Understanding the ecology of medium-sized carnivores (Mammalia: Carnivora) from a Tropical Dry Forest in Colombian Caribbean

Compreendendo a ecologia de carnívoros de médio porte (Mammalia: Carnivora) de uma floresta tropical seca no Caribe colombiano

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Abstract: Fauna in Tropical Dry Forest (TDF) is highly dependent on water availability due to a marked seasonality in precipitation. There are few studies addressing carnivore's ecology and the role of seasonality of TDF in Neotropics. We used scent-station and camera trapping to assess seasonal changes in occurrence and habitat use probability with seasonality. We also described activity patterns and collected fresh scats to describe diet for small sized carnivore species in a TDF fragment in the Colombian Caribbean region. We present information regarding: *Cerdocyon thous*, *Leopardus pardalis*, and *Procyon* spp. The analysis showed a significantly higher occurrence probability during the dry season for the three species, and no differences in the detection probability between seasons. The diet of *C. thous* included 24 different food items; for *L. pardalis* it was composed of seven items, and finally, 25 food items were identified in the diet of *Procyon* spp. We found that the three species presented activity patterns corresponding with previous studies. Finally, our results reflect that these species are probably making more/larger habitat use during the dry season than in the wet season, because the area has permanent water ponds by which limited resources (such as water and food) are available almost constantly in this natural reserve.

Keywords: *Cerdocyon*. Diet. *Leopardus*. Occupancy. *Procyon*.

Resumo: A fauna na floresta seca tropical (TDF) é altamente dependente da disponibilidade de água devido à sazonalidade acentuada na precipitação. Existem poucos estudos que abordam a ecologia dos carnívoros e o papel da sazonalidade do TDF nos neotrópicos. Usamos análises de estação de pegadas, armadilhas fotográficas e fezes para determinar se há mudanças sazonais na ocorrência, ocupação, dieta e padrão de atividade de espécies de carnívoros em um pequeno fragmento de TDF na região do Caribe colombiano. Apresentamos informações sobre: *Cerdocyon thous*, *Leopardus pardalis* e *Procyon* spp. A análise mostrou probabilidade de ocorrência significativamente maior durante a estação seca para as três espécies, e não houve diferenças na probabilidade de detecção entre as estações. A dieta de *C. thous* incluiu 24 itens alimentares diferentes, *L. pardalis* foi composta por sete itens e, finalmente, 25 itens alimentares foram identificados na dieta de *Procyon* spp. Constatamos que as três espécies apresentaram padrões de atividade correspondentes a estudos anteriores. Finalmente, nossos resultados refletem que essas espécies provavelmente estão usando mais um habitat, ou maiores porções desse, durante a estação seca do que na estação chuvosa, uma vez que a área possui lagoas de água permanentes pelas quais recursos limitados (como água e alimentos) estão disponíveis quase constantemente nesta reserva.

Palavras-chave: *Cerdocyon*. Dieta. *Leopardus*. Ocupação. *Procyon.*

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INTRODUCTION

Tropical Dry Forests (TDF) are among the most diverse and threatened ecosystems worldwide (Sánchez-Azofeifa & Portillo-Quintero, 2011). In the Americas, TDF are distributed from Mexico to Argentina, and in South American countries include 51 % of the cover (Portillo-Quintero & Sánchez-Azofeifa, 2010). In addition, disturbances derived from the expansion of agriculture and cattle ranching represent the main threat to this ecosystem, leading to a highly fragmented landscape dominated by small patches throughout its distribution (Portillo-Quintero & Sánchez-Azofeifa, 2010). TDF harbors communities with unique flora and fauna components, characterized by high levels of endemism and β diversity, which are highly dependent on water availability due to a marked seasonality in precipitation (Ceballos, 1995; Pennington *et al*., 2000, 2009). Despite its exclusive characteristics and the threats faced, the components and ecological processes of TDF are not well understood (Sánchez-Azofeifa *et al*., 2005). According to this, faunal and flora communities in TDF are limited by the availability of water and food during dry seasons (Dirzo *et al*., 2011). Terrestrial animals can handle these kinds of limitations in several ways: (1) concentrating in areas with permanent water availability, (2) moving seasonally to follow resources (behavioral adaptation), or (3) showing tolerance to water scarcity (physiological adaptation) (Ceballos, 1995; Schmidt-Nielsen, 1997; Stoner & Timm, 2011). Hence, the marked seasonality exhibited by TDF and the ways animals handle it can involve changes in the local distribution of species, generating spatial and temporal patterns mainly related to the water presence and prey availability throughout the landscape (Mortelliti & Boitani, 2008; Davidson *et al*., 2012; Schuette *et al.*, 2013).

Although the seasonality is recognized as a paramount condition for animal ecology in TDF, it has been a poorly addressed factor in ecological studies of selected animal groups in the Neotropics (Del Coro Arizmendi & Ornelas, 1990; Ornelas *et al*., 1993; Andresen, 2005; Mason-Romo *et al*., 2018). Despite the fact that mammalian medium-sized carnivores are relatively common, more abundant than large carnivores, and are a fundamental component in the ecological dynamic as seed dispersers and as controllers of vertebrate prey (Rocha *et al*., 2004; Cazetta & Galetti, 2009; Kimmel *et al*., 2010), few studies addressing their ecology in TDF are available (Hidalgo-Mihart *et al*., 2001; Maffei & Taber, 2003; Cantú-Salazar *et al*., 2005; Arispe *et al*., 2008; Valenzuela-Galván *et al*., 2013), and the most of them did not consider the role of seasonality (but see Valenzuela & Ceballos, 2000). In the particular case of Colombia, studies carried out with medium-sized carnivores in TDF have been mostly focused on describing the composition of the assemblages (Sánchez-Lalinde & Pérez-Torres, 2008; Pineda-Guerrero *et al.*, 2015). Therefore, the effects of seasonality are unknown yet.

Furthermore, assemblages of medium-sized carnivores mammals associated to TDF in Colombia are composed mainly by widely distributed species, including *Cerdocyon thous* (Linnaeus, 1766), *Procyon cancrivorus* (G. Cuvier, 1798), *Eira barbara* (Linnaeus, 1758), *Leopardus pardalis* (Linnaeus, 1758), *Herpailurus yagouaroundi* (É. Geoffroy, 1803), and *Conepatus semistriatus* Boddaert, 1785 (Díaz-Pulido *et al*., 2014). In general, these species use different ecosystems and habitats with a wide range of precipitation and temperature conditions, and are characterized by opportunistic feeding habits (Sánchez-Lalinde & Pérez-Torres, 2008; Galván-Guevara, 2010; Solari *et al*., 2013; Díaz-Pulido *et al*., 2014; García-Herrera *et al*., 2015; Pineda-Guerrero *et al.*, 2015). Like evidenced in other mammalian species in dry ecosystems (Stoner & Timm, 2004), it is expected that most of medium-sized carnivores in TDF exhibit behavioral adaptations for facing seasonal challenges, rather than physiological ones. These adaptations are likely associated with seasonal shifts in the diet, home range, habitat uses, and daily activity (Núñez-Pérez, 2006; Vieira & Port, 2007), which will be reflected through the changes in the spatial and temporal patterns of the species between seasons.

Moreover, the ecological response of mammalian species to seasonal constrains is directly related to habitat

conditions. That is to say, water availability is a critical factor for maintenance of carnivore assemblages in dry ecosystems, and as a consequence species might adjust their seasonal changes to this resource (Matos *et al*., 2009; Santos *et al*., 2011). In these ecosystems, habitats with a constant water supply (even during dry season) tend to be used more frequently by mammalian species and concentrate higher density of individuals (Western, 1975; Pérez-Cortez *et al*., 2012). In the Caribbean region of Colombia, where a considerable portion of TDF remains, the dry season is characterized by drastic water decrease, and available water sources become restricted to scattered and scarce natural or artificial ponds (Pizano & García, 2014). Consequently, areas containing this kind of water bodies are fundamental habitats for medium-sized carnivore species that inhabit TDF in Caribbean region.

In this study, we compared the patterns of habitat use between seasons, and describe the feeding habits and activity patterns for common medium-sized carnivore species *Cerdocyon thous*, *Leopardus pardalis*, and *Procyon* spp. in a small TDF reserve in the Colombian Caribbean region. We used data from scent station and camera trapping to determinate the seasonal changes in the occurrence probability and habitat use probability. Besides, using the camera records, we also describe their activity patterns. Likewise, we describe main items in the diet of species according to scat analyses. Unlike many TDF areas in Caribbean region, the study area has a constant water supply due to the presence of two natural, permanent ponds that make this area more stable for these carnivore mammals during the dry season. Considering the expected seasonal use of an area with availability of water in a dry ecosystem, we expect higher occurrence probability and habitat use probability for medium-sized carnivore species during dry season.

MATERIALS AND METHODS

STUDY AREA

The study was conducted within the Sanguaré Natural Reserve (9.72017° N, 75.67592° W), north of Morrosquillo Gulf in the Caribbean region, Sucre, Colombia (Figure 1). The area is Tropical Dry Forest, with an annual average rainfall of 1,100 mm, and annual average temperature of 27 °C (Holdridge, 1967; Pizano & García, 2014). It exhibits a markedly seasonal climate, with rainfall concentrated in April-May and October-November, and prolonged dry seasons from December to early April and late June to September (Sánchez-Páez & Álvarez-León, 1997). Within an area of 898 ha, Sanguaré offers a variety of habitats including 80 ha of natural water ponds and flooded habitats, 110 ha of secondary forest, 708 ha composed by shrubland, grassland, and mangrove covers. The forest is dominated by the palm *Attalea butyracea* (Mutis ex L. f.) Wess. Boer, and other trees such as *Sterculia apetala* (Jacq.) H. Karst., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Ceiba pentandra* (L.) Gaertn., *Pseudobombax septenatum* (Jacq.) Dugand, *Bombacopsis quinate* (W. S. Alverson, 1994), *Caesalpinia coriaria* (Jacq.) Willd., *Bursera simaruba* (L.) Sarg., *Lecythis magdalénica* Dugand, *Albizia saman* (Jacq.) Merr., and *Capparis odoratissima* (Jacq.).

DATA COLLECTION

We obtained records of carnivore mammals in Sanguaré Natural Reserve from surveys carried out between 2010 and 2013, covering periods including both dry and wet seasons. Additionally, we implemented as sampling methods scent stations, camera traps, and scat collection, using sampling designs according to each analyzed ecological aspect.

OCCURRENCE PATTERNS

We conducted a scent-station survey during four sampling periods of 5-7 consecutive days, between February 2010 and July 2011, covering two wet (May and June) and two dry (February and March) seasons. During each sampling period, we installed nine stations in secondary forest cover and six in shrublands, using two transects of 2.7 and 1.8 km, respectively (Figure 1A). Stations were placed 0.3 km from each other in each transect, and transects

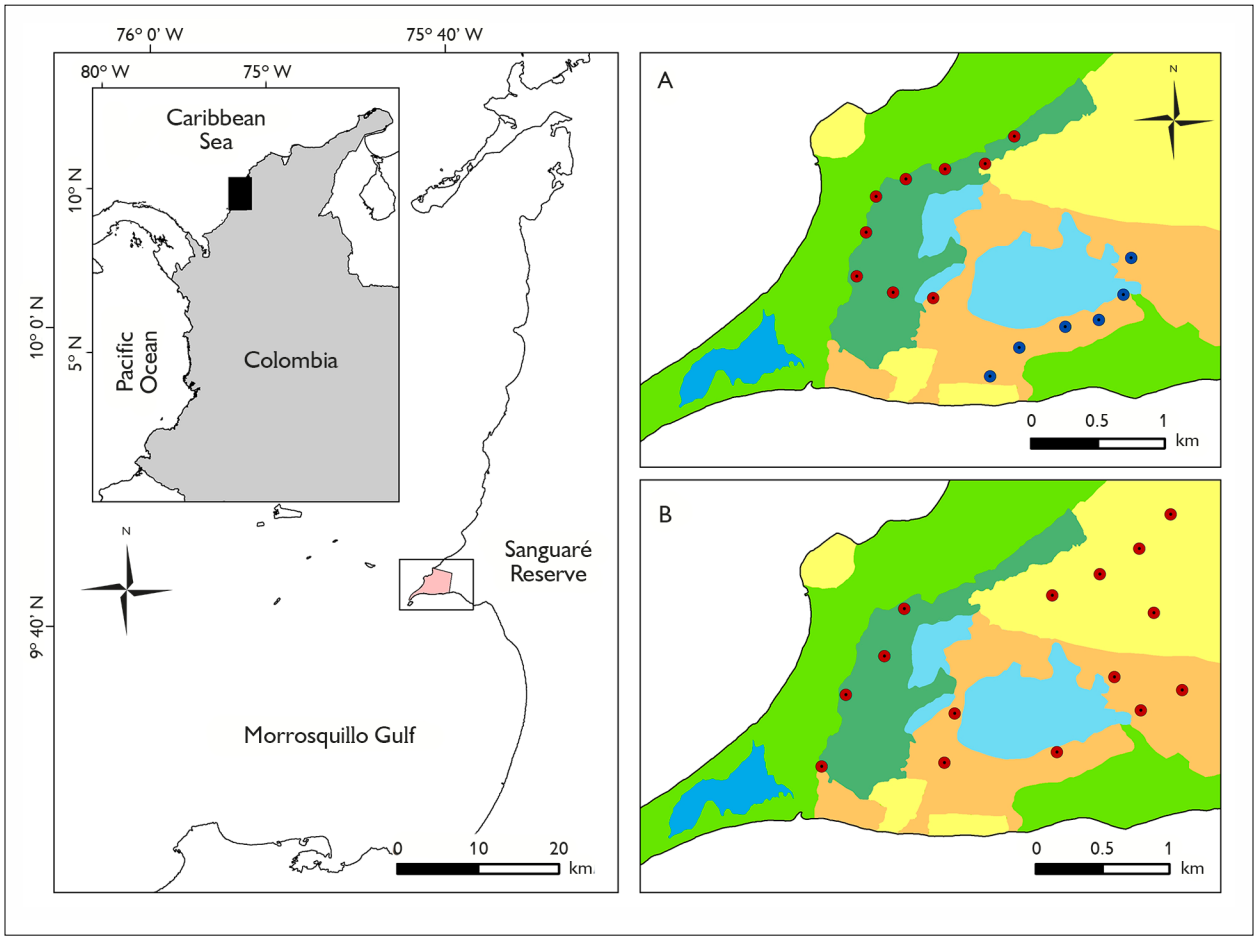

Figure 1. Location of Sanguaré Natural Reserve at Colombian Caribbean coast. Maps showing in detail the cover distribution in Sanguaré Reserve (light blue: freshwater ponds; dark blue: coastal lagoons; dark green: secondary forest; light green: mangrove; orange: shrubland; yellow: grassland), and (A) location of scent-stations within each transect (dark-red dots transect in secondary forest and blue dots transect in shrubland) for occurrence; and (B) location of sampling units (dark-red dots) for occupancy analyses. Map: D. A. Gómez Ruiz (2019).

were separated by 1.8 km, which is far enough to be considered independent from each other (Roughton & Sweeny, 1982; Conner *et al*., 1983; Acosta-Jamett & Simonetti, 2004). Each station was made of soft sand in a thin layer with a dimension of 1 m x 1 m, and due to the type of substrate we did not add water to the station in any of the seasons. Stations were baited with one of three scent lures Pro's choice, Mink Gland Lure, and Skunk Lure (Carman's® Animal Lures) in an alternating pattern.

Also, we walked along transects daily in the morning to check for the presence of fresh tracks and re-scent at each station. Since multiple tracks of the same species can be generated by a single individual at a specific scent-station, we recorded species presence/absence data in stations (Conner *et al*., 1983). Tracks were identified following the field guide of Aranda (2000). Likewise, to verify whether stations were working properly, we left a hand-made mark on it during daily checks and recorded if it was there in the following day. Finally, we recorded the number of stations in which each species occurred per day and the total number of active stations.

HABITAT USE

We implemented a combined camera trap and scent-station survey to record occurrences of carnivore species between February and December 2012. The survey protocol included 15 sampling units or sites randomly selected from a 300 x 300 m grid covering the study area, using the distribution of vegetation cover along the study area (Figure 1B). Each sampling unit was composed of one camera trap (Bushnell Trophy® Cam Trail) and one baited scent-station. Both methods were implemented within the same sampling unit, but camera and scent-stations were located to a minimum distance of 100 m to one another. We implemented the survey in four sampling periods of 12 consecutive days, spanning both the wet (February 22, March 04, and September 14-23, 2012), and dry (June 02-13 and December 04-17, 2012) seasons. During each period the camera traps were active for 24 hours/day, recording 30 s videos with a delay of 15 s between consecutive captures, and scent-stations were checked daily to verify the occurrence of tracks. Therefore, the individual inspection of each video allowed for species identification, following specialized guides (*e.g.*, Eisenberg & Redford, 1989; Emmons & Feer, 1999; Tirira, 2007).

DIET

We obtained fresh scat samples during the same four sampling periods as the scent-station survey. During each sampling period we collected scats opportunistically along dirt roads and trails within the study area. Scats were identified by size, form, location in latrines, and associated tracks following Aranda (2000) and Chame (2003). The scat samples were stored in ethanol (70%), transported to the lab and washed under running water through a fine mesh screen (1 mm); the remains were then inspected under a stereomicroscope for identification (Arruda Bueno & Mota-Junior, 2004). According to this, food items were identified to the lowest taxonomic level possible and separated into the following food categories: Plants, Insects, Arachnids, Chilopods, Crustaceans, Mollusks, and Vertebrates. Food categories were quantified according to their frequency of occurrence, which was calculated as the proportion of scats containing a particular item (number of scats where each item was present divided by the total number of scats) in each season (Rocha *et al*., 2008). Due to the small sample sized in each season and for each carnivore species we present the diet results as a descriptive assessment.

ACTIVITY PATTERNS

Moreover, we used 12 to 15 camera traps installed for 10 to 12 days in six surveys carried out between March, 2011 and August, 2013. The camera traps were located at different places in each survey depending of the quantity of records from the previous survey. Thus, the first and last surveys were aimed to study medium-sized mammals in the area, so we installed the cameras along trails; then, the other four surveys focused on collecting presence data of our target species, and the location of the cameras were almost constant during 2012, but not always along trails (Figure 1A).

We described activity patterns as a probability density functions (Ridout & Linkie, 2009) for each carnivore species per season, which was based on the number and temporal distribution of photographs from camera trapping. Also, we defined as independent detection for a species those records that were more than 30 min apart in a given sampling unit (Zimmermann *et al*., 2016). All estimations were made with package *overlap* in R (R Development Core Team, 2015; Meredith & Ridout, 2018).

DATA ANALYSIS

OCCURRENCE PROBABILITY

We used data from scent station to analyze changes in the occurrence probability of species between rainfall seasons. Besides, we treated the occurrence of a species in a scent-station as a binary response variable: present or absent in a particular station in each sampling day. We fitted Generalized Linear Models (GLMs) using the occurrence of each species with the rainfall season (dry *vs* wet) and vegetation cover

(secondary forest *vs* shrubland) as explanatory variables. We used the *glm* function in R with binomial distribution and logit link function (R Development Core Team, 2015) to fit all models. In this analysis, we did not consider the effects of sampling periods, instead treating observations from the same rainfall season as a group. We adjusted a full model, and models with individual and additive effects from both explanatory variables for each carnivore species, and contrasted the selected model against null model (representing the absence of any effect). The corrected Akaike Information Criterion for small sample sizes (AICc) was used to rank the models, and all models with $\Delta AIC < 2$ were considered equally plausible (Burnham & Anderson, 2004). The contrast with the null model and the selection among plausible models were based on the likelihood-ratio test.

HABITAT USE PROBABILITY

We used data from combined camera trap and scent station surveys to assess the differences in the habitat use of carnivore mammals in relation to seasonality, using an approach based on a multi-season occupancy model (MacKenzie *et al*., 2003). Occupancy models estimate species detection probability (p) based on repeated sampling events over a site, and occupancy probability (ψ) accounting for imperfect detection (MacKenzie *et al*., 2002). Occupancy is defined as the proportion of sites where a species is expected to occur, and detection probability as the probability that a species is detected given it is present, with both parameters being estimated using a likelihood-based method (MacKenzie *et al*., 2002). Multi-season occupancy models include the additional estimation of parameters governing changes in occupancy, namely colonization (γ) and extinction probabilities (ε) (Mackenzie *et al*., 2006). Given that distance between sampling units was less than one kilometer and the vagility capacity of these carnivore species (Maffei & Taber, 2003; Dillon & Kelly, 2008), we considered that the independence assumption was not met. Therefore, assuming that occupancy changed randomly within each season, we interpreted the occupancy parameter as the use probability of the study area (Guillera-Arroita *et al*., 2010; Keane *et al*., 2012).

We built presence-absence matrices of 15 sampling units for each species grouping records from both -camera trap and scent-station- methods into 3-day periods, generating four repetitions for each sampling period. Considering the reduced number of sampling sites, we decided to model the sampling periods from the same season together to improve the inferences about species occupancy. With this approach, modeling included two seasons (dry and wet) each one with eight sampling events, and assumed that occupancy of sites was constant between sampling periods within each season. We modeled detection and occupancy probabilities for carnivore species using a season-dependent detectability model ($\psi(.)\gamma(.)\varepsilon(.)p(season)$) with constant colonization and extinction probabilities. We used the 'unmarked' package in *R* to derived probabilities of occupancy (hereinafter called 'use probability') and detection for each season and their confidence intervals with a bootstrapping approach (Kéry & Chandler, 2012; Fiske & Chandler, 2011, 2019). In addition, we used parametric bootstrapping to evaluate the goodness-of-fit of fitted model for each species (Kéry & Chandler, 2012).

RESULTS

Five carnivore species were recorded during the four years of study: Crab-eating Fox *Cerdocyon thous*, Ocelot *Leopardus pardalis*, Tayra *Eira barbara*, and two Raccoon species *Procyon cancrivorus* (Cuvier, 1798) and *Procyon lotor* (Linnaeus, 1758). Although the identification of the records, including videos, scats, and tracks were straightforward in most cases, the reliable distinction between records of *P. cancrivorus* and *P. lotor* was not possible. Therefore, we classified all records of both species as *Procyon* spp. We did not include *E. barbara* in the analysis due to the small number of records obtained (one track and six videos).

OCCURRENCE PROBABILITY

Altogether, we monitored the 15 scent stations for 46 nights during the entire study, with a total effort of 331 active scent-station nights (Table 1). We obtained 116 detections

from three carnivore species during both seasons, 38 visits of *C. thous*, 31 of *L. pardalis*, and 47 of *Procyon* spp. The most frequent recorded species were *Procyon* spp., visiting 14.2% of the stations, with 22.5% and 6.43% of the visits in wet and dry seasons, respectively (Table 1).

On the whole, the analysis of occurrence probability showed a similar seasonal pattern for the three carnivore species: occurrence was significantly higher in the dry season (*C. thous* [Season model: $z = -3.975$, $p < 0.001$], *L. pardalis* [Season model: $z = -2.898$, $p < 0.0037$], and *Procyon* spp. [Season model: $z = -4.116$, $p < 0.001$]) (Table 2, Figure 2). In the case of *Procyon* spp., cover type was also a significant covariate ($z = -2.398$, $p = 0.0165$) (Table 2) with higher occurrence in secondary forest (Figure 2).

HABITAT USE PROBABILITY

We recorded a total of 71 detections of the three carnivore species; 13 of *C. thous* (eight during the dry season and five in wet season), 28 of *L. pardalis* (16 in the dry season and 12 in wet season) and 30 of *Procyon* spp. (22 during the dry season and eight in wet season), with a total effort of 720 camera days, and 720 scent-station nights. Estimated values from fitted models showed no differences in the detection probability between seasons for all the species, and pointed a trend to higher use probabilities during the dry season, with significant differences only for *Procyon* spp. (Figure 3).

DIET

We collected a total of 72 scats for the three carnivore species during both seasons, 16 of *C. thous*, 14 of *L. pardalis*, and 42 of *Procyon* spp. (Table 3). We found six food categories with 24 different food items for *C. thous*, including fruits from seven plant species, insects from the orders Orthoptera, Coleoptera, Hymenoptera, Hemiptera, and Blattodea; centipedes (Chilopoda), mollusks, reptiles [*Iguana iguana* (Linnaeus, 1758)], and rodents (*Zygodontomys* sp.). The diet of *L. pardalis* was composed of five food categories with seven items, mainly *Iguana iguana*, birds, and rodents of the genera *Diplomys*, *Zygodontomys* and *Rattus*. Finally, five food categories with 25 food items were identified in the diet of *Procyon* spp., including 11 plant species, insects from the orders Coleoptera, Orthoptera, Blattodea, Hymenoptera, crustaceans, mollusks, and vertebrates. Vertebrates were represented mainly by fishes, but also consisted of some (unidentified) birds and amphibians.

ACTIVITY PATTERNS

Likewise, we recorded 114 independent detections for the three carnivore species from all survey periods, investing

Table 1. Number of nights and scent-stations installed during the study. Percentage of visited stations for three carnivore species recorded in Sanguaré Natural Reserve, Sucre, Colombia. Number in parentheses corresponds to the number of visits.

	Dry			Wet			General
	Secondary Forest	Shrubland	Total	Secondary Forest	Shrubland	Total	
Effort							
Nights	11	11	22	13	11	24	46
Active Scent-stations	95	65	160	113	59	171	331
% Visited stations							
Cerdocyon thous	17.89 (17)	21.54 (14)	19.38 (31)	5.31 (6)	1.69 (1)	4.09 (7)	11.48 (38)
Leopardus pardalis	18.95 (18)	7.69 (5)	14.38 (23)	5.31 (6)	3.39 (2)	4.68 (8)	9.37 (31)
Procyon spp.	28.42 (27)	13.85 (9)	22.5 (36)	7.96 (9)	3.39 (2)	6.43 (11)	14.2 (47)

a 1560 camera-days effort. *Cerdocyon thous* was the least frequently detected species with only a total of 15 detections (dry season: eight detections, wet season: seven detections), while *L. pardalis* (dry season: 14 detections, wet season: 27 detections) and *Procyon* spp. (dry season: 21 detections, wet season: 37 detections) were detected 41 and 58 times, respectively. From the combined detections of both seasons, we found that *C. thous* had crepuscular habits, being principally active during the first hours in the night and in the morning (Figure 4). *Leopardus pardalis* was active during the night, with the main activity after midnight, and some scarce records during day time (Figure 4). Finally, *Procyon* spp. presented records mainly during the night (Figure 4).

Table 2. Occurrence probability models compared for three carnivore species in Sanguaré Natural Reserve, Sucre, Colombia. *K*: number of parameters in a model. Delta: between the model AICc and the lowest AICc in the model set. *w*AICc: Akaike model weight.

Species	Model	*K*	AICc	Delta	*w*AICc	Cumulative *w*AICc
Cerdocyon thous	Season	2	94.48	0.00	0.65	0.65
	Season+Cover	3	96.78	2.30	0.20	0.85
	Season*Cover	4	97.43	2.95	0.15	1.00
	Null model	1	112.49	18.01	0.00	1.00
Leopardus pardalis	Season+Cover	3	101.15	0.00	0.58	0.58
	Season	2	103.14	1.99	0.21	0.79
	Season*Cover	4	103.24	2.09	0.20	0.99
	Null model	1	110.51	9.37	0.01	1.00
Procyon spp.	Season+Cover	3	123.82	0.00	0.70	0.70
	Season*Cover	4	126.24	2.41	0.21	0.91
	Season	2	127.88	4.06	0.09	1.00
	Null model	1	143.90	20.08	0.00	1.00

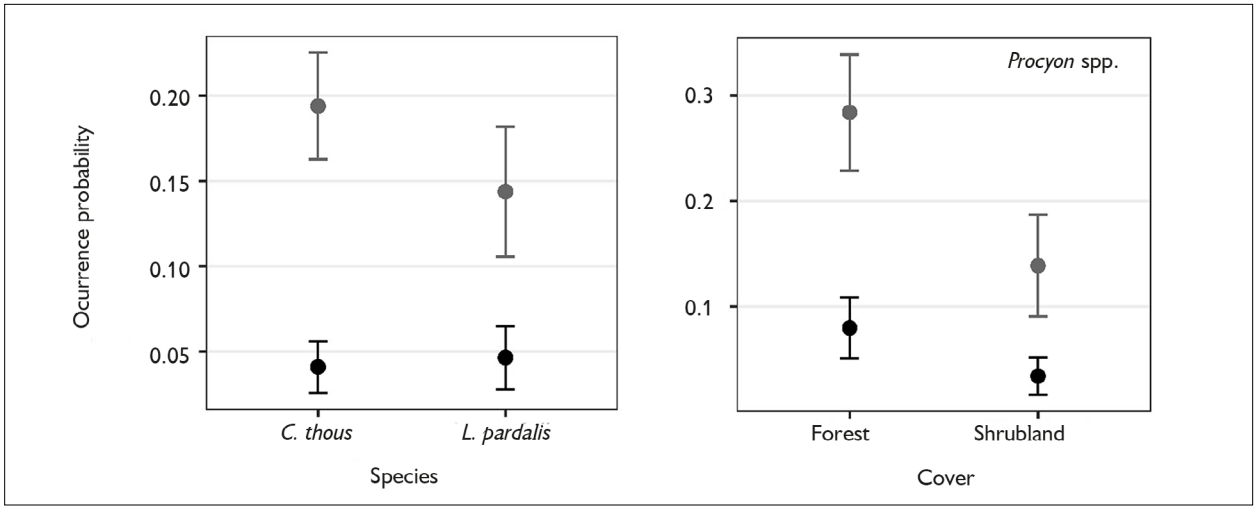

Figure 2. Occurrence probability of *Cerdocyon thous* and *Leopardus pardalis* during the dry (gray bar) and wet (black bar) seasons (left); and occurrence probability of *Procyon* spp. during dry (gray bar) and wet (black bar) seasons in secondary forest and shrubland covers (right), in Sanguaré Natural Reserve, Sucre, Colombia. Bars correspond to standard error.

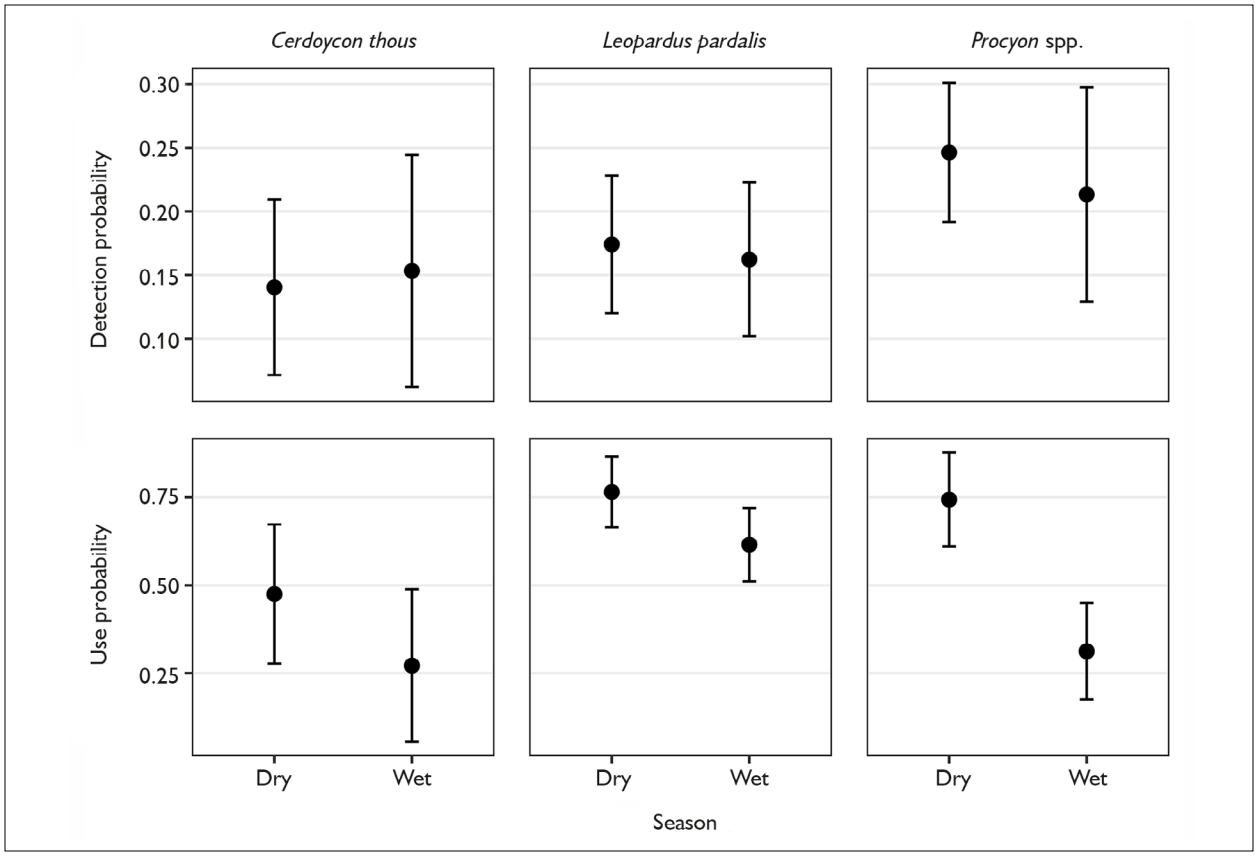

Figure 3. Estimated detection (above) and use probabilities (below) for the carnivore species *Cerdocyon thous*, *Leopardus pardalis*, and *Procyon* spp., in Sanguaré Nutural Reserve, Sucre, Colombia. Bars correspond to standard error.

Table 3. Frequency of each food category and food items in each category in scats collected (number in parenthesis) during dry and wet seasons for carnivore species recorded in Sanguaré Natural Reserve, Sucre, Colombia.

(Continue)

Food Category	*Cerdocyon thous*		*Leopardus pardalis*		*Procyon* spp.	
	Dry (11)	Wet (5)	Dry (12)	Wet (5)	Dry (29)	Wet (13)
Plants	0.45	0.40	0.75	0.60	0.86	0.85
Seeds	0.45	0.40	-	-	0.86	0.85
Other	-	-	0.75	0.60	-	--
Insects	0.27	0.40	0.42	0.40	0.86	0.62
Odonata	0.09	-	-	-	0.04	-
Orthoptera	0.18	-	-	-	0.25	-
Coleoptera	-	0.20	-	-	0.32	0.23
Hymenoptera	-	0.20	-	-	-	-
Blattodea	-	-	-	-	0.25	0.08
Others	-	-	-	-	-	0.31
Crustaceans	-	-	0.33	0.20	0.41	0.62
Arachnids	0.09	-	-	-	-	-

Table 3. (Conclusion)

Food Category	*Cerdocyon thous*		*Leopardus pardalis*		*Procyon* spp.	
	Dry (11)	Wet (5)	Dry (12)	Wet (5)	Dry (29)	Wet (13)
Chilopods	0.18	0.20	0.08	0.40	-	-
Molusks	0.09	-	-	-	0.07	-
Vertebrates	0.64	0.80	1.00	1.00	0.66	0.23
Reptiles	0.63	0.80	0.66	0.6	0.10	-
Birds	-	-	0.78	0.4	0.14	0.07
Fish					0.34	0.15
Amphibians					0.07	0.07
Mammals	0.09		0.44	0.2		

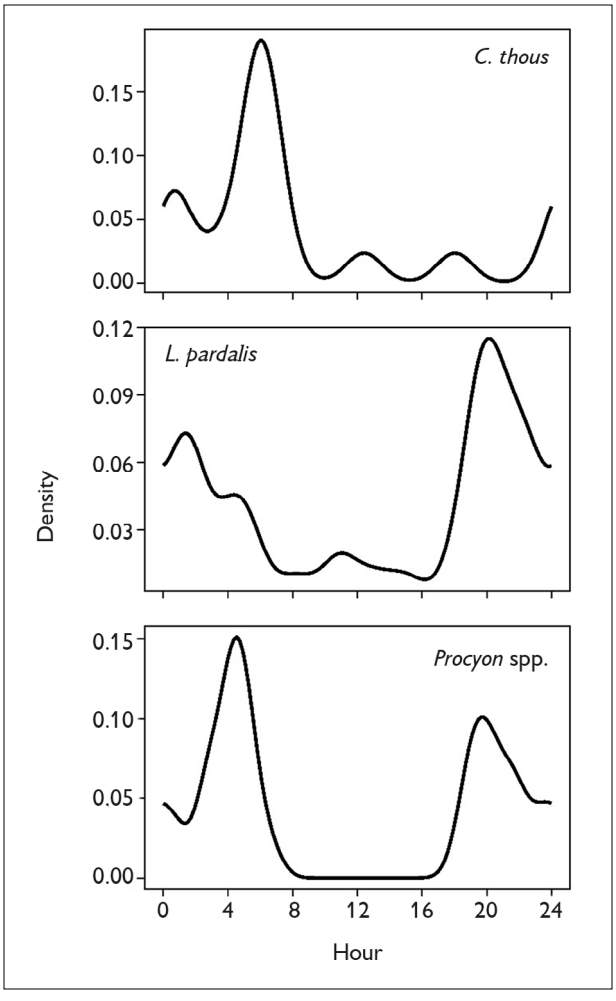

Figure 4. Diel activity patterns from camera trap data using Kernel density function in Sanguaré Natural Reserve, Sucre, Colombia, for the carnivore species: *Cerdocyon thous*, *Leopardus pardalis* and *Procyon* spp.

DISCUSSION

This study is the first attempt to assess the changes in the habitat use patterns of common medium-sized carnivore species (*C. thous*, *L. pardalis*, and *Procyon* spp.) in relation to seasonality in TDF area of Colombian Caribbean. Likewise, it provides information about their diet and activity patterns in this ecosystem. Our results in Sanguaré Natural Reserve were partially congruent with the expected seasonal behavior of medium-size mammals in dry ecosystems, with the occurrence probability of the three carnivore species and the habitat use probability for *Procyon* spp. being higher during the dry season. Study species exhibited behavioral changes to cope with seasonality in TDF, probably associated to variations in local movements during the dry season and the constant water availability. Water availability in Sanguaré Natural Reserve throughout the year contrasts with the predominant one (drought) in the surrounding areas.

OCCURRENCE AND HABITAT USE PROBABILITIES

Our study showed seasonal increase in occurrence probability for the three carnivore species during the dry season. For this reason, it is probably that climatic conditions of the region promote wildlife concentration around the reserve, as animals can have permanent availability of water during the dry season (*e.g.*, Valenzuela & Ceballos, 2000;

Santos *et al*., 2011). The low frequency of tracks records during the wet season would lead to think that such differences in occurrence probability are linked to detection bias (Silveira *et al.*, 2003). However, raw data shows (Table 1) that the number of active scent-stations was not different between seasons. Therefore, we think occurrence pattern responds to seasonality instead detection differences. Furthermore, the non-variation of detection probabilities from habitat use analysis could suggest that occurrence probability is a reasonable inference.

Additionally, seasonal difference in habitat use probability only was found in *Procyon* spp. Lack of significant differences in the habitat use probabilities of *C. thous* and *L. pardalis* can be consequence of our small sample sizes, but it also could be indicating the presence of a stable number of resident individuals in the study area. As has been documented in other dry ecosystems, the occupancy patterns of resident species tend to exhibit negligible seasonal changes because species use regularly the habitat (Martin *et al*., 2017). In this way, Sanguaré Natural Reserve might support a high proportion of resident individuals of both species using the area along year, and although the arriving of individuals during the dry season may happen, it would not generate changes in the habitat use probabilities.

Furthermore, seasonal pattern in *Procyon* spp. could be associated directly to the arriving of individuals to the study area during the dry season as animals move to wet habitats where they can secure food and water resources (*e.g*., Valenzuela & Ceballos, 2000; Maffei & Taber, 2003; Mendes-Pontes, 2004). In addition, the pattern also could be a response to the movements of the resident individuals within the study area during the wet season. Lower habitat use probabilities of *Procyon* spp. in Sanguaré Natural Reserve could be derived from movements of individuals to non-surveyed habitats (*i.e*. mangrove) or to follow seasonal pounds or temporal streams in surrounding areas – which appears in wet season. In coastal and Pantanal systems, *Procyon* species prefer foraging in mangrove stands and freshwater ponds respectively, where food resources as fishes, crabs and mollusks are mostly available (Villa-Meza *et al.*, 2011; Carvalho, 2012).

Finally, habitat preferences are also important behavioral changes to cope with dry season in tropical dry forests, as shown by previous studies (Ceballos, 1995; Stoner & Timm, 2011). For example, *Procyon* spp. habitat preferences have been described as riparian forest and palm forests (Arispe *et al*., 2008), which coincides with our results in showing higher occurrence probability in secondary forest vegetation cover than in shrubland and grassland. The pattern of preference does not change with seasonality, probably since *Procyon* spp. can be found within the most profitable habitat all year around in Sanguaré, near water ponds with secondary forest vegetation, which is also connected to mangrove habitat (Figure 1).

DIET

Few studies on the diet of these mesocarnivore species have been undertaken in Colombia, mostly in Andean ecosystems, for example, the diets of *C. thous* (Delgado-V., 2002; Delgado-V. & Zurc, 2007) and *L. pardalis* (Sánchez *et al*., 2008). We found that *C. thous* is a generalist omnivorous species that consume mainly vertebrates, fruits and insects, as has been previously reported (Macdafem & Marinho-Filho, 2002; Bianchi *et al*., 2014). Previous studies indicate *L. pardalis* is a specialized feline, whose prey includes between eight and 11 different species of vertebrates, mostly mammals in humid forests (Chinchilla, 1997; Sánchez *et al*., 2008) and reptiles in deciduous forests (Villa-Meza *et al*., 2002). However, our study reports just four vertebrate prey species; furthermore, we report a new prey item, a centipede (Chilopoda). Our finding of invertebrates as the main food item for *Procyon* spp. is in agreement with studies on *Procyon cancrivorus* in Brazil (Gatti *et al*., 2006) and Venezuela (Bisbal, 1986).

Moreover, diet descriptive analyses in this study did not show changes in composition between wet and dry seasons for these carnivore species, being these the best examples of trophic generalists in tropical dry forest,

and several studies have documented seasonal variation in the diet of generalist carnivores (Vaughan-Dickhaut & Rodríguez-Sáenz, 1986; Stoner & Timm, 2011 and references therein). For our studied species, there are only studies reporting seasonal changes in diet of *C. thous*, which has been reported feeding on insects during the wet season and small vertebrates during the dry season (Bisbal & Ojasti, 1980; Sunquist *et al*., 1989; Bianchi *et al*., 2014).

Despite of our data does not show changes between seasons, due to the reduced number of scats collected, we believe that, much like *C. thous,* other species present in the TDF may present seasonal changes in their diets. Hence, further studies are needed. These must include a more representative sample sized for each season (scats collected in several months through the years) and to analyze categories informative enough to detect subtler changes than the categories we have evaluated (*e.g*., Bianchi *et al*., 2014).

ACTIVITY PATTERNS

In regard to activity patterns, species in the study area are mainly nocturnal and crepuscular as other studies reported. *Cerdocyon thous* has been reported as a nocturnal species in Bolivia (Maffei & Taber, 2003; Maffei *et al*., 2007) and Brazil (Faria-Correa *et al*., 2009); *L. pardalis* has been described as a nocturnal species without evidence of crepuscular activity (Kolowski & Alonso, 2010; Porfirio *et al*., 2016), and the pattern described to *Procyon* spp. agrees with studies for *P. cancrivorus* reported in a dry forest habitat in Bolivia (Arispe *et al*., 2008). Only for *L. pardalis* seasonal changes in activity patterns have been addressed in Brazil (Porfirio *et al*., 2016), but with no differences detected and assessed with a big set of independent record, which suggest that activity patterns would be a conservative behavior during the marked seasonality of TDF.

Of course, these results highlight the importance of private initiatives for conservation and management of tropical dry forests. Likewise, they represent potential refuge to local fauna due to the matrix of landscape with cattle ranching pastures and few forest remnants. This and other research efforts are contributing towards an effective protection and management of the local biodiversity, as well as its services for local communities in the Caribbean region of Colombia.

CONCLUSIONS

To sum up, three medium-sized carnivore species were recorded at Sanguaré Natural Reserve: *C. thous*, *L. pardalis* and *Procyon* spp. Also, these species showed seasonally changes in occurrence probability with no differences in detection probability between seasons. The observed pattern reflects that these species, in Sanguaré, are probably making more/larger habitat use during the dry season than in the wet season, this because the area has permanent water ponds. This has been already shown in other small carnivore and ungulate species in TDF, where they used areas with available water resources during the dry season (Valenzuela & Ceballos, 2000; Pérez-Cortez *et al*., 2012). Certainly, our result highlights the importance of permanent water to explain the occurrence of medium-sized carnivore species in tropical dry forest. Generalist carnivore species such as the target ones in this study depend on behavioral strategies such as movement during dry season to cope with environmental constraints of this kind of ecosystems.

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