

# Food habits of sympatric jaguars and pumas across a gradient of human disturbance

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## Keywords

jaguar; puma; coexistence; diet; prey depletion; carnivore; livestock.

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## Abstract

Jaguars *Panthera onca* coexist with pumas *Puma concolor* across their entire range. In areas where they occur together their coexistence may be facilitated by differences in diet. This study compared food habits of jaguars and pumas in Belize, Central America, across a protected lowland rainforest and the neighbouring human-influenced landscape. Diets were determined from 362 jaguar scats and 135 puma scats, identified by genetic analysis. In the protected forest, dietary breadths were low for jaguars and pumas and showed little overlap. In this habitat each relied heavily on a single medium-sized (5–10 kg) prey species: armadillos *Dasyus novemcinctus* for jaguars, and pacas *Agouti paca* for pumas. Both cats also took larger prey (> 10 kg), mainly white-lipped peccaries *Tayassu pecari* by jaguars and red brocket deer *Mazama americana* by pumas. In unprotected fragmented lands, jaguar scats rarely contained large wild prey species; rather, a diet of relatively small wild prey was supplemented with larger domestic species. Pumas did not take domestic species and were scarce outside the protected forest, possibly indicating competition with humans for pacas and deer, which are also prized game species in the region. This study is the largest analysis to date of sympatric jaguar and puma diets in both forest and farmland. We suggest that jaguar predation on cattle may be reduced by ensuring that game hunting is sustainable and potentially by augmenting forests within the human matrix with large wild ungulates. The supplementation could benefit both of the cat species, and the local game hunting economy.

## Introduction

The coexistence of similar sympatric species is facilitated by ecological separation along trophic, spatial and temporal dimensions of their environment (e.g. Pianka, 1969), and most commonly through the partitioning of food resources and differential habitat use (Schoener, 1974). For example, similar-sized carnivores may coexist by hunting in different areas (e.g. Durant, 1998), at different times (e.g. Fedriana, Palomares & Delibes, 1999; Karanth & Sunquist, 2000) or by employing different hunting strategies and using different habitats (e.g. Seidensticker, 1976; Fedriana *et al.*, 1999), but perhaps most commonly by using prey of different size-class or taxa (e.g. Bertram, 1982; Bothma, Nel & Macdonald, 1984; Sunquist, Sunquist & Daneke, 1989; Karanth & Sunquist, 2000; Walker *et al.*, 2007). The intensity of competition between sympatric species depends on their niche overlap and resource availability (e.g. Durant, 1998). Phenotypic plasticity reduces competition by facilitating a shift in resource use, provided alternative resources are

available; otherwise the subordinate species may be competitively excluded (Pfennig, Rice & Martin, 2006). The balance of coexistence is thus sensitive to changes in the resource spectrum and the availability of its components (e.g. Bonesi & Macdonald, 2004). Current rates of human population growth are increasing the pressure on natural resources, and the recent increase in hunting of wildlife for meat is considered unsustainable in many areas across the tropics (Milner-Gulland *et al.*, 2003). Large carnivores come into competition with people not only for space but also for prey (e.g. Leite & Galvão, 2002; Salvatori *et al.*, 2002). Their survival is jeopardized by reductions in prey availability, either through direct competition with humans or indirectly through habitat loss (Fuller & Sievert, 2001). Under conditions of globally diminishing diversity and abundances of prey species, Azevedo (2008) suggests that the long-term persistence of large felids may depend on dietary flexibility and their ability to use human-disturbed areas. Changes to habitat and the availability of different prey species will then

alter patterns of coexistence of sympatric felids with differing tolerances to human disturbance (Núñez, Miller & Lindzey, 2000).

This study describes the diets of sympatric populations of jaguars *Panthera onca* and pumas *Puma concolor*, two similar-sized cats that co-occur throughout the neotropics. Jaguar and puma diets are highly variable. Over 85 prey species of jaguars have been recorded across their geographic range, with between eight and 24 prey species documented in the diet at any one site (Rabinowitz & Nottingham, 1986; Emmons, 1987; Seymour, 1989; Aranda & Sánchez-Cordero, 1996; Taber *et al.*, 1997; Garla, Setz & Gobbi, 2001; Crawshaw & Quigley, 2002; Dalponte, 2002; Leite & Galvão, 2002; Núñez, Miller & Lindzey, 2002; Polisar *et al.*, 2003; Crawshaw *et al.*, 2004; Novack *et al.*, 2005; Azevedo, 2008). Similarly up to 20 prey species have been documented in the diet of neotropical pumas (e.g. Leite & Galvão, 2002; Moreno, Kays & Samudio, 2006). In a range-wide review of jaguar and puma feeding habits, de Oliveira (2002) noted a high level of geographical variation in prey use but overall found that the principal prey species of both cats were similar: mainly peccaries, large rodents, deer and armadillos.

Where jaguars and pumas coexist, they often use the same habitats and follow similar activity patterns (e.g. Núñez *et al.*, 2002; Scognamillo *et al.*, 2003). In an undisturbed homogenous forest in Belize, the two species have similar activity patterns and use the same locations (Harmsen *et al.*, 2009b). In such areas, we hypothesize that coexistence may be facilitated by hunting different prey species, as suggested by Rabinowitz & Nottingham (1986). Dietary differentiation may be less pronounced in heterogeneous landscapes that have more potential for habitat partitioning. And, if both species have flexible food habits, dietary overlap may increase in human-disturbed areas that have limited availability of the preferred prey of each (Azevedo, 2008). In the Guatemalan rainforest, Novack *et al.* (2005) described a low degree of dietary overlap between sympatric jaguars and pumas, and detected no dietary differences between an area where people hunt wild game and a non-hunted site. They concluded that human disturbance had minimal effects on the diet and prey selection of jaguars and pumas, but noted that long-term game hunting may eventually lower jaguar and puma carrying capacities. However, no comparison was made between the relative distributions of jaguars and pumas at these two sites. Although diet structure was not influenced by human disturbance, less than one-third of the jaguar scats originated in the hunted site, suggesting a lower jaguar abundance there than at the non-hunted site. In contrast puma scats were more common than jaguar scats, with similar numbers collected at both sites, suggesting a more equal abundance of pumas at both sites. A full understanding of human impacts on patterns of felid coexistence requires knowledge of the relative abundances of the species. In our study, we describe and discuss the food habits of jaguars and pumas in relation to their abundance across a gradient of human disturbance from a protected lowland rainforest, through an unprotected forest buffer, into a

fragmented human-influenced landscape, in Belize, Central America.

Historically, studies of jaguar and puma diets have variously used scat diameter, footprints, ingested hairs and circumstantial evidence to help identify scats to species level (e.g. Emmons, 1987; Olmos, 1993; Aranda & Sánchez-Cordero, 1996; Facure & Giaretta, 1996; Chinchilla, 1997; Garla *et al.*, 2001; Dalponte, 2002; Leite & Galvão, 2002; Núñez *et al.*, 2002; Crawshaw *et al.*, 2004; Azevedo, 2008). However, such methods can incur high errors (e.g. Taber *et al.*, 1997; Farrell, Roman & Sunquist, 2000; Azevedo, 2008). Recently, genetic analyses have successfully identified jaguar and/or puma scats for diet studies (Polisar *et al.*, 2003; Novack *et al.*, 2005; Weckel, Giuliano & Silver, 2006). Sample sizes ranged from 12 scats (jaguar, Weckel *et al.*, 2006) to 145 scats (puma, Novack *et al.*, 2005). Species accumulation curves indicate that samples of ~100 scats are required to fully describe the diet of jaguars and pumas from biodiverse regions such as tropical rainforests (Foster, 2008). Our study is the first to compare jaguar and puma diets in sympatry using genetically identified samples of more than 100 scats for each species, exceeding the threshold sample size required for reliable diet characterization in this region.

## Study area

The study area spanned the eastern half of the protected lowland subtropical broadleaf forest of the Cockscomb Basin, and the mosaic of unprotected habitats and land-use systems extending from the eastern border of the forest towards the sea, across ~525 km<sup>2</sup>. The basin was logged for c. 100 years, creating dense secondary forest. It received protected status in 1986 and today the Cockscomb Basin Wildlife Sanctuary (CBWS) encloses 425 km<sup>2</sup> of forest which supports populations of both jaguars and pumas (Harmsen, 2006). The protected forest is partially buffered from human development by a band of unprotected forest, together forming a contiguous forest block. The unprotected fragmented landscape to the east of this forest block comprises a patchwork of pine savannah, shrubland and forest, interspersed with villages, milpa farms, fruit plantations, cattle pastures and a single highway running north-south. The region supports a diversity of potential prey, including at least 23 species of wild terrestrial mammals (>2 kg) in addition to domestic animals such as cattle, sheep, pigs and dogs. Although the periphery of CBWS is subject to illegal incursions by game hunters, it is likely that wild prey abundances are lower outside the protected forests where the habitat is fragmented by cattle ranches and monocultures, and unregulated hunting is commonplace (Harmsen, 2006; Foster, 2008).

Jaguar density across the study area has been estimated at ~7 individuals per 100 km<sup>2</sup>, ranging from ~10 per km<sup>2</sup> in CBWS to ~2 per 100 km<sup>2</sup> in fragmented lands away from the forest block (Harmsen, 2006; Foster, 2008). Puma density in the study area is unknown, though short-term recognition of pumas from camera-trap photographs in

CBWS indicates that they are less numerous than jaguars (Harmsen *et al.*, 2009a). Camera-trap surveys of jaguars and pumas across the study area have revealed similar activity patterns and habitat use for both species within the contiguous forest block, and jaguars persisting in the fragmented landscape which is almost completely devoid of pumas (Foster, 2008; Harmsen *et al.*, 2009b).

## Methods

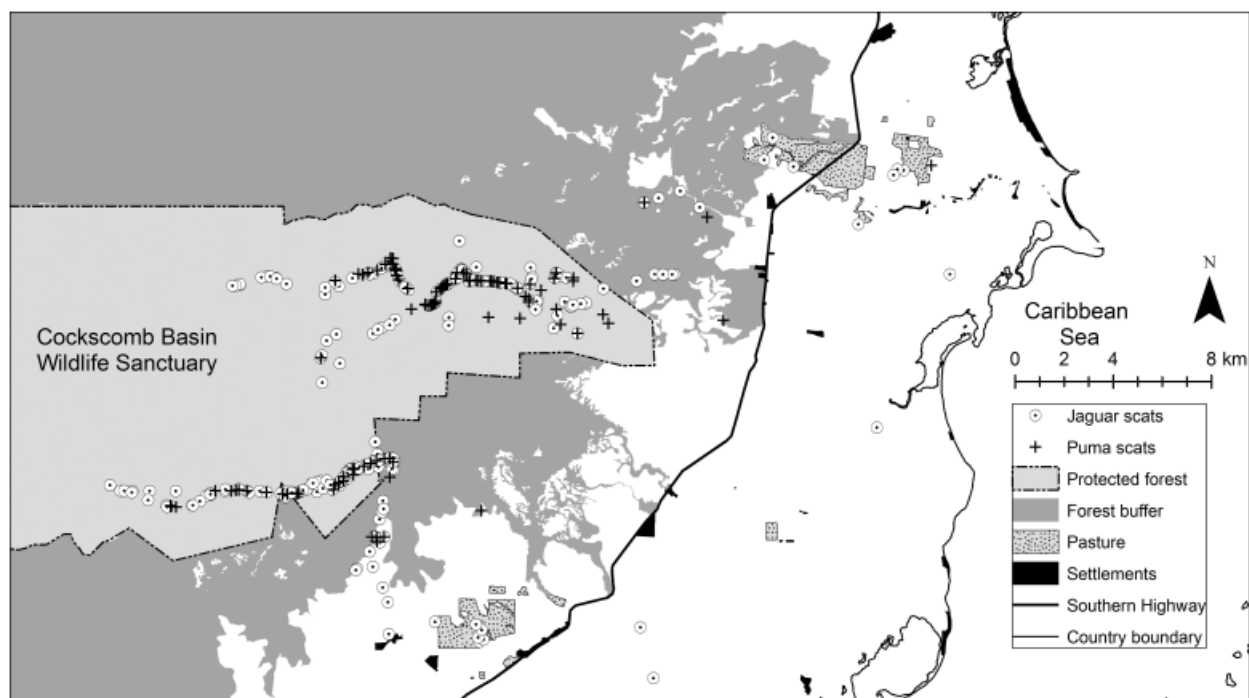
Between 2003 and 2006, 645 carnivore scats were collected opportunistically throughout the study area (Fig. 1). Samples were dried and preserved with silica gel at room temperature until processed. To identify the predator species, genomic DNA was extracted from the external layer of 588 samples using the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA, USA) with minor modifications to the manufacturer's protocol. Primers were adapted from Hoelzel & Green (1992) to amplify 336 bp of the 16S ribosomal RNA gene. Polymerase chain reactions (PCRs) were carried out using Illustra puRE Taq Ready-To-Go™ PCR beads (GE Healthcare Bio-Sciences, Little Chalfont, UK). PCR products were cycle-sequenced with dye-labelled terminators and sequence reactions were analysed in a 3730 DNA analyzer (Applied Biosystem®, Foster City, CA, USA). Obtained sequences were compared with known reference sequences for identification.

Prey items within the scats were identified to species level from macro- and microscopic hair morphology, checked against a reference collection of hairs from local mammals,

and the remains of body parts such as teeth, claws, hooves, scutes and bone fragments. The per cent relative occurrence of each prey species in the diet of each cat species was calculated as  $\{\text{number of prey items belonging to species } X\} / \{\text{total number of prey items}\} \times 100$ , where the number of prey items corresponded to the number of scats containing each species. Relative occurrence tends to overestimate smaller prey species compared with larger prey species (Ackerman, Lindzey & Hemker, 1984). The relative biomass of each species consumed was therefore also calculated, using the correction factor of Ackerman *et al.* (1984) and live masses of potential prey species based on Reid (1997). The correction factor was not used for prey species <2 kg on the assumption that each occurrence in a scat represented a whole individual (Ackerman *et al.*, 1984).

The relative prey consumption of the most commonly eaten prey species ( $\geq 5\%$  occurrence) was compared between jaguars and pumas, and between the protected forest, unprotected forest buffer and the unprotected fragmented landscape, using  $\chi^2$ -tests. Although it was impossible to determine where the contents of the scats had been hunted, it was assumed that scat location equates to the hunting area. Differences between the relative occurrences of a given prey species within the diets of sympatric jaguars and pumas were interpreted to mean that one or both cats were taking prey selectively.

Food niche breadth,  $B$ , was calculated in terms of dietary diversity for jaguars and pumas following Levins (1968). The index was standardized to  $B_{\text{sta}}$  following Colwell & Futuyma (1971), to allow comparisons of diet breadth



**Figure 1** Scat locations within the study area, showing the settlements and cattle farms neighbouring the eastern part of the Cockscomb Basin Wildlife Sanctuary and its unprotected forest buffer. The eastern tip of CBWS is located at UTM 0348113, 1854515 (WGS 84).

between the two felids and between locations. Values of  $B_{sta}$  range between 0 (maximum specialization) and 1 (maximum niche breadth). The overlap in prey use between jaguars and pumas was calculated using the Pianka (1973) measure of niche overlap. A value of 0 indicates complete dissimilarity, and a value of 1 indicates complete similarity. One thousand Monte Carlo simulations were run using the program EcoSim 7 (Gotelli & Entsminger, 2008) to determine whether the observed overlap was greater or lower than random expectation, following Walker *et al.* (2007). The mean weight of the vertebrate prey consumed by each species (MWVP) was calculated as a geometric mean following Jaksic & Braker (1983).

## Results

Predator species was successfully identified for 532 scats, of which 362 were jaguar, 135 puma, 33 ocelot or margay (*Leopardus pardalis* or *Leopardus wiedii*) and two domestic dog *Canis familiaris*. The 322 jaguar and 127 puma scats with identifiable prey items contained, respectively, 378 and 140 distinct items, averaging, respectively, 1.2 and 1.1 prey items per scat, with a maximum of three items for either cat. A further 27 jaguar and six puma scats contained no prey remains and 13 jaguar and two puma scats contained only unidentifiable remains.

### Variation between species

Across the entire study region of protected and unprotected areas, jaguar diet encompassed at least 20 species: 15 wild mammals, three domestic mammals, one reptile and one bird (Table 1). Despite its high species richness, the diet was low in diversity, with  $B_{sta} = 0.143$  due to the dominance of a few prey species. Just four species had  $\geq 5\%$  relative occurrence in jaguar diet. Armadillos were most often consumed (46%) followed by coatis (11%), white-lipped peccaries (10%: 9% adults + 1% juveniles), and collared peccaries (5%: 4% adults + 1% juveniles). The remaining species each comprised  $< 5\%$  of the diet.

Puma diet contained at least 11 species: eight wild mammals, two reptiles and one freshwater decapod crustacean (Table 1). Although puma diet was less species rich than jaguar diet, it was slightly more diverse, with  $B_{sta} = 0.174$ . Five species had  $\geq 5\%$  relative occurrence in puma diet. Pacas were taken most often (58%) followed by red brocket deer (9%), white-lipped peccaries (8%: 4% adults + 4% juveniles), armadillos (7%) and kinkajous (6%). The remaining species each comprised  $< 5\%$  of the diet. Unlike jaguars, there was no evidence that pumas took domestic species.

### Variation between habitats

Within the protected forest, jaguar diet had higher species richness than puma diet (14 vs. nine prey species), though lower diversity (jaguar:  $B_{sta} = 0.113$ , three frequently used prey; puma  $B_{sta} = 0.169$ , five frequently used prey). Jaguars and pumas favoured different species in accor-

dance with their general preferences noted above (Table 1). They had a correspondingly low dietary overlap given by the Pianka index at 0.246, and significantly lower than the random expectation of  $0.479 \pm 0.013$  variance ( $P < 0.05$ ).

The dominant size class of prey within the protected forest was 5–10 kg for both species. The MWVP taken by pumas was 8.6 kg (7.8–9.5 at 95% confidence limits,  $n = 121$ ), higher than for jaguars which was 7.1 kg (6.3–7.8,  $n = 236$ , Table 1). Jaguars ate more armadillos and coatis compared with pumas (armadillo  $\chi^2_1 = 68.9$ ,  $P < 0.0001$ ; coati  $\chi^2_1 = 12.5$ ,  $P < 0.0001$ ). Pumas ate more pacas and red brocket deer compared with jaguars (paca  $\chi^2_1 = 132.7$ ,  $P < 0.0001$ ; red brocket deer  $\chi^2_1 = 5.3$ ,  $P < 0.05$ ). Jaguars and pumas did not differ in the frequencies of white-lipped peccaries or kinkajous (white-lipped peccary  $\chi^2_1 = 2.6$ ,  $P > 0.1$ ; kinkajou  $\chi^2_1 = 0.5$ ,  $P > 0.5$ ). However jaguars tended to take adult white-lipped peccaries more frequently than did pumas: 85% of jaguar scats containing white-lipped peccary remains were identified as adult remains, compared with only 45% for puma.

Outside the protected forest, jaguar diet comprised 15 species, including three domestic mammals (Table 1). Five species were frequently taken, including cattle and sheep, and jaguar diet was more diverse here than inside the protected forest ( $B_{sta} = 0.427$  outside,  $3.8 \times$  higher than inside). In contrast to within the protected forest, where almost 50% of the diet depended on armadillos, the biomass consumed in the unprotected lands was more evenly distributed between armadillos, cattle, sheep and coatis (Table 1), and the MWVP was 9.5 kg (7.5–11.9,  $n = 106$ ). Exclusion of domestic species brings it lower than inside the reserve at 5.1 kg (4.4–5.8,  $n = 77$ ). Further partitioning the unprotected regions, jaguar MWVP was 5.7 kg (5.0–6.6,  $n = 42$ ) in the forest buffer (or 5.6 kg, 4.9–6.4,  $n = 41$ , excluding the single domestic prey item), and 13.2 kg (9.3–18.7,  $n = 64$ ) in the fragmented landscape (or 4.5 kg, 3.6–5.7,  $n = 36$  excluding domestic species).

Jaguars ate no white-lipped peccaries in the unprotected lands, in contrast to their frequent appearance in the diet within the protected forest (Fig. 2). Conversely, no jaguar scats found inside the protected forest contained domestic species, in contrast to their frequent appearance in the diet outside the protected forest (Fig. 2). Jaguars ate the same amount of armadillos in the unprotected forest buffer as in the protected forest ( $\chi^2_1 = 0.1$ ,  $P > 0.8$ , Fig. 2), but more coatis ( $\chi^2_1 = 6.6$ ,  $P < 0.05$ , Fig. 2) and collared peccaries (Fisher's exact test odds ratio = 0.27,  $P < 0.05$ , Fig. 2). Outside the protected forest, jaguars ate more armadillos, coatis and collared peccaries in the forest buffer than in the fragmented landscape (armadillo  $\chi^2_1 = 7.7$ ,  $P < 0.01$ ; coati  $\chi^2_1 = 4.0$ ,  $P < 0.05$ ; collared peccary Fisher's exact test odds ratio = 10.4,  $P < 0.02$ , Fig. 2).

Puma scats were almost entirely confined to the forest block, with 88% inside the protected forest, 9% in the forest buffer, and only 3% in the fragmented landscape. This distribution accords with camera data which recorded a scarcity of pumas outside the forest block, in contrast to

**Table 1** Relative % occurrences (%O) and % consumed biomasses (%B) of prey species in jaguar *Panthera onca* and puma scats *Puma concolor* collected across the study area (449 scats), and partitioned between the protected forest and the unprotected land (421 scats, excluding 26 jaguar and two puma scats from unknown locations within forest block)

Prey species, ordered by mass		Entire study area				Protected forest				Unprotected land <sup>a</sup>			
		Jaguar		Puma		Jaguar		Puma		Jaguar		Puma <sup>b</sup>	
		%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	%O	%B
<b>&gt; 10 kg</b>													
Domestic cattle	<i>Bos taurus</i>	2.9	7.7	–	–	–	–	–	–	10.2	24.2	–	–
White-tailed deer	<i>Odocoileus virginianus</i>	–	–	0.7	1.0	–	–	–	–	–	–	6.3	9.1
White-lipped peccary (adult)	<i>Tayassu pecari</i>	8.7	11.5	3.6	4.9	13.8	18.9	4.1	5.6	–	–	–	–
Sheep	<i>Ovis aries</i>	4.5	5.7	–	–	–	–	–	–	15.7	17.8	–	–
Red-brocket deer	<i>Mazama americana</i>	2.9	3.3	8.6	10.2	3.3	4.0	9.0	10.7	0.9	1.0	6.3	7.9
Collared peccary (adult)	<i>Pecari tajacu</i>	3.7	4.1	2.9	3.3	2.9	3.4	3.3	3.7	4.6	4.6	–	–
Dog	<i>Canis familiaris</i>	0.3	0.3	–	–	–	–	–	–	0.9	0.9	–	–
Unknown peccary (adult)	Family Tayassuidae	0.3	0.3	–	–	0.4	0.5	–	–	–	–	–	–
<b>5–10 kg</b>													
Paca	<i>Agouti paca</i>	4.5	4.3	57.9	57.3	4.6	4.6	58.2	57.2	3.7	3.1	56.3	58.6
Northern tamandua	<i>Tamandua mexicana</i>	0.8	0.7	–	–	1.3	1.2	–	–	–	–	–	–
Northern raccoon	<i>Procyon lotor</i>	0.3	0.2	–	–	–	–	–	–	0.9	0.8	–	–
Nine-banded armadillo	<i>Dasypus novemcinctus</i>	46.4	41.9	7.1	6.7	50.8	47.9	6.6	6.1	33.3	26.8	6.3	6.2
White-lipped peccary (Juvenile)	<i>Tayassu pecari</i>	1.1	1.0	4.3	4.2	1.3	1.2	4.9	4.8	–	–	–	–
Collared peccary (Juvenile)	<i>Pecari tajacu</i>	1.3	1.2	0.7	0.7	1.3	1.2	0.8	0.8	1.9	1.6	–	–
Iguana	<i>Iguana iguana</i>	1.3	1.2	4.3	4.0	1.3	1.2	3.3	3.0	1.9	1.5	12.5	12.3
Unknown peccary (Juvenile)	Family Tayassuidae	0.3	0.3	–	–	0.4	0.4	–	–	–	–	–	–
Paca or armadillo		0.3	0 <sup>c</sup>	–	–	–	–	–	–	–	–	–	–
Unknown mammal	Class Mammalia	0.8	1.0	–	–	0.4	0.4	–	–	0.9	0.8	–	–
<b>2–5 kg</b>													
White-nosed coati	<i>Nasua narica</i>	10.8	9.7	–	–	9.6	9.0	–	–	14.8	11.8	–	–
Kinkajou	<i>Potos flavus</i>	2.6	2.3	5.7	5.2	4.2	3.8	5.7	5.2	–	–	6.3	6.0
Skunk	<i>Conepatus</i> sp.	0.3	0.2	–	–	–	–	–	–	0.9	0.7	–	–
Grey fox	<i>Urocyon cinereoargenteus</i>	0.3	0.2	–	–	0.4	0.4	–	–	–	–	–	–
Greater grison	<i>Galictis vittata</i>	0.8	0.7	–	–	0.8	0.8	–	–	0.9	0.7	–	–
Mexican porcupine	<i>Coendou mexicanus</i>	–	–	2.1	1.9	–	–	2.5	2.2	–	–	–	–
Unknown carnivore	Order Carnivora	1.3	1.2	0.7	0.7	0.8	0.8	0.8	0.7	1.9	1.5	–	–
<b>&lt; 2 kg</b>													
Virginia/common opossum	<i>Didelphis</i> sp.	1.3	0.9	–	–	0.4	0.4	–	–	3.7	2.3	–	–
Unknown rodent	Order Rodentia	0.3	<0.1	–	–	–	–	–	–	0.9	0.1	–	–
Spiny pocket mouse	<i>Heteromys</i> sp.	0.3	<0.1	–	–	0.4	<0.1	–	–	–	–	–	–
Freshwater crustacean	Order Decapoda	–	–	0.7	<0.1	–	–	0.8	<0.1	–	–	–	–
<b>Unknown size</b>													
Unknown mammal	Class Mammalia	1.1	–	–	–	1.3	–	–	–	0.9	–	–	–
Unknown bird	Class Aves	0.5	–	–	–	0.4	–	–	–	0.9	–	–	–
Unknown snake	Suborder Serpentes	–	–	0.7	–	–	–	–	–	–	–	6.3	–
Total prey individuals		378	372	140	139	240	236	122	122	108	106	16	15
Total scats		322	320	127	127	204	202	110	110	92	92	15	14
Mean weight in kg of vertebrate prey (MWVP)		7.6		8.5		7.1		8.6		9.5		8.4	
95% CL in mean MWVP		6.9–8.3		7.8–9.4		6.3–7.8		7.8–9.5		7.5–11.9		6.3–11.2	

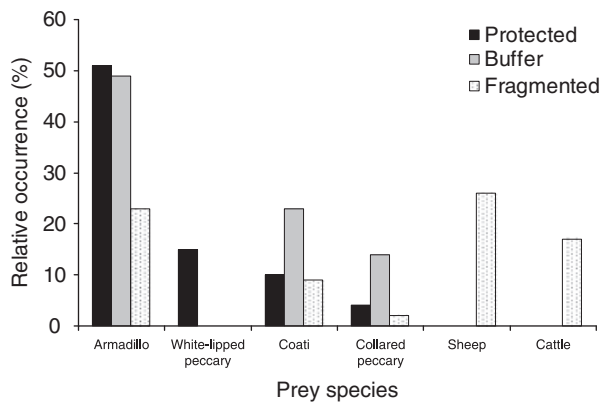
<sup>a</sup>Unprotected forest buffer plus unprotected fragmented landscape.

<sup>b</sup>Only 15 scats available therefore occurrence, biomass and MWVP estimates should be interpreted with caution.

<sup>c</sup>Combined with 'unknown mammal' for biomass calculation.

jaguars which were detected throughout the fragmented lands although at a lower level than in the forest block (Foster, 2008). The 11 puma scats from the forest buffer and four from the fragmented lands were too few for reliable characterization of diet in unprotected areas (Foster, 2008). It is nevertheless worth noting the absence of domestic

species and focus on white-tailed deer, red brocket deer and pacas by pumas outside the protected forest, where the MWVP of wild species taken by pumas was 8.4 kg (6.3–11.2,  $n = 15$ ), higher than that of jaguars. Pacas were equally common in puma diet both inside and outside the protected forest ( $\chi^2_1 = 2.4$ ,  $P > 0.1$ , Table 1).



**Figure 2** Relative occurrences of the frequently occurring prey species in jaguar *Panthera onca* diet, in the protected forest (204 scats), unprotected contiguous forest buffer (38 scats) and unprotected fragmented landscape (54 scats).

## Discussion

In areas where jaguars and pumas are sympatric, pumas are smaller and it has been suggested that they take smaller prey; particularly in dense forest where jaguars may be more efficient at hunting (Iriarte *et al.*, 1990; Taber *et al.*, 1997). However, there is no evidence that average prey size differs between the two cats in sympatry (for a review see de Oliveira, 2002), a finding supported by this study. Published estimates of MWVP in neotropical forests range from 6.2 to 15.6 kg for jaguars and 7.2–12.7 kg for pumas (Núñez *et al.*, 2000; Novack *et al.*, 2005), comparable with estimates here. High decomposition rates associated with hot humid conditions may limit the preferred prey size in tropical rainforests. A solitary cat may not risk attacking a 240 kg tapir over a 22 kg brocket deer if spoilage prevents additional energetic gain (Foster, 2008). This may explain the absence of tapir from the diet in this study and other Mesoamerican forests (e.g. Aranda & Sánchez-Cordero, 1996; Chinchilla, 1997; Novack *et al.*, 2005). However, the small surface area to volume ratio of tapirs, coupled with the paucity of hair, may also explain why few studies detect tapir remains in predator scats. In this study, 7.5% of jaguar scats and 4.4% of puma scats contained no remains, and it is unknown whether these reflect levels of predation on tapirs.

Although rainforest jaguars and pumas may be limited to prey of a similar maximum size, dietary overlap in closed forest habitats is generally low with partitioning between prey species. Harmsen (2006) analysed seven published studies of sympatric jaguars and pumas and found that their diets overlapped by ~80% in open habitats, but were dissimilar in closed rainforest environments (~20% overlap). In this study, jaguars of the protected forest took more armadillos than did pumas, while pumas took more pacas and brocket deer, as documented in the Guatemalan rainforest (Novack *et al.*, 2005). Coatis were absent from puma diet yet contributed 9% of the total biomass taken by jaguars. A similar pattern was observed in the forests of

Guatemala and Mexico (Núñez *et al.*, 2000; Novack *et al.*, 2005). White-lipped peccaries were found more frequently in the diets of both cats than were collared peccaries. Garla *et al.* (2001) found a similar pattern in jaguars and suggested this is because white-lipped peccaries are more conspicuous than collared peccaries. No differences were detected between the two cats in overall use of either peccary species; however jaguars focused on adult white-lipped peccaries while pumas took mainly juveniles. This may reflect the risks associated with preying on adult white-lipped peccaries which will attack defensively. Jaguars are stockier and have a more powerful bite than pumas (Sunquist & Sunquist, 2002) so can probably overpower an adult peccary more quickly with less risk of injury. Polisar *et al.* (2003) also noted that although jaguars and pumas both took collared peccaries, pumas mainly took juveniles.

Within the protected forest, the diversity of prey taken was considerably lower than other areas where jaguars and pumas coexist (cf de Oliveira, 2002). The two cats each relied heavily on a single prey species, jaguars mainly taking armadillos and pumas mainly taking pacas. Both species had similar MWVP and took prey ranging from <1 to 34 kg, demonstrating that both were capable of handling prey of the same size; yet their diets overlapped little. This suggests prey selection by one or both of the cats, rather than opportunistic hunting as Emmons (1987) predicted for solitary predators in dense forests. Our observation of low niche overlap of these two cats provides indirect evidence of resource partitioning in interspecific competition (e.g. Gotelli & Entsminger, 2008).

The jaguar density observed in the protected forest of CBWS is one of the highest recorded in neotropical forests (Silver *et al.*, 2004; Harmsen, 2006). This suggests that local conditions are particularly favourable for jaguars, and armadillos may play an important role in their success. Novack *et al.* (2005) suggested that jaguar encounter rates with armadillos may be positively associated with mesic conditions which favour the arthropod prey of armadillos. The high density of rivers and streams in CBWS (~2.5 km of waterways per km<sup>2</sup>, Foster, 2008) may be particularly favourable for armadillos and jaguars alike. Before the forest was officially protected, the relative occurrence of armadillos in jaguar diet was 54% (Rabinowitz & Nottingham, 1986); and it has not altered (51% this study) after 20 years of protection. Although the forest suffers occasional incursions by poachers seeking game species at the edges, it is likely that prey populations have improved since formal protection. For example, before protection, peccaries comprised only 5% of jaguar diet (Rabinowitz & Nottingham, 1986) compared with 19% in this study. The continued high predation on armadillos despite this four-fold increase in use of larger prey supports the hypothesis that armadillos are abundant in the area and are exploited opportunistically by jaguars. However, simple models predict that intense predation on armadillos may be limited by the high kill rates that would be necessary if larger prey were not also taken. For example, a female jaguar that hunted only armadillos would have to make 500–630 kills per year

to fulfil her own needs and those of her off-spring (Foster, 2008). Therefore it is likely that jaguars, particularly breeding females, must supplement their diet with larger prey (Novack *et al.*, 2005; Foster, 2008). In the protected forest, this role appears to be filled by peccaries. Although jaguars may be capable of taking a wide range of prey, reproduction probably depends on a minimum availability of larger prey, below which the long-term persistence of jaguars may be in jeopardy.

Puma density has not been formally estimated in CBWS but available data suggest that they are less numerous than jaguars (Harmsen *et al.*, 2009a), as observed in the neighbouring Chiquibul Forest Reserve where jaguars were estimated to have approximately twice the density of pumas (Silver *et al.*, 2004; Kelly *et al.*, 2008). Perhaps they are unable to exploit the available food resources as efficiently as jaguars. For example, in CBWS pumas spend more time travelling on trails than jaguars (Harmsen *et al.*, 2009a), potentially limiting their ability to detect the undergrowth-dwelling armadillos. Novack *et al.* (2005) suggested that the tough armadillo carapace may deter pumas from taking them, whereas the powerful bite of the jaguar gives it unimpeded access and minimal handling time. It is therefore possible that intense predation on armadillos is energetically less viable for pumas in CBWS than hunting pacas. A reduced handling effort on pacas compared with armadillos is probably offset against a higher search effort for the relatively agile paca. Because jaguars have short massive limbs associated with reduced cursorial behaviour (Seymour, 1989), they may be less well adapted than pumas to hunting fast-moving prey such as pacas.

Interspecific avoidance has been detected between jaguars and pumas in CBWS (Harmsen *et al.*, 2009b), but it is unknown whether this is mutual or one-sided. In general, however, where jaguars and pumas coexist jaguars tend to be larger (Iriarte *et al.*, 1990) suggesting their dominance; potentially they may interfere with access to key hunting areas for pumas. For example, high paca activity in CBWS is associated with waterways, jaguars also use these areas, but pumas, the main predator of pacas, were never detected near streams (Harmsen *et al.*, 2009a), suggesting a possible deterrence effect by jaguars.

Jaguars took smaller prey and fewer species in the forest buffer than in either the protected forest or the fragmented habitat, presumably because hunters deplete the unprotected forest buffer of larger game species such as deer and peccary and there are no livestock here to supplement jaguar diet. The higher prevalence of coatis and collared peccaries in jaguar diet in the buffer than in the protected forest may reflect either the scarcity of prized game species such as brocket deer and white-lipped peccaries or a higher abundance of coatis and collared peccaries in this edge habitat. For example, Novack *et al.* (2005) detected higher coati densities in a hunted site closer to a settlement than a non-hunted site in a Guatemalan rainforest. Similarly collared peccaries adapt well to disturbed habitats, unlike white-lipped peccaries, which require extensive tracts of undisturbed forest (e.g. Peres, 1996; Novack *et al.*, 2005;

Reyna-Hurtado & Tanner, 2007). The persistence of collared peccaries in areas where other large prey are more quickly depleted by humans may play an important role in sustaining jaguar populations outside protected areas.

Differences in the distributions of jaguars and pumas across this study area are linked to their different feeding habits. Camera-trap data have revealed a decline in the density of jaguars with distance from the contiguous forest block, a finding that is largely attributable to lethal control of jaguars in retaliation for livestock predation outside protected areas (Foster, 2008). Livestock contributed to jaguar diet in the fragmented landscape, replacing armadillos to some extent and supplementing a diet of otherwise small prey. This probably reflects a scarcity of large game species, and the presence of pastures with high densities of livestock. Although jaguars occupying the fragmented landscape may not all take livestock, those with home ranges encompassing pastures have high encounter rates with domestic prey, and potentially a lower availability of wild prey. Azevedo (2008) found that livestock contributed most to jaguar diet in and around Iguacu, a national park of subtropical forest bordered by livestock farms in Brazil. Increased livestock predation in this area correlates with a decline in white-lipped peccaries (Conforti & Azevedo, 2003; Crawshaw *et al.*, 2004; Azevedo, 2008). Indeed the exploitation of domestic prey is often inversely associated with the availability of wild prey (e.g. Hoogesteijn, 2000; Miller, 2002; Polisar *et al.*, 2003). A better understanding of the effect of the availability of domestic versus wild prey on the food habits of jaguars is required, particularly for assessing whether wild prey augmentation, especially large ungulates in the forests of the human-matrix, in combination with sustainable hunting practices, could reduce levels of livestock predation and simultaneously boost the local game hunting economy.

Núñez *et al.* (2000) proposed that the broader prey niche of pumas and their ability to take smaller prey may give them an advantage over jaguars in human-altered landscapes, and suggested that persistence of pumas is more likely than jaguars in disturbed environments. Our study finds contradictory results: pumas took similar-sized or larger prey and fewer species than did jaguars, and their feeding habits, combined with wild prey availability, may partly explain the scarcity of pumas compared with jaguars outside the protected forest. The three most important prey species for pumas within the protected forest (pacas, white-lipped peccaries and brocket deer) are all popular game species in Belize and it is likely that game hunters depress their densities outside the protected forest. Unlike jaguars, there was no evidence that pumas ate livestock. This was also observed in and around Iguacu, where pumas utilized only wild prey (Conforti & Azevedo, 2003; Azevedo, 2008). In the Venezuelan Llanos and Brazilian Pantanal where jaguars and pumas coexist and both kill livestock, pumas tend to focus on the smaller age classes (e.g. González-Fernández, 1995; Crawshaw & Quigley, 2002; Scognamiglio *et al.*, 2002; Azevedo & Murray, 2007). Across Belize, reports of pumas preying on livestock are relatively few

compared with jaguars (Brechin & Buff, 2005; Foster, 2008). Their small size in Belize (Iriarte *et al.*, 1990) may deter them from attacking adult cattle. However, this does not explain why they do not take sheep, pigs, dogs or small calves. A combination of food habits, prey availability and wariness of people may prevent pumas from exploiting the human-matrix (Foster, 2008). In contrast, jaguars are living and breeding across the landscape, albeit at lower densities in the fragmented lands (Foster, 2008). They persist despite utilizing relatively small prey species; although where large wild species have been depleted, livestock may become an increasingly important supplement in their diet, particularly for breeding females. Although flexibility in prey choice may allow jaguars to exploit natural habitats and human-influenced landscapes alike, it also provokes conflict with people and direct persecution, which has important implications for population viability in the long term (Foster, 2008).

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