Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize

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Abstract

To protect and manage an intact neotropical carnivore guild, it is necessary to understand the relative importance of habitat selection and intraguild competition to the ecology of individual species. This study examined habitat use of four carnivores in the Mountain Pine Ridge Forest Reserve, Belize. We calculated photographic trap success (TS) rates for jaguars *Panthera onca*, pumas *Puma concolor*, ocelots *Leopardus pardalis*, grey foxes *Urocyon cinereoargenteus*, potential prey and humans at 47 remote camera stations spaced along roads and trails within the $139 \, km^2$ study site. At each station, we used manual habitat sampling in combination with geographic information systems to estimate habitat characteristics pertaining to vegetation cover. We used negative binomial models to analyse species-specific TS as a response to habitat (including vegetation and landscape variables, prey activity and human activity) and co-predator activity rates. Jaguars [TS = 7.56 ± 1.279 (SE) captures per 100 trap-nights (TN)] and grey foxes (31.5 ± 6.073 captures per 100 TN) were commonly captured by cameras, while pumas (0.66 ± 0.200 captures per 100 TN) and ocelots (0.55 ± 0.209 captures per 100 TN) were rare. Model selection via Akaike's information criterion (AIC) revealed that models including habitat variables generally performed better than models including co-predator activity. Felid captures were positively associated with small bird TS and with the width or length of surrounding roads, while fox counts showed few habitat associations. Ocelot activity was positively related to jaguar captures, an effect probably explained by their shared preference for areas with more roads. Pumas were negatively related to human activity and jaguars showed a similar, though non-significant, trend, suggesting that these felids may be sensitive to human disturbance even within protected areas. Results suggest that these predators do not spatially partition habitat and that the jaguar could function as an umbrella species for smaller sympatric carnivores.

Introduction

The carnivore guild containing the jaguar *Panthera onca*, puma *Puma concolor* and ocelot *Leopardus pardalis* exerts a strong structuring influence within neotropical forest communities (Terborgh, 1990). These cats may limit prey populations to below carrying capacity (Emmons, 1987) and have top-down cascading effects that extend throughout neotropical systems, affecting plant community dynamics (Asquith, Wright & Clauss, 1997; Terborgh *et al.*, 2001, 2006). The jaguar, in particular, has been described as an umbrella species and has been targeted by conservation initiatives meant to preserve entire communities (Noss, 1990; Gittleman *et al.*, 2001; Sanderson *et al.*, 2002). However, the simultaneous protection of multiple carnivores may not be a straightforward endeavor because interspecific competition can result in negative relationships between dominant 'superpredator' and smaller 'mesopredator' populations (mesopre-

dator species concept; Crooks & Soulé, 1999). Competition can also cause niche partitioning and allow dominant competitors to exploit preferred resources to the detriment of subordinate species that are forced to avoid desirable locations used by the larger carnivores (Schoener, 1974; Caro & Stoner, 2003; Gehrt & Clark, 2003). Selecting areas for the preservation of healthy jaguar populations could conflict with the conservation of smaller carnivores such as pumas and ocelots, calling the umbrella species concept into question.

Past research indicates potential for competition within this guild. Jaguars, pumas and ocelots overlap not only in their preference for areas of dense forest but also in the species they prey upon (Rabinowitz & Nottingham, 1986; Sunquist & Sunquist, 2002). Emmons (1987) observed that ocelots and jaguars cover the entire size range of mammalian prey, while the body size of prey eaten by pumas falls in the middle and overlaps with that of prey eaten by jaguars and ocelots. Moreno, Kays & Samudio (2006) proposed that

the absence of jaguars on Barro Colorado Island may allow ocelots and pumas to consume larger prey than in areas with jaguar populations. Researchers have hypothesized that competition with jaguars spatially affects puma activity in both Belize and Venezuela (Rabinowitz & Nottingham, 1986; Scognamillo *et al.*, 2003). Donadio & Buskirk (2006) found that intraguild competition is most intense when species are more predatory, are confamilial, have overlapping diets and have intermediate differences in body size – characteristics common to the neotropical felid guild.

Grey foxes are another carnivore that may interact with neotropical felids, but to our knowledge, no study has examined this interaction. This carnivore, probably too small to compete with jaguars and pumas, may compete for the small mammals consumed frequently by ocelots. The grey fox feeds omnivorously on a variety of items, and some research has found that they select areas with high concentrations of small mammals (Johnson & Franklin, 1994; Sawyer & Fendley, 1994; Novaro, Walker & Suarez, 1995; Fedriani *et al.*, 2000). Ocelots may also compete with grey foxes through intraguild predation due to their intermediate difference in body size (Donadio & Buskirk, 2006).

Our study is unique in that it uses a large number of camera traps combined with manual and geographic information systems (GIS) habitat sampling at camera sites to examine habitat use and interactions among carnivores within the Mountain Pine Ridge Forest Reserve (MPR), Belize. Central American pine forests cover *c.* 111 400 km^2 but are under-represented among protected areas (World Wildlife Fund, 2001). While density estimates exist for jaguars (2.09–3.25 100 km^{-2}) and ocelots (2.11–3. 100 km^{-2}) in the MPR (Davis, 2009; Dillon & Kelly, 2007; Everatt, Andresen & Kelly, 2010), little research has been conducted on carnivore communities in neotropical pine forests. Our study provides a first investigation into interactions among carnivores in this unique and important habitat type.

Our objectives were: (1) to use non-invasive remote camera surveys to describe and compare the habitat use of jaguars, pumas, ocelots and grey foxes with regard to structural vegetation features and potential prey activity in a neotropical pine forest; (2) to examine relationships between co-predator activity rates within this site.

To manage conservation areas that protect co-existing carnivore species, we must understand species-specific habitat use patterns and evaluate the role that competitors play in determining these patterns. We expected that both habitat and co-predator activity would have a significant influence on carnivore activity in the MPR. We hypothesized that multiple carnivores may be attracted by similar habitat features that provide better foraging conditions such as canopy cover, canopy height, understory cover, tree density, streams and roads (which may provide convenient hunting routes, especially when seldom used by humans) (Rabinowitz & Nottingham, 1986; Ludlow & Sunquist, 1987; Sunquist & Sunquist, 2002; Dillon & Kelly, 2007). Additionally, we predicted that these carnivores would avoid areas with human activity while selecting areas with high prey activity. However, smaller carnivores may avoid larger competitors and this may conflict with the desire for optimal habitat. For example, ocelot activity may be negatively related to canopy cover and larger prey, but positively related to human activity because in doing so, they avoid larger felids.

Methods

Study area

The 434 km^2 MPR lies in western Belize (Fig. 1). This neotropical pine forest contains pockets of shrubland and broadleaf forest in riparian areas and is periodically burned by naturally occurring seasonal fires (Kellman & Miyanishi, 1982; Kellman & Meave, 1997). A sequence of fires occurred in May of 2007, 1 month before this study, and affected
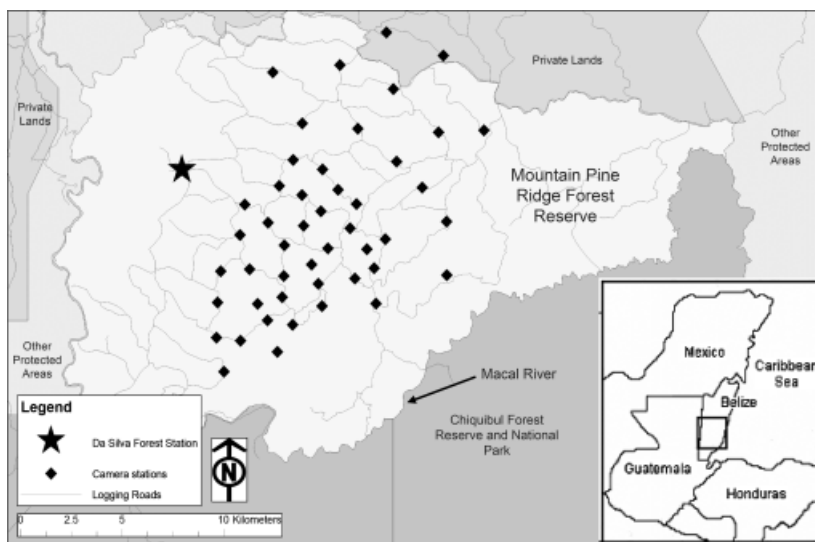
Figure 1 Location of the 47 camera stations established in the Mountain Pine Ridge Forest Reserve (MPR) within Belize, Central America. Camera and habitat surveys were completed in the MPR from June to August of 2007. Each station consisted of two cameras mounted in opposing pairs in a 71-day trapping session from June to August of 2007. The Macal River that delineates the MPR's southern border separates the pine forest of the MPR from the broadleaf forest of the Chiquibul Forest Reserve and National Park.

168 km^2. Da Silva Forest Station (also known as Augustine) is a small (~15 people) settlement in the reserve with a network of old logging roads allowing access to the study site. All of the ~358 km of roads within the site were unpaved (dirt pack) and most were seldom used; many were overgrown with vegetation due to lack of maintenance. The MPR's southern border is delineated by the Macal River, creating a sharp transition between the pine and the broad-leaf forest of the Chiquibul Forest Reserve and National Park (Fig. 1). This adjacent area supports similar densities of jaguars (2.4–8.8 individuals 100 km^{-2}), but higher densities of ocelots (12.8–25.8 individuals 100 km^{-2}) than those found in the MPR (Silver et al., 2004; Dillon & Kelly, 2007; Dillon & Kelly, 2008).

Camera trapping and habitat data collection

We used standardized techniques for remote camera surveys found to be successful in trapping neotropical felids (Silver et al., 2004; Maffei et al., 2005; Kelly et al., 2008). We established 47 camera stations in a grid at intervals of c. 1.5–3.0 km along roads and trails within the MPR (Fig. 1). We used DeerCam (DC200 and DC300 models) passive infrared film cameras (Non typical Inc., Park Falls, WI, USA). Each station included two cameras mounted on opposite sides of trails/roads. The minimum convex polygon linking the camera stations was 139.9 km^2.

We recorded counts of jaguar, puma, ocelot and grey fox captures at each station between 6 June and 18 August 2007. Trap success (TS) of each carnivore was calculated as the number of captures at a station per 100 trap-nights (Dillon & Kelly, 2007). Trap success indicates the relative activity level of these species. To ensure independence of captures, we counted multiple photographs of an animal within an arbitrarily selected 30-min period as only one capture (unless individually distinguishable). The trap success of humans and several 'groups' of prey species were calculated similarly.

Research suggests that while there is dietary overlap, jaguars consume species averaging 15 kg, pumas rely on prey <15 kg (Sunquist & Sunquist, 2002) and ocelots rely on smaller prey, often <1 kg, but take larger prey when available (Konecny, 1989; Abreu et al., 2008). Grey foxes, similar to ocelots, rely on small mammals (Fedriani et al., 2000). We assigned mammals regularly photographed and considered likely prey to the three groups according to species weights: small (<5 kg), medium (5–15 kg) and large (>15 kg) (Reid, 1997, Table 1). Remote cameras captured ground birds that are likely felid prey. Because of the low mass to volume ratio of avian species, we categorized birds separately from mammals as either small (<1 kg) or large

Table 1 Species photographically captured during the remote camera survey in the Mountain Pine Ridge Forest Reserve from June to August 2007. Species considered potential prey were categorized into groups for analysis according to weights from the literature. The mean trap success rate of each species was calculated across 47 camera stations operational during the study period

Scientific name	Common name	Weight from literature (kg)[a]	Group assignment for trap success calculation (potential prey only)	Mean trap success (SE)[b]
Panthera onca	Jaguar	30–100		7.56 (1.279)
Puma concolor	Puma	24–65		0.66 (0.200)
Leopardus pardalis	Ocelot	7–14.5		0.55 (0.209)
Urocyon cinereoargenteus	Grey fox	1.8–3.5		31.5 (6.073)
Dasyprocta punctata	Agouti	3–4	Small mammal	0.06 (0.064)
Dasypus novemcinctus	Nine-banded armadillo	3–7	Small mammal	0.53 (0.155)
Coendou mexicanus	Porcupine	1.4–2.6	Small mammal	0.04 (0.043)
Didelphis marsupialis	Common opossum	0.6–2.4	Small mammal	2.08 (0.313)
Agouti paca	Paca	5–12	Medium mammal	0.42 (0.174)
Tamandua mexicana	Tamandua	3.8–8.5	Medium mammal	0.07 (0.047)
Nasua narica	Coatimundi	2.7–6.5	Medium mammal	0.39 (0.164)
Tayassu tajacu	Collared peccary	12–26	Large mammal	0.17 (0.087)
Dicotyle pecari	White-lipped peccary	27–40	Large mammal	0.16 (0.161)
Mazama americana	Red brocket deer	12–32	Large mammal	0.13 (0.077)
Odocoileus virginianus	White-tailed deer	25–43	Large mammal	1.39 (0.332)
Tapirus bairdii	Tapir	180–300	Large mammal	0.81 (0.236)
Columbina passerina	Common ground dove	0.022–0.041	Small bird	0.32 (0.227)
Nyctidromus albicollis	Common pauraque	0.0532	Small bird	1.24 (0.532)
Ortalis vetula	Plain chachalaca	0.439–0.794	Small bird	3.70 (1.341)
Penelope pupurascens	Crested guan	2.000–2.150	Large bird	0.11 (0.061)
Crax rubra	Great currasow	4.050–4.225	Large bird	0.28 (0.145)
Meleagris ocellata	Ocellated turkey	5.525	Large bird	1.82 (0.623)

[a]Weights were obtained from Reid (1997) in the case of mammalian species and Dunning (1993) in the case of avian species.
[b]All trap success parameters are in units of captures per 100 trap-nights.

(>1 kg) (Dunning, 1993, Table 1). We calculated TS rates for each group as a whole.

Vegetation sampling concentrated on structural characteristics potentially important in providing cover. We recorded canopy cover (present or absent) every 20 m along 200 m transects radiating from the camera stations at 0, 120 and 240°. We estimated canopy height with a clinometer and tree density using the point-centred quarter method with an unbiased estimator (Pollard, 1971) at 50 and 200 m along each transect (six locations). At these points, we also estimated the per cent understory (0–2 m) cover using point intercepts along a 40 m transect. Mean estimates of all variables were calculated at the 50 and 200 m scale and for the whole camera station.

We used ArcGIS to generate landscape variables. We obtained data layers of Belize containing the geographic locations of roads (updated in 2004), rivers and protected area boundaries (updated in 2005; Meerman, 2007), then, following Kelly & Holub (2008), we created 200 m buffers encircling camera stations. These buffers were intersected with appropriate layers to retrieve the total length of rivers and roads within 200 m of each station. Additionally, we calculated the distance to the nearest point along the Macal River (i.e. distance to broadleaf forest) for each station.

Analyses

We treated individual camera stations as the sampling units, assuming that associated habitat characteristics and capture rates were independent due to their wide spacing (≥ 1.5 km between stations). We assumed that sampled habitat was accessible to study species, all capture events of a species >30 min apart were independent and species were absent from stations where they were not photographed (no non-detections).

We used SAS (2008) for analyses. To model species-specific carnivore activity across the site, we used generalized linear models, assuming a negative binomial error distribution, with counts of jaguar, puma, ocelot or grey fox captures at each station as the response. Negative binomial models perform well when data are skewed and over-dispersed containing many low values, as is common with animal counts (Sileshi, 2008). Because stations were operational for varying lengths of time, we included the log number of trap nights at each station as an offset variable in models. We calculated parameter estimates (and standard errors) for all variables to assess effect size, assessing significance with marginal t-tests ($\alpha = 0.05$). We used Akaike's information criterion corrected for small sample sizes (AIC$_c$; Burnham & Anderson, 2002) and calculated the ΔAIC$_c$, and weights to rank and compare all models proposed for each carnivore including a null (intercept-only) model.

To characterize the habitat use of each species with regard to structural features and the activity rates of humans and prey, we modelled captures as a response to a selected set of the habitat variables proposed. We examined correlations between variables using Pearson's correlation coeffi-

cient (r); none showed strong correlations ($r < 0.40$ for all pairs). We narrowed the variable list to those showing *potential* for important effects in the MPR by constructing 'global habitat' models for each carnivore including all proposed variables, calculating the corresponding t-statistic for each parameter and selecting those with $P < 0.1$ (indicating 90% confidence intervals (CIs) not overlapping zero) for inclusion in future 'reduced' habitat models. Then, for each carnivore, we ran models with all possible combinations of the species-specific variable subset. Ranking these models by AIC$_c$ scores allowed us to identify important variables and to compare the strength of habitat-only models against those including co-predator captures.

To examine the relationship between activity levels of possibly competing carnivores, we modelled counts for each of the smaller carnivores while treating the capture rates of larger species as predictors. For example, we assumed that due to their relatively large body sizes, the jaguar, puma and ocelot are dominant to the grey fox and may affect fox activity patterns, but not vice versa. If carnivores prefer the same habitat variables, this could result in a correlation in activities even if they do not interact substantially. Similarly, if a carnivore species avoids another, it might appear to avoid habitats preferred by this competitor. While differentiating between these alternative scenarios is not possible without experimental manipulation, simultaneously adding both important habitat variables and carnivore interactions to models allows statistical control of the one while considering the other. This lends insight into the interplay between habitat use and carnivore interactions.

We included the variables from the highest ranked species-specific habitat model with co-predator capture rates in new 'combination models' for the smaller carnivores. We compared the strength of co-predator parameters in puma, ocelot and fox models with and without the inclusion of habitat variables. Both the co-predator and combination models were ranked according to their AIC$_c$ and included in the final model set for comparison.

Results

Camera traps were operational for 62 (± 0.82) days on average, resulting in 2894 trap nights. Jaguars and grey foxes were commonly captured, while captures of pumas and ocelots were relatively rare. In fact, all but one of the sites used by either ocelots or pumas were also used by both jaguars and grey foxes (Fig. 2). Jaguars were captured 222 times at 41 of the 47 stations and pumas were captured 19 times at 11 stations. Ocelots were captured 16 times at 10 stations. Grey foxes were captured 912 times at 42 stations (for trap success values, see Table 1).

Selection of habitat variable subsets

Considering only variables significant at $P < 0.1$ in the global model reduced the set of potential predictors to five variables for jaguar activity, four for pumas, two for ocelots and two for grey foxes (Table 2).
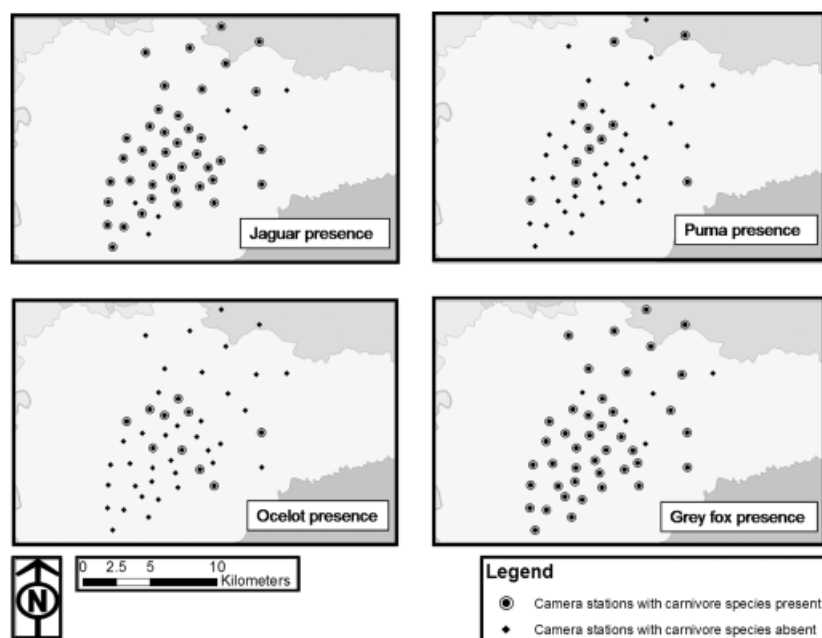
Figure 2 Maps illustrating the individual distributions of jaguar, puma, ocelot and grey fox presence in the Mountain Pine Ridge Forest Reserve are shown. Data were collected using a remote camera survey containing 47 camera stations from June to August of 2007. The presence of each species was inferred from photos obtained at each location, while absence was inferred from lack of photos of that species from that location.

Table 2 Species-specific negative binomial models explaining counts of carnivore captures as a response to 14 habitat characteristics at remote camera stations in the Mountain Pine Ridge Forest Reserve, Belize. Forty-seven camera station locations were sampled between June and August of 2007. These global habitat models allowed the identification of habitat characteristics of potential importance to each carnivore

Parameter	Mean value (SE) across 47 stations	Species-specific parameter estimate (SE)[a]			
		Jaguar	Puma	Ocelot	Grey fox
y-intercept	NA	−8.267 (1.7759)	−2.911 (4.2126)	−1.811 (4.2442)	−1.112 (1.8860)
% canopy cover	26.7 (2.800)	−0.001 (0.0058)	**0.047 (0.0247)** ·	0.033 (0.0313)	**−0.018 (0.0112)** ·
Canopy height (m)	11.8 (0.503)	**0.134 (0.0311)*****	−0.006 (0.1085)	−0.467 (0.3251)	0.032 (0.0519)
% understory cover	78.8 (2.400)	0.014 (0.0093)	−0.012 (0.0353)	−0.032 (0.0386)	0.011 (0.0095)
Log tree density (log number per ha)	6.63 (0.091)	0.318 (0.2474)	−0.847 (0.7666)	−0.721 (0.9162)	−0.208 (0.2829)
Road width (cm)	420 (16.24)	−0.001 (0.0013)	**0.008 (0.0037)***	−0.004 (0.0060)	−0.000 (0.0013)
River length (m)	168 (14.94)	0.001 (0.0007)	0.006 (0.0042)	0.002 (0.0033)	−0.001 (0.0010)
Road length (m)	350 (22.93)	**0.003 (0.0011)****	0.006 (0.0039)	**0.015 (0.0064)***	−0.001 (0.0011)
Distance to the Macal River (km)	7.20 (0.449)	−0.017 (0.0374)	−0.022 (0.1180)	−0.201 (0.1785)	0.029 (0.0559)
Human TS[b]	58.4 (4.486)	**−0.006 (0.0031)** ·	**−0.094 (0.0444)***	0.039 (0.0238)	0.007 (0.0050)
Small bird TS	5.26 (1.742)	**0.020 (0.0072)****	**0.116 (0.0608)** ·	**0.130 (0.0629)***	0.007 (0.0102)
Large bird TS	2.21 (0.661)	0.003 (0.0295)	−0.170 (0.2270)	−0.088 (0.1880)	0.049 (0.0327)
Small mammal TS	1.19 (0.339)	−0.067 (0.0457)	−0.009 (0.1963)	0.065 (0.1745)	0.087 (0.0592)
Medium mammal TS	1.40 (0.269)	−0.088 (0.0735)	0.082 (0.2502)	0.189 (0.2444)	**0.224 (0.0885)***
Large mammal TS	2.67 (0.483)	**0.058 (0.0324)** ·	−0.230 (0.1831)	0.140 (0.1634)	−0.039 (0.0455)

[a]The significance of each parameter was calculated using a t test. Strength of significance is indicated as *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Those marked with a period · are marginally significant at the $\alpha = 0.1$ level and have 90% CIs excluding zero. Bolded values represent parameters selected for inclusion in later models examining the effects of co-predator activity levels shown in Table 3.
[b]All trap success (TS) parameters are in units of captures per 100 trap-nights.

Ocelot captures appeared to be related to road length and small bird TS only: other parameters had 90% CIs overlapping zero. However, human TS showed a potential to be influential ($t_{32} = 1.63$, $P = 0.1035$; Table 2) and we included it in future ocelot models. This was done to be conservative and control for variation due to human activity when considering other variables.

Species-specific results

The model sets (33 for jaguars, 19 for pumas, 11 for ocelots and seven for grey foxes) considered for each carnivore included those with all combinations of that species' subset of potentially important habitat variables, a global habitat model, a null model, a co-predator model and a

combination model including both co-predator predictors and variables from the highest ranked habitat model. As the jaguar is the largest carnivore, no co-predator or combination model was proposed. The top-ranked model of jaguar activity ($\Delta AIC_c = 0$) included canopy height, road length, small bird and large mammal TS (Tables 3 and 4) and had an Akaike weight (ω_i) = 0.29, implying a 29% chance of being the best of the models evaluated. Variables in this model had strong positive relationships with jaguar activity. Small bird TS, road length and canopy height were particularly influential and were predictors in the three highest ranked models. These three competing models had a $\Delta AIC_c < 2$ and were distinguished by the inclusion or exclusion of large mammal captures (positive relationship) and human activity (negative relationship).

The top-ranked puma model had a 31.6% chance of being the best model. Puma counts were positively related to road width and small bird activity while showing a negative correlation with human TS (Table 4). There was one competing model that also included canopy cover ($\Delta AIC_c = 1.14$, $\omega_i = 0.18$; Table 3). Road width was included in all seven models with $\Delta AIC_c < 4$. Puma counts appeared to be unrelated to jaguar activity (Table 4) and, while the combination model ranked third, the co-predator model performed poorly, ranking 18th out of 19 models (Table 3).

The top-ranking model for ocelot counts included significant positive relationships with road length and small bird TS (Table 4; $\omega_i = 0.314$). A second, closely competing model ($\Delta AIC = 0.08$, $\omega_i = 0.302$) included human TS, which

Table 3 Negative binomial models explaining carnivore captures at 47 stations in the Mountain Pine Ridge Forest Reserve, Belize. Models are ordered by rank according to ΔAIC_c, and weights (ω_i). The top five reduced habitat models (including variables from potentially important species-specific subsets), global habitat, co-predator and combination models for each carnivore are displayed for comparison

Species	Model	K^a	ΔAIC_c	ω_i	Rank
Jaguar (33 models tested)	canopy height, roads within 200 m, small bird TS[c] large mammal TS	6	0	0.290	1
	canopy height, roads within 200 m, small bird TS	5	1.06	0.170	2
	canopy height, roads within 200 m, human TS, small bird TS, large mammal TS	7	1.46	0.140	3
	canopy height, roads within 200 m, large mammal TS	5	2.58	0.080	4
	canopy height, small bird TS, large mammal TS	5	3.27	0.057	5
	Global habitat model: all habitat variables[b]	16	27.1	0.000	33
Puma (19 models tested)	Road width, human TS, small bird TS	5	0	0.316	1
	Canopy cover, road width, human TS, small bird TS	6	1.14	0.179	2
	Combination model: jaguar TS, road width, human TS, small bird TS	6	2.23	0.104	3
	Canopy cover, road width, human TS	5	3.24	0.063	4
	Road width, human TS	4	3.54	0.054	5
	Road width, small bird TS	4	3.61	0.052	6
	Co-predator model: jaguar TS	3	10.6	0.002	18
	Global habitat model: all habitat variables	16	23.6	0.000	19
Ocelot (11 models tested)	Roads within 200 m, small bird TS	4	0	0.314	1
	Roads within 200 m, small bird TS, human TS	5	0.08	0.302	2
	Roads within 200 m	3	1.40	0.156	3
	Human TS, roads within 200 m	4	2.07	0.112	4
	Combination model: jaguar TS, puma TS, roads within 200 m, small bird TS	7	2.44	0.093	5
	Human TS, small bird TS	4	7.48	0.007	6
	Co-predator model: jaguar TS, puma TS	4	9.08	0.003	9
	Global habitat model: all habitat variables	16	25.1	0.000	11
Grey fox (seven models tested)	Null	2	0	0.328	1
	Medium mammal TS	3	0.28	0.285	2
	Canopy cover, medium mammal TS	4	1.04	0.195	3
	Canopy cover	3	1.45	0.159	4
	Co-predator model: jaguar TS, puma TS, ocelot TS	5	5.48	0.021	5
	Combination model: jaguar TS, puma TS, ocelot TS, medium mammal TS	6	6.61	0.012	6
	Global habitat model: all habitat variables	16	32.8	0.000	7

[a]K, used to calculate AIC_c, is the number of estimated parameters including the intercept, all predictors, and the overdispersion parameter.
[b]The term 'all habitat variables' indicates the inclusion of all 14 variables in the global habitat model shown in Table 2.
[c]All trap success (TS) parameters are in units of captures per 100 trap-nights.

Table 4 Three sets of species-specific negative binomial models explaining the counts of puma *Puma concolor*, ocelot *Leopardus pardalis* and grey fox *Urocyon cinereoargenteus* captures in the Mountain Pine Ridge Forest Reserve, Belize. The first set of models includes the top-ranked habitat model based on its Akaike score (see Table 3). The second set of co-predator models includes only the trap success rates of relatively larger carnivores as predictors while the third set of combination models includes both co-predator trap success rates and the selected habitat parameters (from the top-ranking habitat model)

Species	Parameter[a,b]	Selected habitat model Estimate (SE)	Co-predator model Estimate (SE)	Combination model Estimate (SE)
Jaguar	y-intercept	−5.393 (0.5452)		
	Canopy height	0.128 (0.0297)***		
	Roads within 200 m	0.002 (0.0010)*		
	Small bird TS[c]	0.017 (0.0061)**		
	Large mammal TS	0.059 (0.0288)*		
Puma	y-intercept	−6.611 (1.4223)	−5.099 (0.4158)	−6.50 (1.360)
	Road width (cm)	0.007 (0.0025)**		0.007 (0.0024)**
	Human TS	−0.047 (0.0232)*		−0.047 (0.231)*
	Small bird TS	0.0506 (0.0201)*		0.057 (0.0225)*
	Jaguar TS		0.009 (0.0300)	0.023 (0.0381)
Ocelot	y-intercept	−9.926 (1.4111)	−5.91 (0.5419)	−10.79 (1.6869)
	Roads within 200 m	0.010 (0.0027)***		0.011 (0.0029)***
	Small bird TS	0.042 (0.0182)*		0.031 (0.0197)
	Jaguar TS		0.057 (0.0235)*	0.052 (0.0291)·
	Puma TS		0.137 (0.2068)	0.123 (0.2257)
Grey fox	y-intercept	−1.341 (0.2326)	−1.046 (0.2305)	−1.223 (0.2717)
	Medium mammal TS	0.117 (0.0773)		0.107 (0.0820)
	Jaguar TS		−0.017 (0.0172)	−0.014 (0.0172)
	Puma TS		0.026 (0.1001)	0.010 (0.0979)
	Ocelot TS		−0.009 (0.0919)	−0.015 (0.0946)

[a]See Table 3 for detail on within species comparison of models based on AIC$_c$ and weights.
[b]The significance of each parameter was calculated using a t test. Asterisk(s) indicate significance, with 95% confidence intervals that exclude zero. Strength of significance is indicated as *$P<0.05$, **$P<0.01$, ***$P<0.001$. Those marked with a period · are marginally significant at the $\alpha=0.1$ level.
[c]All trap success (TS) parameters are in units of captures per 100 trap-nights.

was positively associated with ocelot captures ($t = 1.76$, $P = 0.078$). Road length was included in all three competing models with ΔAIC$_c<2$ (Table 3). Neither the co-predator nor the combination model performed well; however, ocelot counts showed a significant positive association with jaguar activity ($t_{44} = 2.43$, $P = 0.0150$) in the co-predator model. In the carnivore–habitat combination model for ocelot counts, road length was the strongest predictor of ocelot counts, while jaguar TS had a more modest effect ($t_{44} = 1.78$, $P = 0.0753$; Table 4).

When modelling grey fox counts, the null model ranked the highest, with a 32.8% chance of being the best model tested (Table 3). None of the competing models included co-predator predictors. The second-ranked model (ΔAIC$_c = 0.28$, $\omega_i = 0.285$) included only medium mammal TS with a non-significant effect ($t_{45} = 1.51$, $P = 0.1299$). All parameter estimates in the other competing models were similarly non-significant (Table 4), implying that in the original habitat model, these parameters appeared important only after controlling for other variables. Fox models including co-predator activity rates performed poorly and all associated coefficients had 95% CIs overlapping zero.

Discussion

Ecological implications

Contrary to our expectations, we found that the activities of potentially competing species were poor predictors of carnivore captures in the MPR. Smaller carnivores did not appear to avoid areas used by larger competitors nor was there much evidence of habitat partitioning. In fact, ocelots may have used sites with higher jaguar activity more frequently (Table 4). The niches of these predators may be too distinct for competition to take place (e.g. differential use of prey species), or it is possible that these species find similar habitat desirable. The benefits of using areas with preferable habitat features (e.g. high prey activity) may outweigh the costs of proximity to dominant competitors; this could be the case when predators exist at low densities and direct confrontations are uncommon. Also, the lack of relationships among ocelots, grey foxes and the larger carnivores may indicate that these two mesopredators are too small to be considered substantial competitors with jaguars and pumas (Donadio & Buskirk, 2006).

Habitat models performed best when predicting ocelot activity and puma activity. While the third-ranking model for puma activity included a positive (non-significant) relationship with jaguar TS, on its own, this variable was not a strong predictor of puma captures. Additionally, the fact that the relationship between jaguar and ocelot activity was less significant after controlling for habitat characteristics (in the combination model) supports the possibility that common preferences lead to the co-occurrence of these predators. The three felids all appeared to respond to similar habitat characteristics. Small bird activity and variables related to road cover (length or width) were generally important, appearing in the top-ranked models for all the three species. As the most frequently photographed prey group (Table 2), it is possible that small birds provide reliable prey for felids in the MPR; however, these cats are not known to prey extensively on small birds (Sunquist & Sunquist, 2002). It is, therefore, likely that this relationship was caused by a shared use of areas with more roads and edge vegetation, as has been observed for the species in this prey group (see Table 1; Jones, 2003). The felids' selection of areas with higher road cover is consistent with previous camera trapping studies in Belize (Dillon & Kelly, 2007) and is likely because the old and partially overgrown roads may provide access to edge habitat where many prey are vulnerable.

There was little evidence of resource partitioning. Pumas used areas with more human activity less frequently and jaguars showed a similar trend; this relationship was not shared by the smaller carnivores and it is possible that ocelots selected areas with higher human activity (marginally significant trend in the second-ranked model). Ocelots may be more tolerant towards human activity than pumas or jaguars (Crawshaw & Quigley, 1991; Bisbal, 1993), but given that none of these carnivores avoided each other spatially, it is difficult to conclude that this indicates habitat partitioning.

Jaguars and grey foxes displayed unique associations with prey activity. The positive relationship between jaguars and large mammal activity makes sense, given that jaguars consume species averaging 15 kg in weight (Sunquist & Sunquist, 2002). The relationship between fox counts and medium mammals was non-significant and unlikely to reflect predation because this canid is probably incapable of taking prey weighing 5–15 kg. The null model performed best of those proposed for fox counts, which implies that they are either habitat generalists or that the variables chosen were not relevant. Foxes may be consuming plant material (Fedriani et al., 2000) or relying on prey too small to be captured by the cameras (e.g. we frequently photographed grey foxes carrying iguanas and snakes).

In high-ranking models, variables associated with prey activity and roads were important in describing carnivore activity, while there were few relationships with vegetation characteristics. However, there was a positive association of jaguars with canopy height, which is consistent with the selection for dense undisturbed forest previously observed for jaguars (Sunquist & Sunquist, 2002). The absence of strong relationships between ocelots and vegetation is parti-

cularly interesting, given previous evidence that canopy cover is key to ocelot habitat use (Tewes, 1986; Ludlow & Sunquist, 1987; Shindle & Tewes, 1998). The pine forest, with low canopy cover ($26.7 \pm 2.8\%$; Table 2), may provide poor ocelot habitat, causing low population density (Dillon & Kelly, 2007). The resulting low capture rates could make it difficult to observe habitat use. Puma activity was similarly low and conclusions regarding puma habitat use may be similarly restricted.

Another possibility is that our results were affected by the placement of cameras along roads. Scognamillo et al. (2003) and Taber et al. (1997) suggested that documenting the use of roads does not necessarily imply use of surrounding habitat, merely travel through those areas. Alternatively, competition may take place without resulting in spatial habitat partitioning and be manifested as temporal avoidance or intraguild predation (Schoener, 1974; Palomares & Caro, 1999). Smaller mesopredators may visit areas at different times or only after signs of recent visits by competitors have faded. Harmsen et al. (2009) found that jaguars and pumas in central Belize had similar space-use patterns and activity schedules, but did not use locations simultaneously. While detection of intraguild predation is beyond the scope of this study, if such aggressive interactions were regular and ecologically important, it seems likely that noticeable spatial avoidance would result.

Conservation and management implications

Our results indicate that pumas (and possibly jaguars) may select against areas with high human activity; this should be considered when regulating recreational use of conservation areas. Past research on a variety of carnivores suggests that human activity, even within protected areas, can restrict foraging activities, limit access to resources and, theoretically, inhibit healthy populations (Kerley et al., 2002; Boydston et al., 2003; Paviolo et al., 2009). Felid activity was positively associated with roads in the MPR, but this should be interpreted cautiously as roads with extensive human traffic might not yield the same results. The old roads in this site are likely analogous to animal paths used by felids to forage in undisturbed forests (Emmons, 1987; Sunquist & Sunquist, 2002). While we found few associations with vegetation characteristics, our results are broadly consistent with previous evidence that dense forest and abundant prey are important to neotropical felids (Rabinowitz & Nottingham, 1986; Ludlow & Sunquist, 1987; Sunquist & Sunquist, 2002; Scognamillo et al., 2003).

This study suggests that the jaguar could fulfill the role of an umbrella species with respect to sympatric carnivores in the MPR; none of the smaller predators avoided centers of jaguar activity, leaving no reason to believe that competition with jaguars limits habitat use. Selectively protecting large areas with healthy jaguar populations may also meet the requirements of other predators, allowing simultaneous conservation of these species. However, this is a unique study area and low counts for some species may have limited the analysis. Ideally, population densities of multiple species

at multiple sites (including broadleaf forests) are necessary to draw large-scale conclusions about the jaguar as an umbrella species. Further research examining the relationship between habitat use and co-predator ecology could elucidate mechanisms driving carnivore co-existence and aid in the prioritization of conservation areas.

Acknowledgements

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