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Habitat use patterns and conservation of small carnivores in a human-dominated landscape of the semiarid Caatinga in Brazil

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Abstract

In today's increasingly degraded world, private lands are becoming integral components of wildlife conservation. The Caatinga biome possesses the largest tropical dry forest in the Americas; however, it has experienced high levels of habitat loss. Natural vegetation cover in this biome is highly fragmented, and the few protected areas tend to be privately-owned. In this context, carnivores are particularly vulnerable to anthropogenic threats. Identifying factors that influence carnivore habitat selection in privately-owned areas is crucial for effective conservation actions. To this end, we assessed the habitat preferences of northern tiger cats (*Leopardus tigrinus*), jaguarundis (*Herpailurus yagouaroundi*), crab-eating foxes (*Cerdocyon thous*), and crab-eating raccoons (*Procyon cancrivorus*) on a private reserve in the Caatinga. We sampled the area with camera traps during a 4-year period and examined habitat use patterns through occupancy models. Caatinga cover was strongly favoured by northern tiger cats. Areas near human household had higher jaguarundi occupancy and crab-eating fox detection. Edge effects did not influence any of the species. The results suggest that in the absence of poaching and provided there is enough natural vegetation cover left, private lands indeed have potential conservation value for some carnivorous species. Nevertheless, because these areas tend to be small, connectivity with larger habitat patches is important for long-term conservation.

Keywords Caatinga · Occupancy models · *Leopardus tigrinus* · *Herpailurus yagouaroundi* · *Cerdocyon thous* · *Procyon cancrivorus*

Introduction

Agricultural encroachment, habitat loss and poaching all represent major threats to the world's carnivores (Ripple et al. 2014; Marneweck et al. 2021). These threats, along with biotic factors, such as prey availability, vegetation, etc., dictate habitat use patterns of carnivores in their distribution. With a growing worldwide human population, existing wildlands are becoming ever more fragmented, forcing several carnivorous species into fragmented landscapes with high human prevalence (Crooks 2002; Ordeñana et al. 2010; Moll et al. 2018). Provided there is suitable habitat and prey available, carnivores are generally able to live in close proximity with humans (Bateman and Fleming 2012). However, not all carnivorous species respond the same to human activities and among the so-called mesopredators, though some species are known to be tolerant of human presence (Monteiro-Alves et al. 2019; Reshamwala et al. 2021), while others respond negatively to human activity (Marinho et al. 2018; de Oliveira et al. 2020; Lombardi et al. 2020). Mesopredators are mid-ranking carnivores in the food

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web of an ecological community (Prugh et al. 2009) and this group includes generalist, common species as well as threatened ones. Understanding the patterns of habitat selection by mesopredators is important to their long-term conservation.

Several mesopredator species, including small felids, foxes and procyonids, are known to occur in the semi-arid Caatinga domain of north-eastern Brazil. The Caatinga is the largest dry forest ecoregion in South America (Beuchle et al. 2015). It is characterized by a semi-arid climate, with 250–1000 mm of annual rainfall and is composed of several vegetation formations. Caatinga vegetation types include semi-open shrublands, thorny scrubs, and dense tropical dry forests. Low, shrubby Caatinga is associated with sandy soils and is composed of small shrubs (< 1 m tall). The taller Caatinga forests (woodland Caatinga) are associated with eutrophic soils and consist of dense closed-canopy dry forests. This heterogeneity results in high biodiversity including 178 mammals, 591 birds, and 1200 vascular plants (MMA 2019; WWF 2021). About 46% of Caatinga vegetation has already been converted to agriculture and livestock ranching areas (MMA 2019) Most of the remaining areas of Caatinga are composed of small fragments that suffer from chronic anthropogenic disturbance (Antongiovanni et al. 2020), and only 7.5% of the biome is currently under some form of protection; the vast majority of which is represented by small, privately-owned conservation areas (MMA 2019). As such, these areas are crucial to the long-term survival of wildlife in the Caatinga biome.

Given the importance of private lands to the conservation of Caatinga habitats, it is imperative to discern how carnivores fare in the human-dominated landscapes of this semi-arid biome. To assess this, a privately-owned environmental protection area in the Caatinga biome was monitored for a 4-year period. We analysed habitat use patterns of the following four species of small carnivores (Fig. 1): the crab-eating fox (*Cerdocyon thous*), the crab-eating raccoon (*Procyon cancrivorus*), the northern tiger cat (*Leopardus tigrinus*) and the jaguarundi (*Herpailurus yagouaroundi*). The first two are generalist omnivores that exhibit great environmental flexibility and are classified as Least Concern by the IUCN (Lucherini 2015; Reid et al. 2016). The northern tiger cat (*Leopardus tigrinus*) is Globally Vulnerable (Payan and de Oliveira 2016), while the jaguarundi (*Herpailurus yagouaroundi*) is classified as Vulnerable in Brazil (Queirolo et al. 2013). Our goal was to identify which environmental and anthropogenic features most influence habitat use by

Fig. 1 Study species (clockwise from top-left): Jaguarundi (*Herpailurus yagouaroundi*), Northern tiger cat (*Leopardus tigrinus*), crab-eating fox (*Cerdocyon thous*), crab-eating raccoon (*Procyon cancrivorus*)

mesopredators in a human-dominated context. It is expected that the two felids be more dependent upon natural vegetation cover and avoid humans more than the two generalists. It was also desirable to assess the possible role that private lands might have on the conservation of carnivores in the ever increasingly fragmented semi-arid Caatinga.

Materials and methods

Study site

Tamanduá Ranch (TR) is a private natural heritage reserve (RPPN—Reserva Particular de Patrimônio Natural in Portuguese) located in the state of Paraíba, in north-eastern Brazil (Fig. 2). According to federal legislation in Brazil, an RPPN is a privately owned protected area in which agriculture, deforestation, hunting or other extractive activities are forbidden (Souza et al. 2012). TR is roughly 3073 ha in size, one-third of which is comprised of native Caatinga shrublands and dry forests. The remaining area is used for dairy farming, small-scale organic agriculture, beekeeping and fruit harvesting. Several man-made structures, including residential dwellings and processing facilities, exist on the property. The houses tend to be isolated rather than being organized into settlements. Human presence within the farm is wildlife-friendly, with domestic dogs being required to be leashed at all times. The climate is hot and semi-arid (BSh according to the Köppen system), with a mean annual rainfall of 700 mm and mean annual temperatures of 20.8–32.9 °C (Filho et al. 2015) and the elevation ranges from 200 to 400 m above sea level.

Camera trapping

The study site was divided into a grid with 30 cells of 1 km^2 each. Then 19 of these cells were selected for sampling purposes, covering areas ranging from open shrublands to dense tropical dry forests. Sampled cells were selected based on accessibility, as some of the grid cells fell on areas that were not accessible by car or foot. Though it must be acknowledged that this does not allow us to make inferences to the whole study area, there is greater interest in habitat associations and species persistence. Furthermore, the selected sampled cells cover a wide range of the selected covariates (Supplementary Table 1). In each of these 19 cells, one non-baited camera trap (model TIGRINUS Digital 6.5D, Tigrinus®) was installed at a height of 30–40 cm above ground level. Cameras were located at the centre of each grid to keep a constant distance between adjacent cameras,

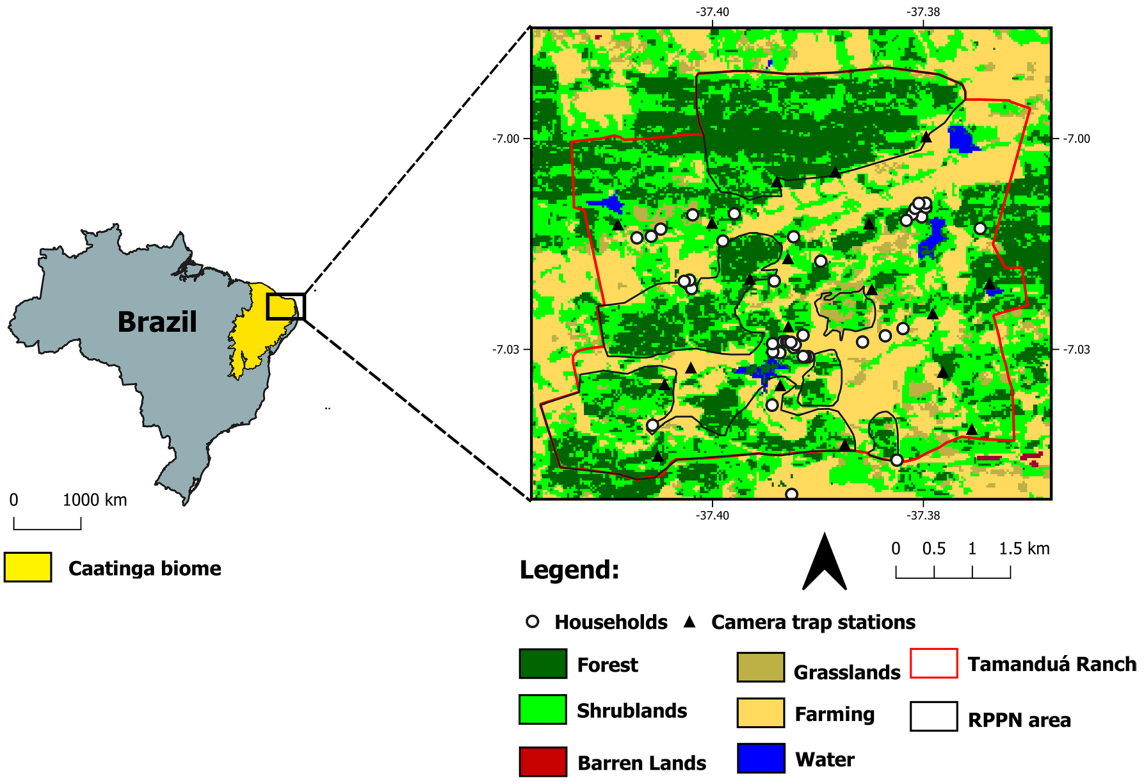


Fig. 2 Location of the study site in the Brazilian Caatinga biome. Red line indicates the limits of Tamanduá Ranch, black lines show the areas under protection (RPPN proper)

except when this was not feasible due to accessibility. Cameras were on average spaced out at 812.73 m. Cameras were deployed along wildlife trails and roads to maximize the detection of carnivores and other wildlife (Srbek-Araujo and Chiarello 2013). The study area was sampled over a 4-year period (2010–2014; sampling effort: 15,748 trap-nights), and the batteries were changed and the films collected from the cameras every 2–3 months. Cameras were programmed with a 1-s delay between pictures and were active 24 h/day.

Site covariates

Data was collected on one anthropogenic and four environmental variables at each sampling point. It was hypothesized that these variables could influence mesopredator habitat use at the local level (Table 1). The environmental variables were associated with habitat quality and include (i) percentage of forest cover, (ii) percentage of shrublands, (iii) percentage of grasslands, and (iv) distance to the edge of the habitat. The vegetation at our site is composed of forest formations, thorny scrub, and open grasslands. Forest was defined as formations in which at least 10% of the vegetation is closed canopy and ≥ 5 m tall (Hansen et al. 2013). Shrublands are characterized by a semi-continuous canopy and scrub (Souza et al. 2020), while grasslands are dominated by herbaceous plants. It was hypothesized that there would be a positive effect of increasing forest cover and shrubby vegetation on habitat use for both felid species (Oliveira et al. 2010; Marinho et al. 2018; Cruz et al. 2019). Conversely, it was expected that crab-eating foxes and racoons would favour areas with lower vegetation cover based on studies conducted in other semi-arid and dry environments (Monteiro-Alves et al. 2019; Weiler et al. 2020). Habitat edges at the TR represent the limit between habitat and non-habitat patches (i.e., agriculture, cattle ranching areas, old fields, and barren land; Fig. 2), and it was expected that there would be negative effects caused by the edges on northern tiger cat's intensity of habitat use (Marinho et al. 2018) and positive effects on crab-eating foxes, jaguarundis, and raccoons (Coronado-Quibrera et al. 2019; Monteiro-Alves et al 2019). Finally, (v) the distance to the nearest household was measured, as a proxy for human activity, with higher anthropogenic pressures in areas near households. Lower occupancy by northern tiger cats and jaguarundis was expected near households (Marinho et al. 2018; Dias et al. 2019; de Oliveira et al. 2020). All variables were extracted ex-situ in Q-GIS version 3.4 (QGIS Development Team 2009) using shapefiles and digitalization of features from satellite imagery. The "Distance to…" variables were measured in relation to the precise location of the camera traps. The percentage of Caatinga cover was calculated according to a 200-m buffer around each camera, as that was the largest distance that could be used without overlapping adjacent cameras. The variables for collinearity were tested using Spearman's rank test (not all variables were normally distributed) and highly correlated variables ($|r| > 0.7$) were excluded. All variables were transformed into z scores for a mean of 0 and a standard deviation of 1 before model construction.

Occupancy modelling

To estimate habitat use, single-season single-species occupancy models were run (Mackenzie et al. 2002). These models estimate the following two parameters: occupancy (Ψ), the probability that the species is present at a site; and detection (p), the probability of detecting the species at a site given that it is present. The model assumes that sampling sites are closed to changes in occupancy during the survey period; that occupancy and detection probabilities are either constant across sites or with differences modelled by covariates; species detections are spatially and temporally independent; that all species are identified correctly (i.e., no false positives).

Table 1 Covariates and predicted effects on the species' respective habitat use parameters

Covariate	Code	Description	LTI[a]		HYA[b]		CTH[c]		PCA[d]	
			Ψ	p	Ψ	p	Ψ	p	Ψ	p
Forest cover	FC	% Forest cover on an 8-ha buffer around each camera	+	+	+	+	NA	−	−	+
Shrubland cover	SHR	% Shrubland cover on an 8-ha buffer around each camera	+	+	+	+	NA	+	+	+
Grassland cover	GRA	% Grassland cover on an 8-ha buffer around each camera	−	−	−	−	NA	+	+	+
Distance to households	HDT	Euclidean distance from each camera to the nearest household	+	+	+	+	NA	−	−	−
Distance to edge	EDG	Euclidean distance from each camera to nearest non-habitat patch (plantations, barren land)	NA	+	NA	−	NA	−	NA	−

[a] Northern tiger cat (*Leopardus tigrinus*)

[b] Jaguarundi (*Herpailurus yagouaroundi*)

[c] Crab-eating fox (*Cerdocyon thous*). The species was detected at all stations, hence we only tested covariates on its detection probability

[d] Crab-eating raccoon (*Procyon cancrivorus*)

Each site-year combination was considered to be a distinct site because our interest was in discovering habitat use patterns among the species, as opposed to occupancy dynamics across years (Fuller et al. 2016; Meyer et al. 2020). Furthermore, temporal replication among years was limited, with some cameras being moved from one year to the other. This resulted in a total of 55 unique site-year combinations. The sampling period was collapsed into six 2-month occasions, and this occasion length was chosen because our dataset was too sparse for shorter sampling occasion lengths. Periods of 2 months, 1 month and 15 days per occasion were compared using a chi-square goodness of fit test (MacKenzie and Bailey 2004); however, 2 months (60 days) represented the optimum sampling period per occasion to maximize model fit for all four species (Supplementary Table 2). Because our four species are highly mobile and some of our sites did not meet the closure assumption, ψ was interpreted as the probability of habitat use rather than true occupancy and p was interpreted as the intensity of habitat use (Cassano et al. 2014; MacKenzie et al. 2018). In addition to the five spatial covariates described above, the possibility of yearly variation in detection and occupancy probabilities was tested by defining a categorical variable, which represented the 4 years of sampling (Table 2).

A two-step approach was used to model habitat use preferences of each species. Detection was first modelled with the occupancy parameter fixed to the global parameterization. The best detection covariates were then used and these were fixed to model habitat use. Each candidate model represented a biologically relevant a priori hypothesis (Table 1). Models were ranked by $\mathrm{AIC_C}$, and those with a $\Delta\mathrm{AIC_C} < 2.0$ were considered to have support (Burnham and Anderson 2002). A Pearson's Chi-square test was run on the most parameterized model of each species (MacKenzie and Bailey 2004) using 1000 bootstrap iterations to assess model fit and overdispersion.

All statistical analyses were conducted using the R program version 3.3.3 (R Development Core Team 2019) using the packages *AICcmodavg* (Mazerolle 2016) and *unmarked* (Fiske and Chandler 2011).

Results

From January 2010 through February 2014, we obtained 386 photographic records of crab-eating fox, 54 records of crab-eating racoon, 52 records of northern tiger cat, and 21 records of jaguarundi. The goodness of fit tests indicated no overdispersion for any of the species, with $\hat{c}$ values ranging

Table 2 Model selection table

Model	*K*	$\mathrm{AIC_C}$	$\Delta\mathrm{AIC_C}$	*w*	LL
Leopardus tigrinus					
p(EDG)Ψ(FC + GR + YR)	8	204.92	0.00	0.40	−92.86
p(EDG + FC)Ψ(FC + GR + YR)	9	206.76	1.85	0.16	−92.34
p(.)Ψ(FC + GR + YR)	7	206.94	2.02	0.14	−95.25
p(FC + GR + EDG)Ψ(FC + GR + YR)	10	207.28	2.36	0.12	−91.08
p(EDG + GR)Ψ(FC + GR + YR)	9	207.55	2.64	0.11	−92.73
Herpailurus yagouaroundi					
p(FC + GR)Ψ(HDT)	5	129.57	0.00	0.31	−59.17
p(FC)Ψ(HDT)	4	129.87	0.30	0.26	−60.53
p(.)Ψ(HDT)	3	130.33	0.76	0.21	−61.93
p(.)Ψ(SH)	3	131.81	2.24	0.10	−62.97
p(.)Ψ(.)	2	133.10	3.53	0.05	−64.43
Cerdocyon thous					
p(HDT + GR + FC)Ψ(.)	5	296.27	0.00	0.50	−142.52
p(HDT + FC)Ψ(.)	4	297.51	1.24	0.27	−144.35
p(HDT + SH + GR + FC)Ψ(.)	6	298.13	1.86	0.20	−142.19
Procyon cancrivorus					
p(EDG)Ψ(HDT)	4	204.31	0.00	0.30	−97.76
p(.)Ψ(HDT)	3	204.38	0.06	0.29	−98.95
p(FC + EDG)Ψ(HDT)	5	205.55	1.24	0.16	−97.16
p(.)Ψ(HDT + GR)	4	206.20	1.88	0.12	−98.70
p(GR + FC + EDG)Ψ(HDT)	6	207.65	3.34	0.06	−96.95

Models with a cumulative AICC weight of 0.95 are shown

w model weight; *LL* log-likelihood of each model from 0.61 to 1.11 and p values > 0.05 (Supplementary Table 2). Northern tiger cat habitat use was significantly affected by the percentage of forest cover ($\beta = 1.65 \pm 0.78$; 95% CI 0.13–3.17; Fig. 3a). Distance to households significantly influenced occupancy probability of jaguarundi ($\beta = -1.09 \pm 0.53$; 95% CI −2.13 to −0.05; Fig. 3b). It also affected the occupancy probability of crab-eating racoon, though not significantly ($\beta = -9.84 \pm 6.00$; 95% CI −21.61 to 1.92). Detection probabilities ranged from 0.20 ± 0.05 for jaguarundi, 0.24 ± 0.03 for crab-eating raccoon, 0.39 ± 0.04 for crab-eating fox, to 0.40 ± 0.05 for northern tiger cat. Detectability of crab-eating foxes was higher in areas closer to households ($\beta = -0.56 \pm 0.17$; 95% CI −0.89 to −0.24; Fig. 4a) and with higher forest cover ($\beta = 0.40 \pm 0.16$; 95% CI 0.09–0.72; Fig. 4b). Distance to habitat edge had a significant positive influence on the detection probability of northern tiger cat ($\beta = 0.48 \pm 0.23$; 95% CI 0.03——0.93; Fig. 4c), and nonsignificant positive effect on that of the crab-eating raccoon ($\beta = 0.38 \pm 0.25$; 95% CI −0.10 to 0.86). All other variables did not have any significant effect on the occupancy or detectability of none of the species (Supplementary Table 3).

Discussion

Overall, the four species had different responses to the covariates evaluated. The northern tiger cat, the only globally threatened species of our sample, was highly dependent on remaining forest cover, and was the only species whose habitat use probability was significantly affected by this covariate. The species is known to favour areas with higher tree cover (Marinho et al. 2018; de Oliveira et al. 2020; Lima 2020) and, at Tamanduá Ranch, arboreal Caatinga patches represent the densest areas. Though it was also expected that shrublands would positively influence the tiger cat's habitat use, this was not the case at our study site, with the species preferring denser vegetation formations than the remaining natural habitat. Interestingly, in the northern savannas, the species seems to be favouring denser shrublands to woodland savanna (de Oliveira et al. 2020; Lima 2020). However, this difference could simply be a consequence of vegetation structure and provision of cover between shrublands in the Caatinga and savannas. Our results suggest that dense woodland cover is important for the long-term conservation of this globally threatened felid in semi-arid habitats. In contrast to our previous expectations, the varying Caatinga formations did not influence jaguarundi habitat use parameters. Jaguarundis are known to use open habitats, but even in these areas they tend to favour denser vegetation cover (Oliveira 1994, 1998; Caso et al. 2015; Boron et al. 2018; Porfirio et al. 2018). It is worth noting that most of our sampled sites had a high percentage of Caatinga cover (forest and shrublands combined; mean = 78.36%); therefore, we expect that on a wider scale jaguarundis will have a significantly higher probability of occurrence and/or detectability in natural Caatinga vegetation sites.

Neither forest cover, grasslands, nor shrublands influenced the habitat use parameters of crab-eating raccoons. This was expected since the species is a generalist and is able to use different vegetation formations (Regolin et al. 2017). In the Paraguayan Chaco, another dry-forest ecoregion, the crab-eating raccoons' occupancy and detection probabilities were not influenced by tree cover (Weiler et al. 2020), which is in agreement with our findings. On the other hand, crab-eating foxes were detected more often in areas with higher forest cover. Elsewhere in South America, the species has been found to avoid dense vegetation formations in moist forests (Mendes-Oliveira et al. 2017; Dechner et al. 2018; Monteiro-Alves et al. 2019). However, in the semiarid environment of the Caatinga, forest patches may provide shelter against extremes temperatures (Astete et al. 2017), and this

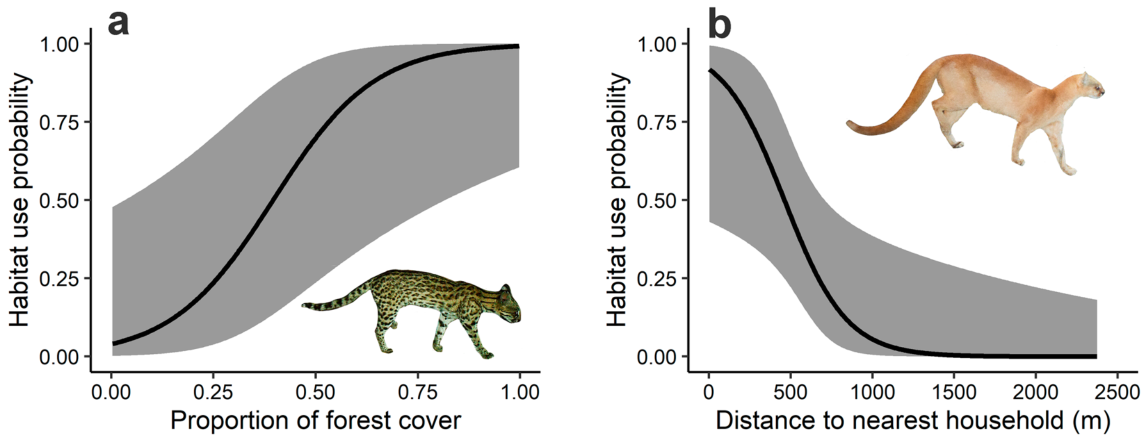
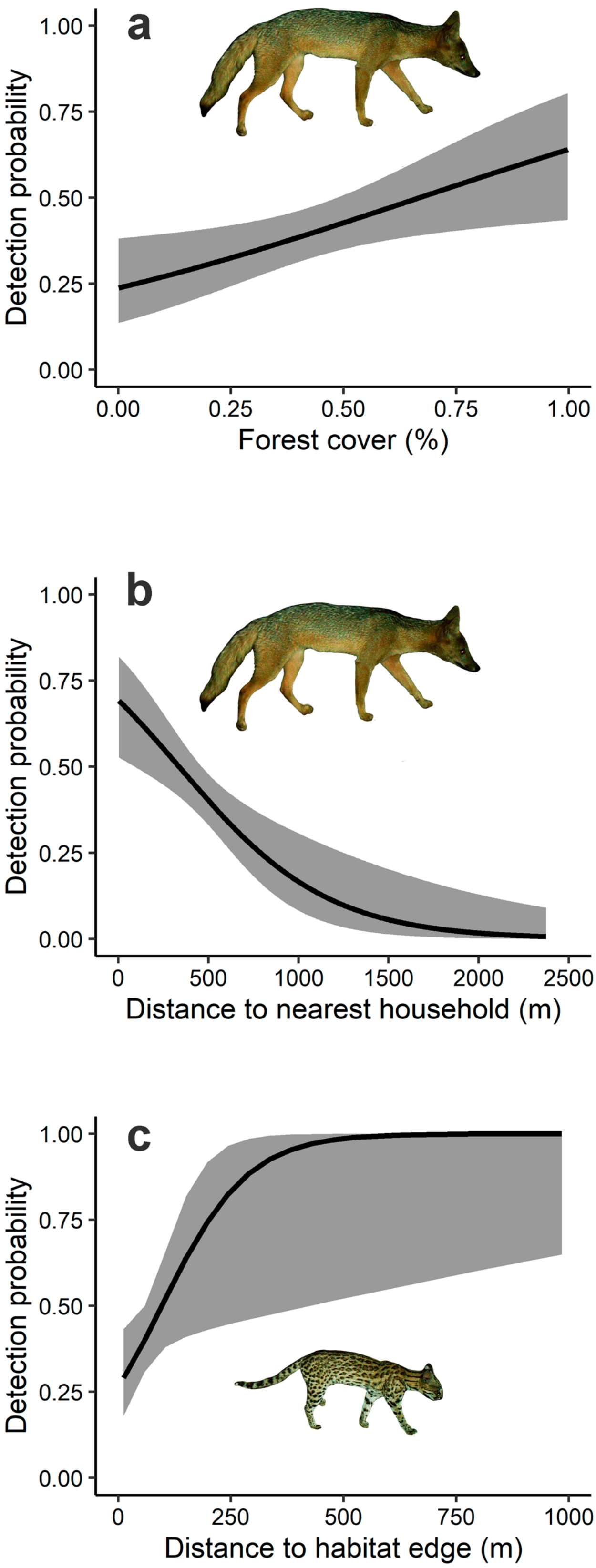


Fig. 3 Influence of covariates on habitat use probability of **a** Northern tiger cat; **b** Jaguarundi. Gray band indicates 95% confidence interval

Fig. 4 Influence of forest cover (**a**) and distance to nearest household ▸ (**b**) on crab-eating fox detection probability, and influence of distance to habitat edge (**c**) on northern tiger cat detection probability. Gray band indicates 95% confidence interval



may result in wildlife frequently using forest patches. At another Caatinga site in Alagoas, crab-eating foxes were recorded more frequently in shrublands and forest patches than in other habitats (Dias and Bocchiglieri 2016).

Interestingly, it was noted that distance to households did not have a negative effect on the occupancy and detection rates of any of the species. In fact, in the case of crab-eating foxes, a closer distance to households significantly increased the detection probability. Crab-eating foxes are not threatened and they tend to be tolerant of human presence (Lucherini 2015; Dias and Bocchiglieri 2016). At Boqueirão da Onça, another region in the Caatinga domain, crab-eating foxes were found to have a higher occupancy (though not detectability) in areas closer to human settlements (Dias et al. 2019). Distance to households also improved model fit of crab-eating raccoon occupancy; however, the 95% confidence interval included zero, so the effect of this covariate is not clear. Although crab-eating raccoons do not seem to be as adaptable to human presence as northern raccoons (*Procyon lotor*) (Reid et al. 2016), they are not among the commonly poached mammalian species in the Caatinga (Alves et al. 2016). It is likely that both species make use of areas closer to households due to higher food availability in the form of trash, as is the case for other generalist species elsewhere (Theimer et al. 2015; Reshamwala et al. 2021).

For the two cats, distance to human households did not have a negative impact on habitat use. Jaguarundi habitat use was, in fact, higher in areas closer to households, which is a pattern also witnessed by Coronado-Quibrera et al. (2019) in Central México. Prey availability, in the form of rodents and domestic animals (i.e., poultry), could potentially explain jaguarundi preference for areas near households, provided poaching is low. At TR, most households are adjacent to plantations and agricultural fields. These areas often have a high prevalence of rodents and birds, which may be easier to catch due to open visibility, as has been suggested for leopard cats in Borneo (Rajaratnam et al. 2007). In the Colombian Llanos, jaguarundis also made heavy use of plantations and they were detected there more often than in adjacent riparian forests (Pardo et al. 2021). Thus, it is likely that jaguarundi usage of areas near households at our study site is driven by the availability and catchability of prey.

The lack of negative effects of households on the carnivore species suggests that these animals are able to persist in fairly close proximity to humans provided there is no pressure from poaching. In fact, residents of the ranch have a positive attitude towards wildlife. At TR, there are few problems with poaching, and poachers tend to be people living in communities outside the property who target grey-brocket deer (*Mazama gouazoubira*), yellow armadillo (*Euphractus sexcinctus*) and other game animals that are not carnivores (Landolt pers. comm.). Although the opportunistic killing of small carnivores by outside poachers may occur, the incidence of this should be minimal, if any. Throughout our 4 years of sampling, not a single poacher was recorded on our cameras, which was a vast contrast to other study sites. For instance, in other regions of the Caatinga biome, both tiger cats and jaguarundis have been found to have lower occupancy and detection rates in areas closer to human settlements (Marinho et al. 2018; Dias et al. 2019). These studies were conducted over large areas, at which poaching and retaliatory killing are major threats for the small felids for some of these areas. At our site, where poaching is controlled, human presence seems to be rather innocuous in terms of habitat selection for northern tiger cats and even beneficial to some degree for the other three species.

Negative edge effects on carnivores include increased mortality due to direct persecution (Balme et al. 2010), as well as a higher vulnerability to disease transmission from domestic dogs (Lacerda et al. 2009; Home et al. 2018). Conversely, the border of small-scale agricultural fields adjacent to natural vegetation can actually be favourable for small felids due to prey abundance (Oliveira et al. 2010) and, at our study site workers, have reported seeing tiger cats near agricultural fields (Landolt pers. comm.). Despite this, the distance to the habitat edge only had a significant influence on the detection probability of the northern tiger cat, with the species being detected more often at sites farther away from the edges. Elsewhere edge habitats have been positively associated with crab-eating foxes and raccoons (Di Bitetti et al. 2009; Dechner et al. 2018). Jaguarundis in the Atlantic Forest showed lower occupancy, but higher detection probabilities near forest edges (da Silva et al. 2018). Currently, in the entire Caatinga biome, more than 75% of remaining natural vegetation fragments is within 1 km of the nearest habitat edge (Antongiovanni et al. 2020), and all our sampled sites were within that distance from the nearest edge (Supplementary Table 1). Further research in larger areas could yield more insight on the effects of edge on habitat use by our sampled species.

Across the 4-year sampling period, no significant changes were detected in the occupancy of any of the species. The "year" covariate did not improve model fit for crab-eating foxes, raccoons, and jaguarundis. It was present in the top model of the northern tiger cat, yet it was not significant (Supplementary Table 4) and was likely an uninformative parameter (Arnold 2010). This suggests that our study site is effectively conserving the four mesopredator species. Lack of poaching and protection of natural vegetation cover likely enhance this. Despite the apparent stability in occupancy for the four species across our sampling period, it must be noted that 4 years is a short time frame when compared to the average lifespan of these species. Long-term monitoring of occupancy trends and population fluctuations would be needed to draw more solid conclusions. For instance, although evidence of breeding by jaguarundis (Supplementary Fig. 1) and tiger cats was detected during our sampling period, and preliminary density estimates suggest that their population has actually declined between 2011 and 2018 at our study site (de Oliveira unpublished data).

Conservation implications

Although our results suggest that mesopredators are able to survive and even thrive in private landscapes, lack of persecution and preservation of natural habitat cover are important. Little to no poaching may be sufficient for generalist species such as crab-eating foxes and raccoons. Nevertheless, for species such as the northern tiger cat, retention of natural habitat within these landscapes is key. Currently, less than less than 1% of the Caatinga biome is fully protected in the form of national and state parks, and ecological stations (MMA 2019). Most of the protected areas in the biome are privately owned and the majority of the areas that the four focal species use within the Caatinga are unprotected. For the two felid species, private lands have been identified as priority conservation areas due to interspecific competition with the ocelot (*Leopardus pardalis*) in larger protected areas (Oliveira et al. 2010). Thus, effective conservation measures on private lands are key for the long-term survival of these species. In the long term, due to the fact that most of the land area of the Caatinga biome is not protected, ongoing loss of habitat is expected to continue for the foreseeable future. Conservation efforts should focus on preserving the natural cover available and minimizing human-wildlife conflict. Further studies on carnivore habitat use patterns conducted on public lands (national parks and unprotected areas) in the Caatinga are needed to draw more conclusions about the advantages of private lands for carnivore conservation when compared to public landscapes.

It is also important to mention that most of the private lands in the Caatinga tend to be small. Indeed, at roughly 19 km^2, our sampled area is smaller than some of the reported home ranges for the jaguarundi and the northern tiger cat (Konecny 1989; Oliveira et al. 2010). Most of the individuals of these two species that were detected were likely using unprotected habitats outside of the reserve, which could potentially be converted to other land uses in the future or where the threat of poaching is greater. Therefore, conservation actions should consider securing safe connectivity between private lands. Globally, the number one threat for both the northern tiger cat and the jaguarundi is habitat loss (Caso et al. 2015; Payan and de Oliveira 2016), which further highlights the importance of connectivity among core habitats. Crab-eating foxes and raccoons tend to have smaller home ranges (Lucherini 2015; Reid et al. 2016) and are not threatened. However, with increasing habitat loss across the Caatinga biome, both of these species would also benefit from corridors linking a mosaic of small private lands.

Our study suggests that with poaching control and natural habitat preservation, private lands in the Caatinga contribute greatly to conservation, not only of generalist carnivores but also of threatened ones. Additional research is needed to assess threats that are particular to these areas. For example, while poaching is very rare at the Tamanduá Ranch, cattle ranching is extensive, which could potentially impact wildlife populations in the area (Schieltz and Rubenstein 2016; Filazzola et al. 2020). Another threat that should be evaluated more carefully is the potential for disease transmission from domestic dogs, which is considered to be one of the main threats to crab-eating fox and northern tiger cats in some parts of their range (Lucherini 2015; de Oliveira et al. 2020). Lastly, a higher human prevalence in private lands when compared to large protected areas could result in human-wildlife conflicts and hence retaliatory killing. Addressing these issues is key to ensuring wildlife conservation in private lands of the semi-arid Caatinga.

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Declarations

Conflict of interest The authors have no competing interests to declare.

Code availability Not applicable.

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