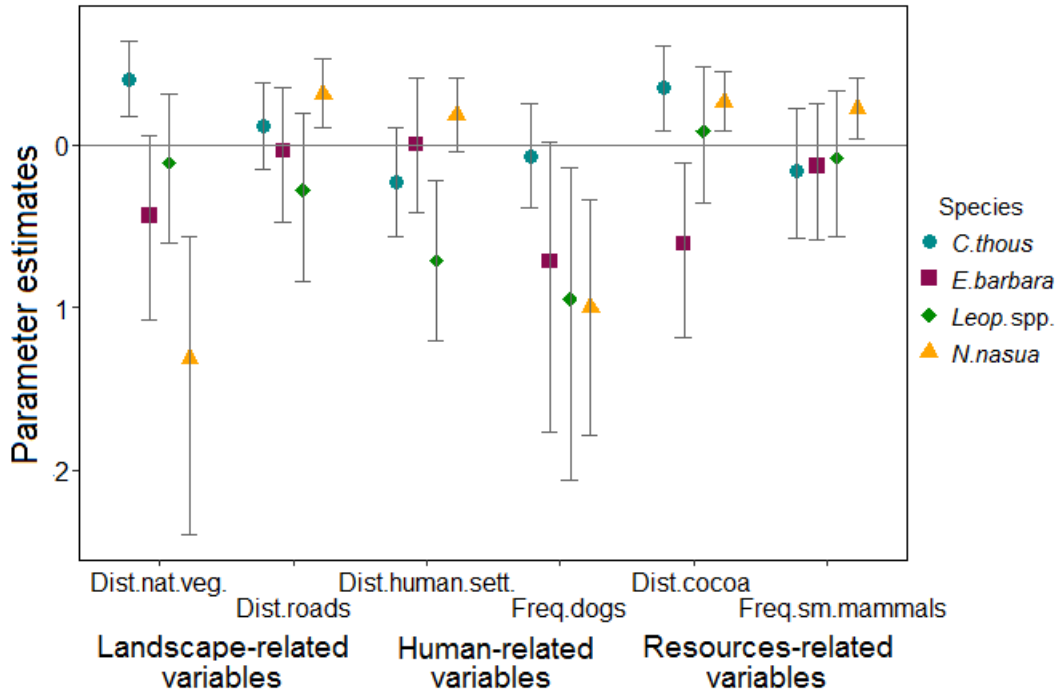


Figure 2.3. Mean and 95% posterior intervals for parameter estimates resulting from the different sets of models tested per species. Intervals crossing zero suggest no statistical significance.

Distance to native arboreal vegetation had a significant positive effect on crab-eating foxes and a negative effect on South American coatis. The distance to roads had a significant positive effect only on South American coatis. The distance to human settlements had a significant negative effect on the wildcats and although not significant at 95% Bayesian posterior interval, it exhibited a certain positive effect on South American coatis. The frequency of site use by domestic dogs had a significant negative effect on both wildcats and South American coatis, and although non-significant at 95% Bayesian posterior interval, it showed a trend of negative effect on tayras. Distance to cocoa exhibited significant positive effects on crab-eating foxes and South American

coatis, and an opposite, negative effect on tayras. Finally, the frequency of site use by small mammals only exhibited a significant positive effect on South American coatis (Figure 2.4).

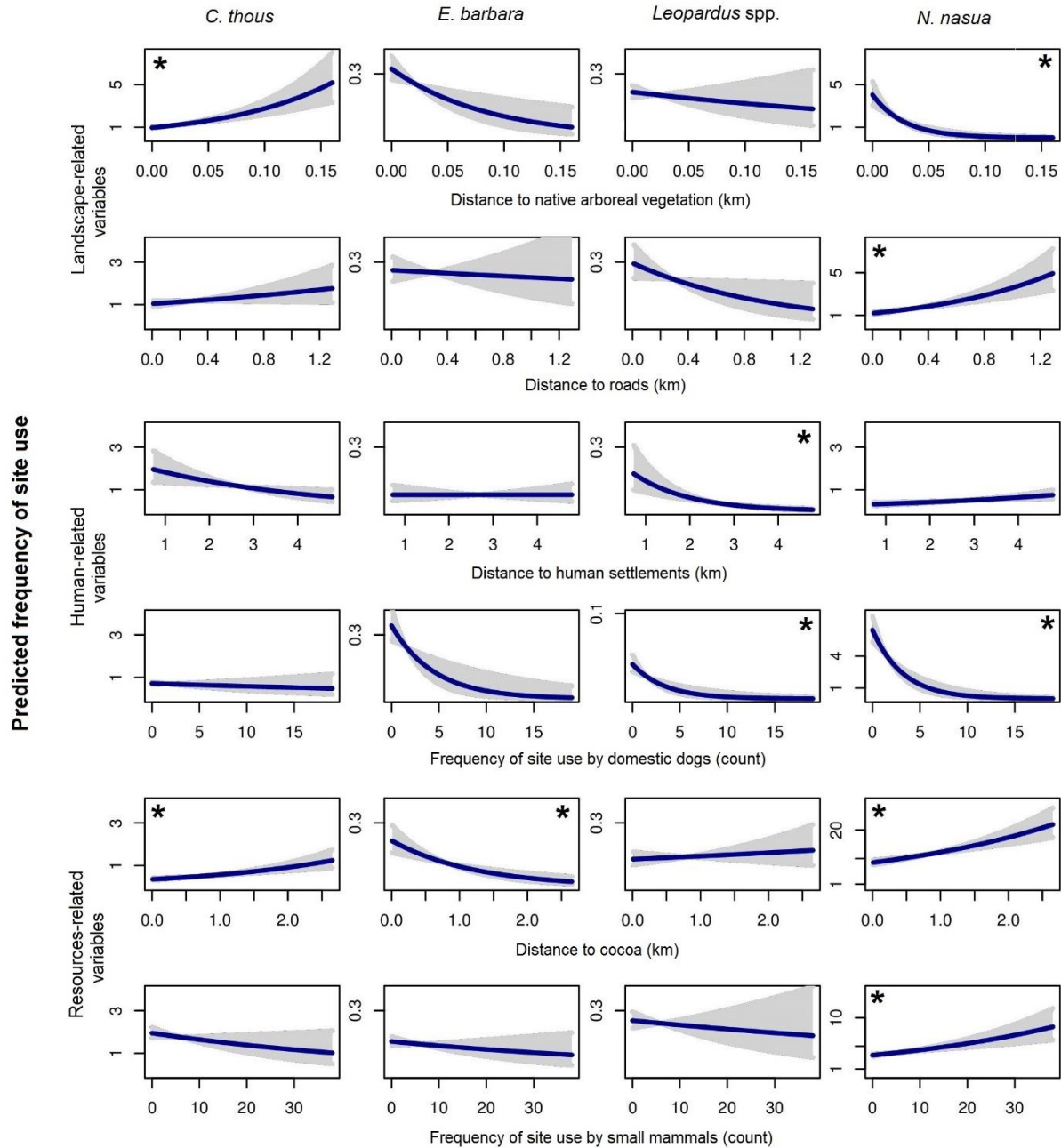


Figure 2.4. Predicted frequency of site use by four carnivore species as a function of six variables. The gray areas represent the standard deviation. The * indicates significance at a 95% posterior interval.

Table 2.2 Posterior predictive p-values for the mean (ppp-val.m) and the standard deviation (ppp-val.sd), WAIC and LOO values.

Model	ppp-val.m	ppp-val.sd	WAIC	LOO
<i>Fox (Cerdocyon thous)</i>				
Landscape-related vars.	0.48	0.42	200.4	200.5
Human-related vars.	0.54	0.58	210.74	210.95
Resources-related vars.	0.57	0.66	205.24	205.34
<i>Tayra (Eira barbara)</i>				
Landscape-related vars.	0.55	0.7	129.03	129.24
Human-related vars.	0.55	0.7	128.22	128.34
Resources-related vars.	0.55	0.67	125.2	125.3
<i>Wildcats (Leopardus spp.)</i>				
Landscape-related vars.	0.56	0.95	124.72	124.94
Human-related vars.	0.56	0.88	116.2	116.4
Resources-related vars.	0.56	0.95	125.43	125.52
<i>Coatis (Nasua nasua)</i>				
Landscape-related vars.	0.54	0.51	294.4	295
Human-related vars.	0.58	0.58	302.15	302.24
Resources-related vars.	0.64	0.62	306.3	306.38

In terms of which models predicted better than others the frequency of site used by the different species in this community, I found that the frequency of site use of crab-eating foxes and South American coatis was best predicted by landscape-related variables, whereas tayras' frequency of site use was best predicted by resource-related variables, and wildcats' frequency of site use by human-related variables. The high values, yet ≤ 0.95 , of posterior predictive p-values for the standard deviation of the wildcats indicated that the actual dataset had standard deviations greater than most the simulated datasets (Table 2.2).

DISCUSSION

The differences in carnivores' responses to different factors associated with agricultural landscapes demonstrate the necessity of understanding this variability at the species level to propose more inclusive actions towards the different members of the carnivore communities and their roles in ecosystem functioning. Although I am aware of the non-exclusive effect of the models here tested, and that other combinations/additions of factors may increase their predictive ability, the fact that for all species the difference in WAIC and LOO values between the best model and the others is equal or higher than three, allows me to conclude that there is a clear difference in terms of the predictive abilities of the tested models under a parsimony principle.

The increase in frequency of site use by crab-eating foxes in areas farther from native arboreal vegetation is consistent with results from other studies that have shown the preference of this species for open, agricultural areas (Chapter 1, Lyra-Jorge et al. 2008; Cassano et al. 2012). This would also explain the fact that the model that best predicted the frequency of site use by this species was the one that accounted for variables at the landscape level. Their increase in frequency of site use in areas further from cocoa crops can be explained by the fact that relatively young cocoa crops, like the ones in the study area may not provide as many resources to this non-scansorial species, whose diet depends solely on the resources found on the ground. The lack of resources of the cocoa crops could also be the result of their intensive management. The cocoa crops in the area have been described as providing few fruit resources, partly due to the open understory and the absence of secondary forest vegetation (Flesher 2006). In addition, it is likely that the abundance of small vertebrates and invertebrates, which are also part of the diet of the crab-eating foxes (Gatti et al. 2006; Rocha et al. 2008), are reduced in these areas given the

frequent usage of herbicides (i.e. glyphosate), fungicides and insecticides in the cocoa crops adjacent to my study site (Flesher 2006). The use of these chemicals has been demonstrated to have a short-term direct and/or indirect negative effect on the abundance of many small sized wildlife species (Santillo et al. 1989; Lautenschlager 1993). The lack of effect of human-related variables is not surprising as their nocturnal behavior reduces encounters with humans and domestic dogs (Chapter 1). The lack of effect of the site use by small mammals is also not surprising as small mammals are only part of the broad diet of this opportunistic feeder.

In the case of the tayras, the higher frequency of site use in areas closer to cocoa is consistent with other studies that have found this scansorial species to be common in cocoa crops (Harvey et al. 2006; Cassano et al. 2009). Their higher frequency of site use in these areas is related to their consumption of cocoa and banana (Flesher 2006; Soley 2012), the latter planted only in the initial years of the cocoa crops establishment. Although not statistically significant at 95% Bayesian posterior interval (PI), the PI slightly crossing zero for the effect of native vegetation cover may indicate that given the scansorial locomotion of this species, there may be a trend for tayras to prefer sites with closed/continuous canopies (regardless of being native vegetation or tree crops) over open sites. This may be because they can forage and move on the ground and on the trees. The similar trend for the effect of frequency of site use by domestic dogs indicated that tayras could tend to avoid using sites frequently used by domestic dogs (chapter 1). However, the non-significance at 95% Bayesian posterior interval for this effect may be the result of the fearless behavior of this mostly diurnal species, as described by farmers in the area, and to the fact that their climbing abilities would allow them to avoid direct confrontation with this non-native predator. The relative absence of conflict between farmers and this species in the region (chapter 2) and the fact that tayras are not a prime quarry for hunters (Flesher 2006) may also explain the

non-effect of distances to human settlements and roads. Their generalist diet may explain the no effect of site use by small mammals (Presley 2000).

Wildcats presented significantly less frequency of site use in areas further from human settlements, yet this frequency decreases significantly in sites frequently used by domestic dogs. This pattern can be explained by the more specialized diet of this group which includes mainly vertebrates (Wang 2002; Bianchi et al. 2010; Bianchi et al. 2011) and which would attract them to poultry and small vertebrates associated with the multi-crop systems near the houses in the settlements. The nocturnal behavior of the wildcats (chapter 1) would allow them to roam around the settlements while avoiding encounter with the inhabitants. Although this nocturnal behavior also reduces the chances of encounters with dogs, the avoidance of sites frequently used by dogs can be explained by the demarcation of the territory that dogs display. This is supported by other studies that have reported felid's avoidance of areas used by dogs (Lenth et al. 2008). Although some species of spotted cats, such as the margay and the ocelot, have been found to be highly associated with forested areas (Michalski et al. 2011; Massara et al. 2015; Jordan et al. 2016), it is possible that the lack of effect of factors such as distance to native arboreal cover found in here, is related to the fact that this group includes several species and that each species may have a different response to the variables here examined. However, even with this limitation derived from the inclusion of all the species into one group, this study showed that, all wildcats' frequency of site use was significantly affected and best predicted by human-related variables.

In the case of the coatis, their decrease in frequency of site use in areas farther from the native arboreal vegetation is supported by earlier studies that have shown that this is mainly a forest

species (chapter 1, Desbiez & Borges 2010; Trovati et al. 2010; Cassano et al. 2012). This, may be due to a need of robust canopies that can offer resting places to their large groups (Desbiez & Borges 2010). In addition, their significant avoidance of sites near roads, cocoa crops, sites frequently used by dogs, as well as their trend to avoid human settlements, is consistent with previous studies, which have demonstrated that this species avoids encounters with humans and dogs (Alves 1990; Espartosa 2009). Coatis' avoidance of humans can be explained by a local vulnerability to hunting in the area. Such vulnerability is due their large size, group and diurnal behavior (Flesher 2006). The positive significant effect of the frequency of site use by small mammals on the site use of coatis, may be explained by the fact that since coatis avoid humans and dogs, they cannot fully exploit agricultural food resources, so they must rely on resources that are not strictly associated with agricultural lands such as small mammals.

With exception of the frequency of site use by dogs, all the variables studied had a different and in most occasions opposite effects on the different members of the carnivore community. The frequency of site use by dogs had either no effect or negative effect on all species, which is consistent with other findings related to the negative effect of domestic dogs on wildlife (Espartosa 2009; Lacerda et al. 2009; Young et al. 2011; Hughes & Macdonald 2013; Vanak et al. 2014). Differences with other studies on species specific responses to dog-related effects, can be explained by the fact that effects may vary depending on factors such as, the dog's relative position within the carnivore community, their roaming behavior, dependency on human resources, and dogs' population density (Vanak et al. 2014). Most of the dogs in my study area can be classified as "village dogs", which are characterized for being affiliated to a household, heavily dependent on human-resources but that are not confined (Miller et al. 2014). The strong affiliation of the dogs

with their owners was observable while doing the field work; it was common to see the workers biking or walking to their field labors in the morning along with their dogs. The weak correlation found in preliminary analyses between distance to human settlements and frequency of site use by dogs (-0.32), indicates that the roaming behavior of the dogs was not associated with the distance from the settlements, but more likely to happen while accompanying their owners during their field labors.

In terms of conservation, my findings demonstrated that there is a necessity for understanding the species-specific responses of carnivores to agricultural-related factors to propose more appropriate actions for the conservation of carnivore communities and their role on the ecosystem functioning. The observed variation in the responses among species implies a higher complexity in the actions required to conserve these species. This is especially true in many areas in the neotropics where governmental assistance, appropriate governmental policies, landscape planning and management, are extremely weak due to a complex mixture of socio-economic reasons beyond of the scope of this paper. Cocoa and cocoa/rubber crops in the area can become more wildlife friendly by partial tree enrichment in a *cabruca*-like style (Cocoa crops shaded by native forests), which is common towards the South of my study site and which would increase the diversity of primary producers and in turn of their associated resources. In addition, research on the usage of herbicides and pesticides in the area may be useful in elucidating the patterns and factors associated with such usage including misuse. Misuse of pesticides have been reported to be common in areas in the Brazilian Amazon (Schiesari et al. 2013), and there is no reason to believe that such misuse is absent in other parts of the country. The management of dogs is an extremely sensitive topic as they play an important role in the daily activities of the rural workers (e.g. company, vigilance).

They also play a role in conservation by decreasing human-native carnivores' conflicts by protecting livestock and crops from native carnivores (Sepulveda et al. 2014; VerCauteren et al. 2014). In a study conducted in Chile, Sepulveda et al. (2014) found that dogs-wildlife interactions are influenced by the dogs' owners and related to the role of the dog in the household. The same author found that the factor that best explained dog-wild carnivore interactions was related to the ownership of livestock, while the factor that best explained dog-wild prey interactions was low quality food. The latter was also reported by Silva-Rodriguez and Sieving (2011). These findings suggest that the strategies concerning the management of dogs require better knowledge on the human dimensions of the dog-wildlife interactions. This, to propose more realistic strategies that would contribute to the carnivore conservation in agricultural landscapes.

PERMITS – ETHICAL CONSIDERATIONS

I conducted this research with approval of the Animal Care and Used committee (IACUC) of Michigan State University under the AUF # 11/12-208-00. In addition, I collected the data with approval of the Brazilian government under the CNPq permit # 001308/2012-2.

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CHAPTER 3. HUMAN DIMENSIONS OF THE HUMAN-CARNIVORE CO- OCURRENCE IN AN AGRICULTURAL LANDSCAPE IN BRAZIL³.

ABSTRACT

Understanding the factors that affect tolerance towards carnivores is critical for proposing strategies for the conservation of these species, particularly in landscapes where human-carnivore co-occurrence is high and conflicts, consequently, more frequent. The objectives of this research were: 1) to identify the stakeholders' perceived negative effects derived from their co-occurrence with carnivores, and 2) to determine the effect of situational factors (stakes involved, exposure and previous interactions) and psychological factors (likability and perceived benefits, perceived negative effects, and perceived risks) on the tolerance for pumas (*Puma concolor*) in an agricultural landscape in the Northeast of Brazil. I conducted 109 semi-structured interviews in five different human groups in the South of the State of Bahia. Results showed that, at the group level, carnivores, in comparison with non-carnivores (i.e. 12 species, non-members of the order Carnivora), were not the group with the highest frequency of reported negative effects by stakeholders in this agricultural (crop-based) landscape. At a lower taxonomic level, the puma was the second species with the highest frequency of reported negative effects (after the snakes (suborder Serpentes)), and the first among carnivores. The negative impact associated with the puma was in all cases due to fear caused by its presence. I used cumulative link models to assess the factors that most affect tolerance towards pumas. I found that a model containing evaluative

³ This chapter will be submitted for review as a research paper

attitudes (likability) and perceived benefits as explanatory variables, had a 99% probability of being the best model given the data and the set of candidate models. These results suggest that social-based strategies for carnivore conservation must consider the role of psychological factors (e.g. perceived benefits derived from their presence) on the tolerance for these species.

Keywords: Brazilian Atlantic forest, human dimensions, tolerance, carnivores, Puma (*Puma concolor*).

INTRODUCTION

Biodiversity conservation in agricultural landscapes is key to the long-term existence of many species as the areas dedicated to conservation are disproportionately less than the areas dedicated to agricultural purposes. It is estimated that 48.6% of the land surface on the planet is under agricultural use (permanent and temporal crops and pastures), while 14.8% is under some level of protection (The World Bank 2016). In addition, although the rural population have been decreasing over the last decades, it is estimated that as of today 46% of the total world population still lives in rural areas (The World Bank 2016). Given this situation and that human-wildlife interactions are generally more intense in agricultural areas or in areas adjacent to natural areas, especially in those with higher population densities (Distefano 2005), it is clear that human-wildlife interactions determine partially the future of many species. Therefore, understanding how the different dimensions of the human-wildlife interactions influence the tolerance for wildlife is essential in devising strategies for biodiversity conservation.

Theories on behavior, judgments and decision making under risk, have demonstrated that these processes are highly dynamic, multidimensional and strongly influenced by factors such as emotions, anticipated outcomes, subjective probabilities, situational variables and even evolutionary aspects (Loewenstein et al. 2001; Kobbeltvedt & Wolff 2009). Consequently, it is clear that the ways in which humans react towards wildlife would depend, among other factors (e.g. needs), on the perceived benefits, impacts and risks associated with it. In the case of the carnivore species, the largest members of the order are among the species with higher conflict with humans (Treves & Karanth 2003). Conflicts with the smaller species of the order may not be different but have been less studied as their size limit the kind, magnitude and the spatial extent of their perceived effects by the human communities.

The situation of the Atlantic forest of Brazil is particular in the field of human dimensions of carnivore conservation given that 1) nearly 70% of the Brazilian population, about 120 million people, inhabits this heavily fragmented hotspot (Ministry of Environment of Brazil 2013), 2) this biome accounts for 80% of the Brazilian GDP (Ministry of Environment of Brazil 2013), and 3) it is the second richest Brazilian biome in terms of carnivore species with 20 species (Paglia et al. 2012).

To better understand the factors that affect tolerance for carnivores in an agricultural landscape in the state of Bahia, I present here the case study of the puma (*Puma concolor*). I chose the puma as the subject for this study case because: 1) although Jaguars (*Panthera onca*) have been the focus of attention of most of the studies on human-carnivore interactions conducted in Brazil (Marchini & Crawshaw 2015), pumas present also numerous conflicts with human communities due to

predation on livestock and fear associated with their presence (Marchini & Crawshaw 2015), 2) although the puma's relative tolerance of human activities allows them to persist in areas with higher human disturbance in comparison to other carnivores (Ripple et al. 2014), the status of the puma in Brazil is vulnerable (Ministry of Environment of Brazil 2014), and 3) given their role as top predators in places where jaguars have been extirpated, it is important to determine the factors that affect the tolerance for this large predator in order to propose actions for its conservation.

The objectives of this study were: 1) to identify the stakeholders' perceived negative effects derived from their co-occurrence with carnivores, and 2) to determine the effect of situational factors (stakes involved, exposure and previous interactions) and psychological factors (likability and perceived benefits, perceived negative effects, and perceived risks) on the tolerance for pumas. Given that in most parts of the globe, carnivore conservation is partially dependent on the tolerance of human communities towards carnivore species (Treves & Karanth 2003; Treves & Bruskotter 2014), the results presented here provide helpful insights for managers to establish conservation strategies with the aim of increasing tolerance for carnivores.

THEORETICAL BACKGROUND

Tolerance for wildlife

Tolerance for wildlife has been defined as the passive acceptance of wildlife populations (Bruskotter & Fulton 2012). In turn, wildlife acceptance capacity has been defined as the wildlife population level that is acceptable by different groups of stakeholders (Carpenter et al. 2000). Tolerance/acceptance for wildlife, therefore, is expected to vary among stakeholders and in turn among wildlife species, and to be determined by multiple factors, including: situational specifics,

sociodemographic traits, stakes involved, previous experiences and socio-psychological variables such as attitudes and beliefs (Carpenter et al. 2000; Zinn et al. 2000; Wieczorek Hudenko et al. 2010).

Psychological factors

The socio-psychological theory behind the study of the human dimensions of wildlife management is based on a cognitive approach that explores the relationships between values, value orientations, attitudes, behavioral intentions and behaviors associated with wildlife (Vaske & Manfredo 2012). Previous studies on wildlife conservation have focused on cognitive factors, such as attitudes, because of their effect on the tolerance/acceptance towards wildlife species (Zimmermann et al. 2005; Engel et al. 2016).

Under this cognitive approach, attitudes have been defined as evaluations of a person or object (Vaske & Manfredo 2012). Attitudes are considered to have two dimensions, evaluative and cognitive, the first is related to the positive or negative evaluation of an object (e.g. like/dislike wildlife), while the second is related to what a person believes is true about such object (e.g. beliefs regarding benefits related to wildlife) (Vaske & Manfredo 2012). Attitudes are one of the most popular cognitive factors in social studies because their relatively easiness to be studied and interpreted, as well as their direct effect on behaviors (Manfredo 2008). In addition, such popularity is also related to their broad coverage of elements because it includes aspects such as preferences, opinions and perceptions (Manfredo et al. 2004).

Specific perceptions about benefits, negative impacts and risks associated with wildlife have been frequently considered in studies on human dimension of wildlife conservation, because of their effect on the tolerance/acceptance towards these species (for a review see Bruskotter & Wilson 2014). Impacts have been defined as perceived effects, either positive or negative, derived from the interactions between humans and wildlife (Riley et al. 2002). Such perceived effects have been previously classified into different categories including ecological, economic, health and safety, psychological and social (Wieczorek Hudenko et al. 2010).

Furthermore, negative impacts lead to judgments derived from their occurrence, which are the focus of studies on risk perception (Slovic 1987). There are two ways in which risks may be analyzed. The first is from an analytical system, which has a strong logical component (e.g. probabilities of occurrence), and which is referred to commonly as cognitive risk or risk as analysis, and hereafter as analytical risk. The second is from an emotional system, which has a strong affective component (e.g. concern, fear), and which has been referred to as affective risk or risk as feelings and hereafter as emotional risk (Slovic et al. 2004).

METHODS

Study site and description of the communities

I conducted this research in the South of the state of Bahia, Brazil, between the municipalities of Ituberá and Igrapiúna (39°10'W 13°47'S and 39°13'W 13°54S) (Figure 3.1). The study landscape encompasses a 3,386-ha private natural reserve (Reserva Ecológica Michelin - REM) and its surrounding areas. The REM includes forests (of different successional stages), riparian areas, wetlands and rubber crops that were extracted until the middle of 2014, after which they were

abandoned for restoration purposes. Outside of the reserve the agricultural landscape is characterized by the presence of farms of different sizes with tree crops dominating the landscape. In the region there are more than 60 cultivars with a predominance of cocoa (*Theobroma cacao*), rubber (*Hevea brasiliensis*), cloves (*Eugenia caryophylla*), West African oil palm (*Elaeis guineensis*), bananas (*Musa* sp.) and Manioc (*Manihot esculenta*), among others (Flesher 2006). Livestock farming for commercial purposes is not common, and the people who raise animals, raise mainly poultry for their own consumption. There are nine human communities (>10 households) settled in an approximate distance of 2 km from the boundaries of the reserve. A social diagnosis conducted in these communities in 2011 determined that, on average, only 23% of the people living in those communities were born there, showing the transient character of some of those communities that are mainly composed of a transient rural work force (Ação Ambiental 2011). The majority (59%) of the households in these communities have a monthly income above the Brazilian minimum salary (~US\$ 270 as of August/2016), and the estimated average illiteracy is 14% (Ação Ambiental 2011).

Data collection

I conducted 109 semi-structured interviews between January 2013 and April 2014 in four communities located around the Reserva Ecológica Michelin (REM) (Figure 3.1). The four communities chosen were those that were previously identified as stakeholders by the REM for the purposes of their outreach program (Ação Ambiental 2011). Besides the people who inhabit these communities, I identified as stakeholders the people that came to work in the reserve every day in multiple capacities and that, although they may not live in the nearby communities, are in constant interaction with the wildlife.

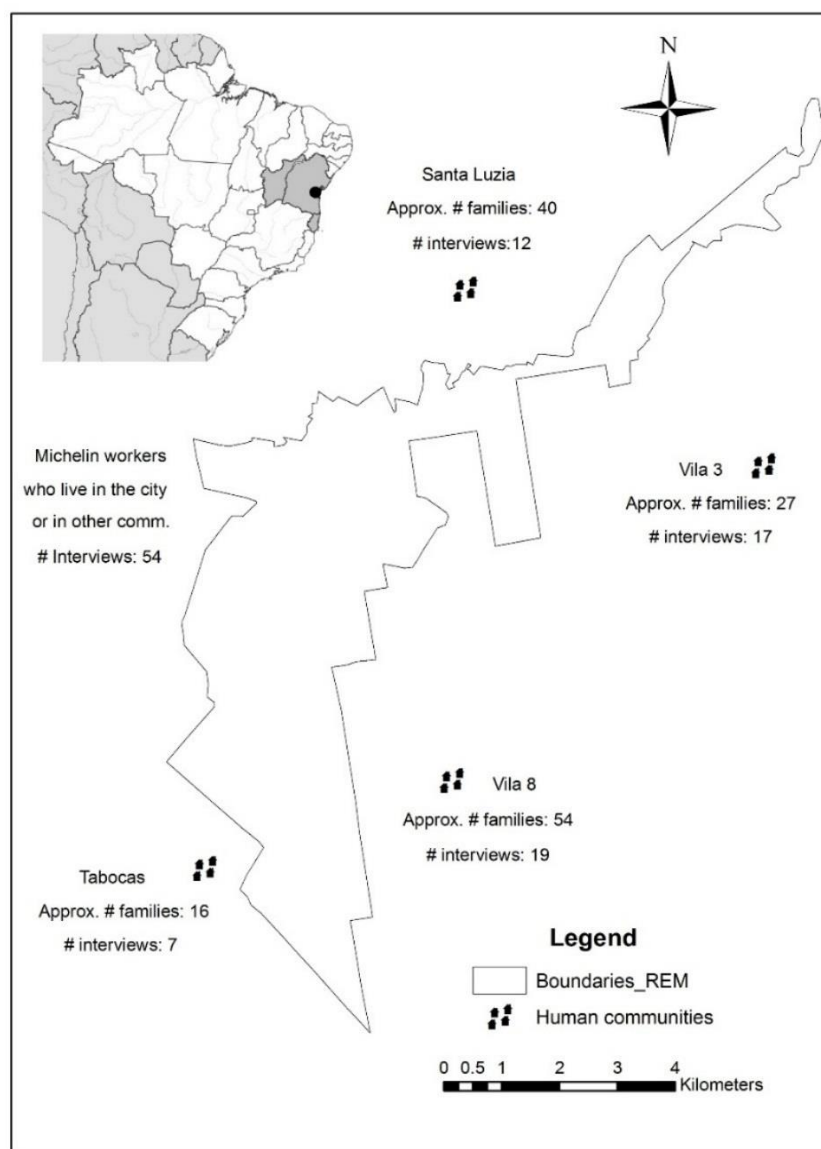


Figure 3.1. Communities interviewed and number of interviews by place of residence. The approx. number of families in each community was taken from Ação Ambiental (2011).

An earlier version of the questionnaire used was tested ($n=31$) during a pilot study conducted in the area in 2009. In addition, I tested the wording of the questions and answers with help from members of Ação Ambiental, an organization that has been working on environmental education projects in the area since 2007. During the interviews, following a series of demographic and socioeconomic questions such as gender, place of residence, employment, and ownership of farm

and animals (pets and livestock included) in rural areas. Respondents were asked an open-ended question about the animals that have a negative effect on their lives (*prejudicam*), in this open-ended question participants could mention all the animals that cause them a negative impact. Afterwards, respondents were asked about their previous experiences with pumas. Responses to this question were distributed in a three-ordered categorical scale representing the maximum level of interaction of the participant (animal never seen, animal never seen but encountered tracks, scats and/or animals thought to be predated by it, and animal seen personally).

Perceptions about pumas' current population size in the study area were registered in a three-ordered categorical scale (few, some and many). Evaluative attitude (referred here also to as likability) towards pumas was measured by asking how much the participants like the idea of having pumas in the area. Their answers were registered in a 5-point ordered categorical scale (absolutely no, mostly no, more or less, yes, very much). Negative impacts derived from the presence of pumas were measured by asking the participants, separately, if pumas have a negative effect (*prejudica*) on them (hereafter referred to as self) and on people acquainted with them (hereafter referred to as others). Responses to these questions were registered separately in a 5-point ordered categorical scale (absolutely no, mostly no, more or less, yes, and very much). The emotional risk (measured as the worry that the occurrence of a puma's attack on the participant produces) was registered in a 5-point ordered categorical scale (absolutely no, mostly no, more or less, yes, very much). The analytical risk was measured, not by inducing the participants to think objectively about the probabilities of occurrence of an impact related to pumas, as done in other studies (Riley & Decker 2000), but as the perceived probability of the occurrence of an attack on the participant. The analytical risk was registered in a 5-point ordered categorical scale

(impossible, extremely unlikely, unlikely, somewhat likely, extremely likely). The perceived benefit was measured by asking the participants if there is a benefit derived from the presence of the animal in the area and was registered in a 5-point ordered categorical scale (absolutely no, mostly no, more or less, yes, very much).

Finally, tolerance for pumas was measured as the desired future population size of the pumas (Inskip et al. 2016). Such desire was measured in a 5-point ordered categorical scale (to disappear, to decrease, to remain the same, to increase, to increase greatly). Given the transient residency of many of the participants in the area, I did not include a fixed temporal scale in the question about the desired future population size (e.g. desired future population size in the next 10 years). “Don’t know” was provided as an option in all questions and were entered into the dataset as NAs (See full questionnaire in appendix).

Statistical analysis

All statistical analyses mentioned in this section were conducted in R (R Core Team 2016). In order to determine the interactions and the perceived effects by stakeholders in the area in terms of response frequency, I used the `balloonplot` function in the `gplots` package (Warnes et al. 2016), which provides a visual examination by plotting a graphical matrix where the dot size reflects the relative response frequency.

Previous studies on the factors that affect tolerance for wildlife have demonstrated the utility of statistical methods with capacity to assess unobservable (latent) constructs and the links between such constructs. However, the applicability of such methods, conducted frequently through

structural equation modeling (SEM), requires in most cases large samples sizes for achieving adequate statistical power (Fritz & Mackinnon 2007; Wolf et al. 2013). In this study, sample size was limited by the population size of the human communities in the study area.

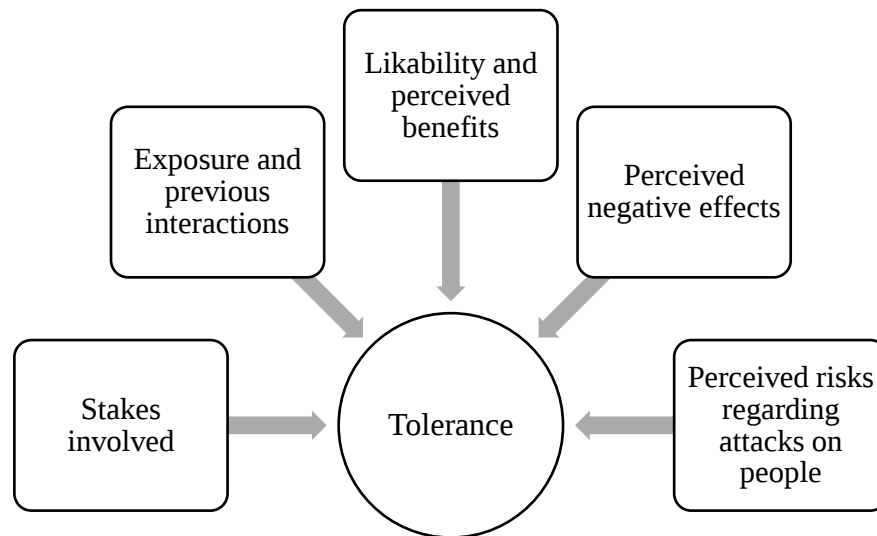


Figure 3.2 Theoretical tolerance model.

Therefore, to determine the effect of the stakes involved, exposure and previous interactions, likability and perceived benefits, perceived negative effects, and perceived risks on the tolerance for pumas (Figure 3.2), I used a set of five cumulative-link models (Agresti 2012), each with two explanatory variables (Table 3.1).

Table 3.1. Models specification and explanatory variables per model.

Model	Explanatory Variables	Input
Stakes involved	Land ownership	Indicator variable (0,1)
	Animal ownership	Indicator variable (0,1)
Exposure and interactions	Living in rural areas	Indicator variable (0,1)
	Previous interaction	Indicator variable (0,1)
Likability and perceived benefits	Likability	Ordinal (1-5)
	Perceived benefits	Ordinal (1-5)
Perceived negative effects	Neg. Impacts on self	Ordinal (1-5)
	Neg. Impacts on others	Ordinal (1-5)
Risk perception about attack on people	Analytical risk	Ordinal (1-5)
	Emotional risk	Ordinal (1-5)

Each one of the cumulative-link models defined above (Table 3.1) was then specified as:

$$\begin{aligned} \text{logit} (P(Y_i \leq j)) &= \theta_j - \beta_1(\text{Variable1}_i) - \beta_2(\text{Variable2}_i) \\ i &= 1, \dots, n, \quad j = 1, \dots, J - 1 \end{aligned}$$

Where $P(Y_i \leq j)$ is the cumulative probability that the response i th has of falling in the tolerance category j th or below, θ_j is the intercept for each one of the j th cumulative logits, and β_1 and β_a represent the effects of the variable 1 and the variable 2 on tolerance respectively. The *theta* parameters are also known as thresholds or cut-points between categories (Christensen 2015). Preliminary assessments of correlations between explanatory variables was conducted using the Spearman rank correlation for the ordinal variables, and for the indicator variables I used the phi coefficient in the psych package (Revelle 2016) (all correlations ranged from -0.42 to 0.62). Collinearity among the explanatory variables was tested using the vif function in the package usdm (Naimi 2015); in all cases the variance inflation factors (VIF) were ≤ 1.90 , indicating that there was no collinearity in the data. I fit the cumulative link models through maximum likelihood with the clm function in the ordinal package (Christensen 2015). I assessed model identifiability by looking at the condition number of the Hessian with values $< 10^4$ considered acceptable (Christensen 2015).

Model selection was done by using the Akaike's information criterion for small sample sizes (AICc), with the best models being identified for having lower AICc values (Burnham & Anderson 2002). To assess the probability of each model being the best model given the data, I estimated the Akaike weights (w_i), which are specified as: $w_i = \frac{\exp(-1/2 \Delta_i)}{\sum_{r=1}^R \exp(-1/2 \Delta_r)}$, where Δ_i is the difference between each model in the set and the best model ($\Delta_i = AICc_i - AICc_{min}$) (Burnham & Anderson 2002). To assess the explanatory power of the models, I used a generalized R^2 , which is estimated

as: $R^2 = 1 - \exp[-\frac{2}{n} \{\ell_1 - \ell_0\}]$, where ℓ_1 and ℓ_0 are the log likelihoods of the fitted and the null model respectively (Nagelkerke 1991). All analyses were conducted only with the complete cases matrices (i.e. excluding NAs).

RESULTS

Descriptive information

Most the 109 participants were men (90.8%, n=99) given that women in the area were not commonly found working in the field, and in the communities on many occasions they preferred that the men participated in the interviews. According to most women, the men knew more about wildlife given that they were, with some exceptions, the ones that worked the land. Most the participants (57.8%, n=63) owned a farm, and less than half (48.6%, n=53) had animals (pets and/or livestock) in the rural area. In terms of employment, 45.9% (n=50) of the interviewees were employed either by the reserve or by the farms around the reserve, 37.6% (n=41) were employed but also worked on their own land, and only 16.5% (n=18) worked on their own land exclusively. Most respondents (59.6%, n=65) lived and worked in the rural area while the rest only worked in the rural area but lived in the city.

Perceived negative effects derived from the co-occurrence with carnivores

Most of the participants (64.2%, n=70) reported a negative impact on their lives due to at least one animal species, while only 35.8% (n=39) of the respondents affirmed that there were no animal species that caused damage to them. Those respondents who reported negative animal-related

impacts, mentioned a species 143 times (Figure 3.3). At the group level, non-carnivore species, had the highest relative frequency of mention (73.4%, n=105), mostly due to their negative effect on the crops. Carnivore species on the other hand, were mentioned only 26.6% (n=38) of the times. The group here referred as to non-carnivores, included 12 species, non-members of the order Carnivora. The 12 species (or lower taxa) incorporated in this group included snakes (suborder Serpentes), deer (*Mazama* spp.), and white collared peccary (*Pecari tajacu*), among others. All snakes were kept grouped in their suborder because the difficulty for participants to differentiate between species.

At a lower taxonomic level, the puma is the second species, after the snakes, with the highest frequency of reported negative effects (mentioned 14% of the times, n=20), and the first among carnivores, due to the fear related to their presence. The second carnivore species with highest frequency of reported negative effects was the crab-eating fox (*Cerdocyon thous*) (mentioned 4.9% of the times, n=7), with all negative impact associated with predation on poultry. The wildcats (*Leopardus* spp.) and the South American coati (*Nasua nasua*) had an equal relative frequency of mention (2.8% each, n=4) because of effects on the poultry and the crops (especially cocoa among other fruits) respectively. The domestic cat (*Felis catus*) was mentioned 1.4% (n=2) of the time, because of their predation on chicks, and because their nocturnal activities on the roofs affected the participants' sleep. The species with the least frequency of mention (0.7%, n=1) was the tayra (*Eira barbara*) and its only reported impact was associated with their fearless behavior as one participant affirmed having been chased by a tayra once before.

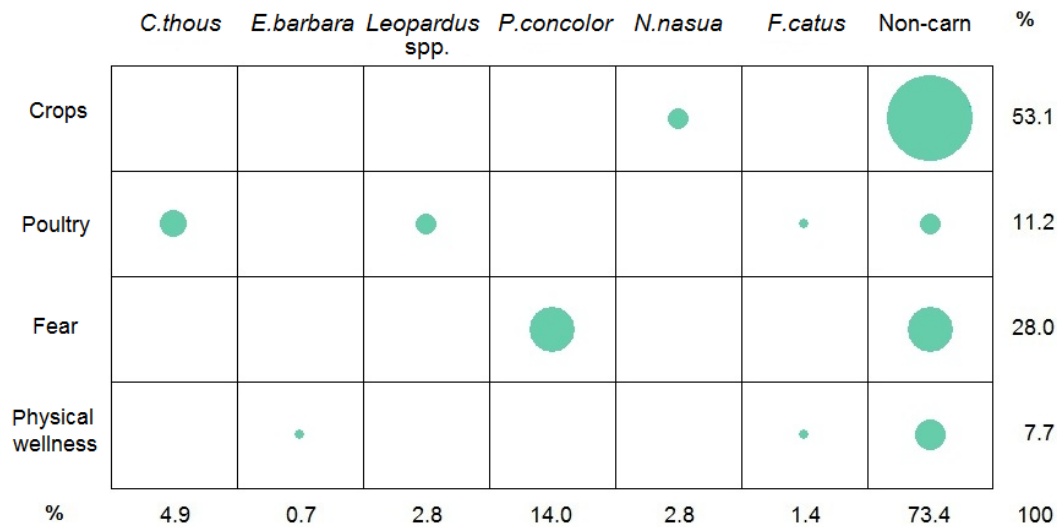


Figure 3.3. Relative frequency of reported negative effects of human-carnivore interactions. Circle area is proportional to relative frequency of mention (Total number of mentions=143).

Tolerance for pumas

Interactions with pumas were reported to be rare as only 7.3% (n=8) of the interviewees had seen the animal. 45.9% (n=50) of the participants had seen only traces associated with pumas, while 45.9% (n=50) had never seen the animal nor any trace. Most the respondents (50.5%, n=55) believed that in the area there were few pumas, 25.7% (n=28) believed that there were some, while 14.7% (n=16) believed that there were many of them. None of the interviewees had ever heard of a puma attack on humans in the region, and only 2.8% (n=3) of the participants had heard about cases of attack on animals; in all cases those attacks occurred on animals owned by others in the region.

Results from the set of five models fit to explain tolerance for pumas, showed that the model that includes evaluative attitudes (likability) and perceived benefits regarding pumas, had a 99%

probability of being the best model at explaining tolerance given the data and the set of candidate models (Table 3.2).

Table 3.2 Estimated coefficient, standard error, Z-value, Wald p -value, AICc, Akaike weight and generalized R^2 for each one of the five tolerance models fit ($n=93$). * Risk perception regarding a puma's attack on the participant.

Model category	Explanatory Variables	Estim.	Std.Err.	Z-value	p -value	AICc	Δ_i	W_i	Gen. R^2
Stakes	Land ownership	-0.38	0.43	-0.87	0.38	285.54	59.33	1.3E-13	0.02
	Animal ownership	-0.14	0.43	-0.32	0.75				
Exposure interactions	Living rural	-0.81	0.39	-2.10	0.04*	278.55	52.34	4.3E-12	0.09
	Prev. interaction	0.78	0.38	2.04	0.04*				
Likability benefits	Likability	1.32	0.28	4.66	3.2E-06 ***	226.21	0.00	0.999	0.48
	Perc. Benefit	0.70	0.24	2.91	3.6E-03 **				
Perceived neg. effects	Impact on self	-0.92	0.24	-3.86	1.2E-04***	270.43	44.21	2.5E-10	0.16
	Impact on others	-0.09	0.42	-0.22	0.83				
Risk perception*	Analytical risk	-0.11	0.2	-0.55	0.59	279.40	53.19	2.8E-12	0.08
	Emotional risk	-0.36	0.17	-2.08	0.04*				

In terms of explanatory power, the generalized R^2 values suggest that the model containing evaluative attitudes (likability) and perceived benefits regarding pumas, explained almost half (0.48) of the variability in the tolerance for pumas (Table 3.2).

DISCUSSION

The small size (in term of inhabitants) of the communities included in this study precluded me from making inferences at a larger scale (i.e. by including the communities as a random factor), thus the interpretation of the results presented in here is limited to the communities sampled. Nevertheless, this study demonstrates several issues to be considered in the field of human dimensions of carnivore conservation in the Atlantic forest of Brazil and worldwide.

In the studied area, where most of the economy is based on crop production, carnivores, in comparison with non-carnivores, are not the group with the highest frequency of reported negative effects by stakeholders. This result is consistent with another study conducted 150 km south of my study area, in which non-carnivore species presented the highest frequency of complaints from farmers (Lobão & Nogueira-Filho 2011). Although reported less frequently, all of the small and medium-sized carnivores reported here as having negative impacts on stakeholders, were also found to have perceived negative effects in other agricultural areas in South America, due to their predation on small-sized farm animals (e.g. poultry and pigs) and on crops like banana and papaya (Naughton-Treves et al. 2003; Lobão & Nogueira-Filho 2011).

Even though in the study area, direct human-puma interactions and predation on animals by pumas were rare, the frequency of reported negative effects of this carnivore was higher in comparison with the frequency of other species that cause economic losses and with whom interactions are more frequent (e.g. deer, crab-eating foxes). This, added to the fact that, at a lower taxonomic level, the puma is the second wildlife species with the highest frequency of reported negative effects, demonstrates that the low frequency of interactions or fact-based effects, does not necessarily imply an absence of perceived effects (either positive or negative). This is also true in the opposite case, in which the absence of perceived effects does not necessarily imply an absence of interactions. A good example of this case is provided by the interactions with tayras, which are frequent according to the interviewees. However, interactions with tayras are not considered to be problematic because, as expressed by one of the participants, “it only comes to eat one banana and continues on its way”. This, demonstrates the importance of perceptions and not only fact-based aspects in the study of the human-wildlife interactions, and in turn in carnivore conservation.

The importance of psychological factors on the tolerance for carnivores is also demonstrated by the fact that the model that presented a 99% probability of being the best model at explaining tolerance for pumas, included 2 psychological variables: evaluative attitudes (likability) and perceived benefits. Although the perceived negative effects derived from the presence of pumas in this area, may not be comparable to those perceived by stakeholders in areas where the presence of large carnivores represents economic losses or life threatening interactions, my results agreed with other studies on large carnivores in Brazil and in Nepal, and that also found that positive attitudes and perceived benefits are among the best predictors of tolerance/acceptance (Carter et al. 2012; Engel et al. 2016). Benefits mentioned by participants, ranged from indirect benefits (e.g. their presence is good for the forest and in turn the forest is beneficial to me) to direct benefits (e.g. their presence keeps thieves outside of agricultural lands).

The moderate generalized R^2 value (0.48) of the best model (i.e. tolerance $\sim$ likability + perceived benefits) indicates that, despite having only two explanatory variables, this model explained almost half of the variability in the tolerance for pumas. Although the other models presented significant factors, their large AICc differences and low Akaike weights and generalized R^2 values, suggested a lack of support for these models. In terms of analytical methods, I want to highlight the use of cumulative probability models for the analysis of categorical ordinal data (Agresti 2012). The suitability of these models are due to their capability of treating the response variable as it is, categorical and not continuous, while taking advantage of its ordinal character (i.e. increased magnitude) (Christensen 2015). Cumulative probability models are also useful in those cases where the sample size is not large enough to use structural equation models (SEM), which despite their benefits, depending on the proposed model (i.e. number of factors, number of indicator

variables, number of mediators etc.), may require several hundreds of observations (Wolf et al. 2013).

The necessity to integrate concepts as tolerance into carnivore conservation is more needed today than ever before in the history of humanity. Carnivore conservation actions and strategies, in the studied area and beyond, should be focused partly on communicating not only tactics on how to avoid or reduce carnivore-related risks and negative impacts but also on the benefits associated with the existence of these species (Bruskotter & Wilson 2014). In my study area, communicating the importance of pumas in controlling populations of herbivores with negative impacts on crops, such as deer and white collared peccary, would contribute to increase tolerance for this, regionally speaking, vulnerable species. Further research is needed for assessing of how tolerance influence behavioral intentions (i.e. beliefs about how one would behave in a specific situation (Manfredo et al. 1995)) as well as behaviors, even more, considering that behavioral intentions themselves may have a stronger and actual impact on carnivore populations than tolerance itself (Bruskotter & Fulton 2012). Finally, expanding the research on human dimensions of carnivore conservation is essential for clarifying concepts and relationships, and therefore proposing specific actions for the conservation of these species.

PERMITS – ETHICAL CONSIDERATIONS

I conducted this research with approval of the Institutional Review Boards (IRBs) of Michigan State University under the IRB#: X09-465 - ID# i033079. In addition, I collected the data with approval of the Brazilian government under the CNPq permit # 001308/2012-2.

APPENDIX

APPENDIX

Questionnaire used during interviews

Date:	Location:
Question	Answers
Gender	F M
Place of residence	
Occupation (Estimated salary)	
Do you own a farm?	Yes No
Do you own animals in the rural area (e.g. pets, chickens, ducks, cattle)	Pets Yes No Non-pets Yes No
Which animals do affect you negatively?	
Have you seen pumas?	Yes No Don't know
If not, have you seen traces?	Yes No Don't know
Do you think there are a lot of, some, or few pumas in this area?	Many Some Few Don't know
Do you like the idea of having pumas in this area?	Absolutely no Mostly no More or less Yes Very much Don't know
Do pumas affect you negatively? If yes, how? : _____	Absolutely no Mostly no More or less Yes Very much Don't know
Do you know people who have been affected negatively by pumas? If yes, how? : _____	Absolutely no Mostly no More or less Yes

	Very much Don't know
Do you feel worry about a puma attacking you?	Absolutely no Mostly no More or less Yes Very much Don't know
How likely do you think is that a puma attacks you?	Impossible Extremely unlikely Unlikely Somewhat likely Extremely likely Don't know
Are there any benefits for having pumas in this area?	Absolutely no Mostly no More or less Yes Very much Don't know
In the future, would you prefer pumas' populations to disappear, to decrease, to remain the same, to increase, or to increase greatly?	To disappear To decrease To remain the same To increase To increase greatly Don't know

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