

Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos

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(Accepted 25 June 2002)

Abstract

Jaguar *Panthera onca* and puma *Puma concolor* are sympatric throughout the jaguar's distribution. Although several studies have focused on the interactions between these two predators, the ecological and behavioural factors that promote their coexistence remain unclear. The goal of this study was to identify those factors that facilitate the coexistence of these cats in a mosaic landscape in the Venezuelan llanos. The study was conducted from January 1996 until November 1998. Five jaguars and six pumas were captured and radio-collared. A high degree of spatial overlap was observed between jaguars and pumas, which may be related to the abundance and distribution of prey species. At a fine scale, there was little overlap of puma locations with jaguar locations. Both species were more active at night than during daytime, but seasonal differences were detected in the activity levels of these predators. Major segregation was found in food habits. Jaguars selected for large prey and pumas for medium-sized prey. Jaguars selected for capybara *Hydrochaeris hydrochaeris* and collared peccary *Tayassu tajacu* and consumed caiman *Caiman crocodilus* and white-tailed deer *Odocoileus virginianus* less than expected. Pumas selected just for collared peccary and also killed caiman less than expected. It is suggested that the abundance of medium-sized prey is an ecological factor that is facilitating the coexistence of jaguar and puma in the study area. Habitat heterogeneity may be another influential factor leading to the coexistence. Seasonal differences in activity levels probably reflect differences in the size and species of prey taken by these cats.

Key words: *Panthera onca*, *Puma concolor*, coexistence, mosaic landscape, Venezuela

INTRODUCTION

The ecological interactions and the mechanisms promoting the coexistence of sympatric species have been studied and debated for many decades (MacArthur & Levins, 1967; Schoener, 1974, 1982; Weins, 1977; Gordon, 2000). The traditional approach has been to look at how sympatric species partition resources (Schoener, 1974; Gordon, 2000), principally along the axes of diet, space and time. Depending on quantitative differences in these axes, coexistence has been suggested to be related to selection for one or more variables, including different prey species (Karanth & Sunquist, 1995, 2000), different prey sizes (Gittleman, 1985; Karanth & Sunquist, 1995, 2000; Taber *et al.*, 1997), different activity patterns (Fedriani, Palomares & Delibes, 1999; Karanth & Sunquist, 2000), different habitats (Palomares *et al.*, 1996; Fedriani *et al.*, 1999), and differential use of space (Creel & Creel, 1996; Palomares *et al.*, 1996; Durant, 1998).

The jaguar and the puma are sympatric throughout the jaguar's distribution in the Neotropics. Several studies have been conducted on these two species, but few have examined the ecological interactions between them. Trophic separation has frequently been studied (Jorgenson & Redford, 1993; Aranda & Sánchez-Cordero, 1996; Taber *et al.*, 1997; Nuñez, Miller & Lindzey, 2000; Crawshaw & Quigley, 2002; de Oliveira, 2002), but only two studies have considered variables other than diet (Emmons, 1987; Nuñez *et al.*, 2002).

The goal of this study was to identify the ecological and behavioural factors that mediate the coexistence of jaguar and puma in a mosaic landscape in the Venezuelan llanos. An understanding of these mechanisms is critical to the development of conservation and management plans for these two predators in an area where both are threatened by loss of preferred prey and by persecution for depredation on livestock.

Study area

This study was carried out in the llanos of west-central Venezuela from January 1997 to November 1998. It was a

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continuation of a study initiated in 1996 by Farrell (Farrell, 1999) and for that reason part of her data are included. Hato Piñero, the study site, is located in the south-eastern corner of the state of Cojedes ($8^{\circ}40' - 9^{\circ}00'N$, $68^{\circ}00' - 68^{\circ}18'W$). Piñero's 80 000 ha support both a working ranch of 10 000 cattle, and a thriving ecotourism business. Average annual precipitation between 1961 and 1965 was 1469 mm, with 86% of the rain falling between May and October. During the rainy season up to 80% of the ranch is flooded, with water depths ranging from a few cm to 1.5 m, and the workable study area is reduced to about 30 000 ha. During the wet season, the average low temperature is $19.8^{\circ}C$, and the average high temperature is $31.8^{\circ}C$. In the dry season, the average low temperature is $17.9^{\circ}C$, and the average high temperature is $34.6^{\circ}C$.

The topography on the ranch includes permanent rivers, temporary creeks (semi-permanent, seasonally drying water bodies), grassland or open pasture, savanna woodland, non-flooded evergreen forest and dry forested uplands. The ratio of open to forested areas is roughly 50:50. While many of Piñero's streams are bordered by forests, relatively large areas of semi-deciduous forest are not adjacent to streams. In general, the landscape can be characterized as a complex mosaic of interdigitated forests and open areas with vegetation types based on interactions of elevation, substrate and hydrology.

Prey diversity and abundance vary greatly across the landscape (Polisar, 2000). Overall, prey diversity declined as elevation increased and was lower in savannas than forests. During the wet season, prey species seemed to become more dispersed within large annual use areas, making use of more dispersed resources, less surface water constraints and the phenology of favoured plant foods (Polisar, 2000).

METHODS

Cats were captured with trained hounds or rubber padded leg-hold traps. Captured pumas and jaguars were chemically anaesthetized using a projectile dart (TELINJECT, rifle model IV; Soledad, CA, U.S.A.). A combination of 2 drugs was used to immobilize the animals: medetomidine (Zalopine; Farnos, Orion Corp., Turku, Finland, and Wildlife Pharm. Inc., Fort Collins, CO, U.S.A.) and ketamine (Wildlife Pharm. Inc., Fort Collins, CO, U.S.A.); a reverter, atipamezole (Farnos, Orion Corp., Turku, Finland), allowed the quick recovery of the sedated cats.

Drug dosages varied with type of capture. With traps, the dosage was $50 \mu g/kg$ medetomidine (concentration 10 mg/ml) + $5 mg/kg$ ketamine (concentration 200 mg/ml) (Hoogsteijn *et al.*, 1996). As a consequence of the stress of being followed by dogs, the dosage was increased to $150 \mu g/kg$ medetomidine + $5 mg/kg$ ketamine for cats captured with this technique. The dosage of the antagonist was always 3 times the dosage of medetomidine. Immobilized animals were examined for

general body condition, measured, weighed, and fitted with radio-collars (160–164 MHz, Telonics, Inc., Mesa, AZ, U.S.A. and ATS/Advanced Telemetry Systems, Isanti, MN, U.S.A.). Relative age was estimated on the basis of dentition and tooth wear (Shaw, 1987).

Telemetry locations were obtained through ground triangulation, using hand-held antennae, and aerially by wing-mounted antennae attached to ultralight aircraft. When a radio signal was heard, 2 or 3 azimuths to the cat were taken where the angle between any 2 azimuths was between 20° and 120° , and the time between successive measurements was <30 min. Aerial locations were determined with a GPS unit while circling the animal's location. Radio-locations were distributed over 24 h. Activity was determined at 15-min intervals based on radio-transmitter signal integrity (Lord, Bellrose & Cochran, 1962). When the radio signal was unsteady for 5 min, a consequence of local or long distance movements, the animal was noted as active (Lord *et al.*, 1962; Schaller & Crawshaw, 1980; Sunquist, 1981).

Dietary habits of puma and jaguar were determined from scats and kills. Scats were collected opportunistically from trails and roads and the identity of the predator was assigned by the presence of tracks. Scats were air dried and stored until analysed. Prey contents of the collected scats were visually identified to the lowest taxa possible by examination of teeth and/or hair scale pattern by comparing them to a reference collection. Carcasses of prey animals were located by tracking the radio-tagged cats and from the presence of scavengers and predator sign. If the predator was unknown, ancillary evidence such as tracks, scats, teeth marks, type of killing injury, feeding method and caching behaviour was examined to identify the predator involved. Where the identity of the predator that left the scat or made the kill was unknown, these data were excluded from the analysis. In addition to the species of prey killed, records were made of age-class, based on the descriptions given by Ojasti (1973) for capybara, and by Dimmick & Pelton (1994) for peccary and white-tailed deer.

Data analysis

Home range

Location error was estimated from the polygon error method of White & Garrot (1990). The longest diagonal between opposite corners of the error polygon for a radiolocation was estimated at 150 m when the distance between the individual and the researcher was 500 m. Locations were plotted on a vegetation map of the study area (1:50 000) with UTM coordinates. Home ranges were calculated by the 95% minimum convex polygon method (Mohr, 1947) and 95% utilization distribution (UD) kernel estimator with 1.4 km band width (H) (Powell, 2000; Kernohan, Gitzen & Millspaugh, 2001) using the software LOAS and BIOTAS (Ecological Software Solutions, 2000).

Activity

Activity readings were divided into daytime readings (06:00–18:00) and night-time readings (19:00–05:00), and further divided into 3-h blocks for analysis.

Habitat use

At the fine scale, the percentage of jaguar and puma locations that overlapped in forest patches of 300 ha or larger were determined. Then the percentage of each cat's location that fell within the outer 0–500 m band of the patch and the percentage that fell in the interior (> 500 m from the edge) of the patch were determined. Assuming that the jaguar is the social dominant species (Morse, 1974; Persson, 1985) and for this reason pumas probably avoid jaguars, a second analysis examined the percentage of puma locations that were included in jaguar ranges and those that fell within a 200-m diameter circle generated around each jaguar's location (Seidensticker, 1976).

For the coarse-scale analysis, the Skillings–Mack non-parametric test for arbitrary unbalanced block design (Hollander & Wolfe, 1999) was used to determine whether there was a significant difference between the observed proportion of use of each habitat type and the expected use of habitat types. Polisar (2000) described the habitat types used in this analysis.

Diet composition

The frequency of occurrence and biomass of each prey species consumed was calculated. The frequency of occurrence for all prey types is the number of scats with the item *i*th divided by the total number of scat samples for predator species. The relative biomass of the different vertebrate prey taken was calculated using the formula $y = 1.98 + 0.035x$ given by Ackerman, Lindzey & Hemker (1984) for puma, where *y* is weight of food consumed per scat and *x* is the live weight of the prey. Mean weight of vertebrate prey (MWVP) was calculated as the grand geometric mean obtained by summing the products of the numbers of individual prey items times their natural-log-transformed weight (g) and dividing by the total number of prey items used in the calculation (Jaksic & Braker, 1983). Diet breadth was calculated using Levins' index (B) (Levins, 1968), which considers prey taken in relation to the species available and ranges from 1 to the number of prey taxa categories taken. This index was used to estimate the Colwell and Futuyma's standardized index (B_{sta}), which allows comparisons of niche breadths among different studies or locations (Colwell & Futuyma, 1971). Values of the standardized index range from 0 to 1, and values approaching 1 indicate that all prey items were taken in equal proportion to each other, while a value approaching 0 means that a few prey items were taken at a high frequency and many prey items were taken at a low frequency. The degree of diet overlap was calculated following Pianka (1973).

Prey size selectivity

Prey were divided in 3 size categories based on their mean adult body weight: small <1 kg, medium 1–15 kg, and large >15 kg (Iriarte *et al.*, 1990). Chesson's index (Chesson, 1978) was used to estimate puma and jaguar selectivity for prey size categories. The values of this index range between 0 and 1, where higher values indicate higher selectivity.

Prey species selectivity

Chi-square tests (Zar, 1996) were used to make statistical inferences about prey species selectivity, based on the null hypothesis of random, non-selective predation by cats. The sample counts of scats containing each prey species were compared to expected numbers of scats containing that prey in the environment (Karanth & Sunquist, 1995). When the χ^2 test showed significant differences ($\alpha = 0.05$), Bonferroni confidence intervals were used to evaluate selection for or against prey species (Neu, Byers & Peek, 1974; Byers, Steinhorst & Krausman, 1984).

RESULTS

Five jaguars (three females and two males) and six pumas (four females and two males) (Table 1) were captured. When captured in 1996, female jaguar JF1 was with small cubs and still lactating (see Farrell, 1999). In 1997, one of her cubs (JF3), who was 14–18 months old and still travelling with her mother and sibling, was captured. Although jaguar JM4 was radio-collared for 14 months, he was seldom located even by aerial tracking. He was an elderly male, estimated to be *c.* 20 years old, and he obviously ranged over a vast area.

Home ranges

A total of 1090 radio-locations was obtained from collared animals. After eliminating locations with high error, 817 locations (458 for jaguars and 359 for pumas) were used to estimate home-range size (Table 2). Locations of one female jaguar (JF3) were not considered for home-range size estimation because they were collected while she was travelling with her mother. There was considerable overlap in the home ranges of jaguars and pumas during the dry season (60%) and rainy season (50%). Evidence (tracks, sightings) was also found of an uncollared male jaguar moving within the home ranges of female pumas FP1 and FP2 and male puma MP6 (1996–97).

Activity patterns

A total of 3027 activity readings was obtained from the 10 tracked animals (1269 for jaguars and 1758 for pumas). In general, both jaguars and pumas were significantly more active at night than during daytime (jaguar: $Z = 2.32$, $P = 0.02$; puma: $Z = 8.82$, $P < 0.001$; see Fig. 1). On a

Table 1. Body measurements, sex and age class of jaguars *Panthera onca* and pumas *Puma concolor* captured in Hato Piñero, Venezuela, during 1996–98. a, Adult; j, juvenile; m, male; f, female

Animal ID	Species	Age, sex class	Weight (kg)	Total length (cm)	Tail length (cm)	Head length (cm)	Shoulder height (cm)
JF1	Jaguar	a, f	46	180	56	25	65
JF2	Jaguar	a, f	58	–	–	–	–
JF3	Jaguar	j, f	41	181	60	27	57
JM4	Jaguar	a, m	82	177	61	33	81
JM5	Jaguar	a, m	93	–	–	–	–
PF1	Puma	a, f	24	178	63	23	–
PF2	Puma	a, f	25	143	69	22	59
PF3	Puma	a, f	25	167	64	21	55
PF4	Puma	a, f	28	203	66	22	52
PM5	Puma	a, m	52	196	64	26	73
PM6	Puma	a, m	50	223	68	25	62

Table 2. Estimated home-range size (km²) of jaguars *Panthera onca* and pumas *Puma concolor* in Hato Piñero, Venezuela. Range sizes, 95% minimum convex polygon (MCP)/95% UD kernel (K) and band width (H) 1.4 km. JF, Female jaguar; JM, male jaguar; PF, female puma; PM, male puma

Animal ID	Species	Dry season (km ²) (MCP/K)	Rainy season (km ²) (MCP/K)	Total no. of radio-locations (dry/rainy)
JF1	Jaguar	80/83	51/66	86/369
JF2	Jaguar	–	53/47	–/45
JM4	Jaguar	99/93	–	24/–
JM5	Jaguar	100/108	–	20/–
PF1	Puma	47/48	–	54/–
PF2	Puma	29/85	23/55	30/138
PF3	Puma	23/69	–	20/–
PM5	Puma	104/100	83/91	117/131
PM6	Puma	17/57	–	16/–

Table 3. Comparisons of the activity levels of jaguars *Panthera onca* and pumas *Puma concolor* between day and night during dry and rainy season in Hato Piñero, Venezuela

Day–rainy season	Jaguars more active than pumas	Z = 3.51, P < 0.001
Night–rainy season	Pumas more active than jaguars	Z = 2.81, P = 0.005
Day–dry season	Pumas more active than jaguars	Z = 3.83, P < 0.001
Night–dry season	Pumas more active than jaguar	Z = 2.27, P = 0.023

seasonal basis, jaguars were significantly more active than pumas during the daytime in the wet season, but in all other comparisons pumas were more active than jaguars (see Table 3).

Habitat selectivity

Data on habitat use (% of locations in each habitat type) vs habitat availability (% of each habitat type within home range) for each animal are presented in Table 4. The Skillings–Mack test (Hollander & Wolfe, 1999) indicates that jaguars used different habitat types in the same proportion as available within their home ranges (SM = 1.32, P = 0.45). This test also indicates marginal selection by puma for open habitats (SM = 9.153,

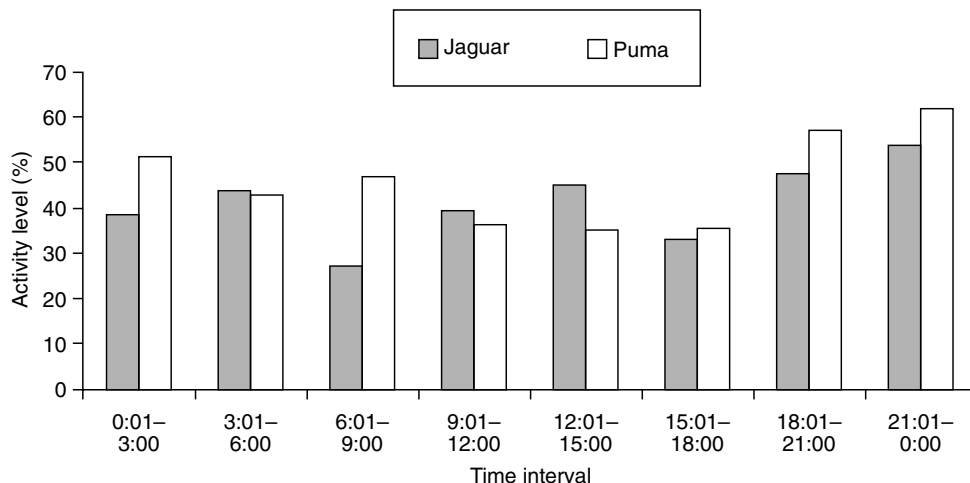


Fig. 1. Activity patterns (% of ‘active’ records) of jaguars *Panthera onca* and pumas *Puma concolor* in relation to time of the day in Hato Piñero (Estado Cojedes, Venezuela) during 1996–98.

Table 4. Habitat use (% of locations in each habitat type) and habitat available for each animal (% of each habitat type within home range) for four jaguars *Panthera onca* and five pumas *Puma concolor* at Hato Piñero, Venezuela during 1996–98. SI, Flooding savanna; BS, dry forest; SS/CH, dry savanna with chaparro; BSD, semi-deciduous forest; PS, dry pasture; BSV, evergreen forest

		JF1	JF2	JM3	JM4	PF1	PF2	PF3	PM5	PM6
SI	Use	31.7	2.2	29.0	65.0	29.6	16.0	0.0	37.3	18.7
	Available	27.7	11.1	55.0	30.6	46.0	15.1	0.0	26.1	19.5
BS	Use	21.4	11.1	0.0	10.0	37.0	34.8	5.0	3.2	37.5
	Available	7.5	14.4	4.4	1.3	26.0	35.4	10.2	4.0	32.5
SS/CH	Use	3.2	46.7	0.0	0.0	1.8	14.5	45.0	4.0	18.7
	Available	4.0	24.3	0.2	1.8	4.6	21.8	69.1	7.3	23.6
BSD	Use	43.4	33.3	71.0	25.0	16.6	0.7	35.0	55.5	0.0
	Available	60.3	44.4	40.4	66.2	19.0	23.2	13.2	60.9	0.0
PS	Use	0.0	6.7	0.0	0.0	9.2	33.3	15.0	0.0	25.0
	Available	0.0	5.7	0.0	0.0	2.5	23.9	6.4	1.7	23.5
BSV	Use	0.0	0.0	0.0	0.0	5.5	0.7	0.0	0.0	0.0
	Available	0.0	0.0	0.0	0.0	0.8	1.4	0.0	0.0	0.0

Table 5. Densities, and standing crop biomass estimates of potential prey of jaguars *Panthera onca* and pumas *Puma concolor* for each habitat type in Hato Piñero, Venezuela (adapted from Polisar, 2000)

Species	Habitat	Density (individuals/km ²)	Biomass (kg)
<i>Odocoileus virginianus</i>	All forests	1	
	Dry forest	1.5	
	Flooded savanna	8.3	
	All habitats		78 890
<i>Tayassu tajacu</i>	All forests	7.5	35 890
<i>Tayassu pecari</i>	All forests	167 ^a	5000
<i>Hydrochaeris hydrochaeris</i>	Water bodies	547 ^a	22 654
		4	181
<i>Dasypros novemcinctus</i>	Dry forest		
	Semi-deciduous forest	4	756
	All forests		937
<i>Caiman crocodilus</i>		15 408 ^a	167 826
<i>Sylvilagus floridanus</i>	Semi-deciduous forest	0.8	
	Dry forest	1.7	
	All forests		183
<i>Dasyprocta agouti</i>	All forests	1.2	1072
<i>Myrmecophaga tridactyla</i>	All forests	0.4	2787

^a Data refer to estimated number of individuals in the entire study area.

$P = 0.086$), otherwise puma did not select for habitat types.

Space use patterns

In forest patches of 300 ha or larger, 83% and 81% of jaguar and puma locations, respectively, were in the 0–500 m band. About 17% and 9% of jaguar and puma locations, respectively, fell in the interior of the patch (>500 m from edge). Only 144 (37.3%) of 386 puma locations fell within known jaguar home ranges. Of these

144 locations, 21 locations (14.6%) were within a 200-m diameter buffer zone around each jaguar location.

Scat analysis and prey selectivity

A total of 94 scats (42 for pumas, 42 for jaguars, 10 unidentified) was collected from 1996 to 1998, with almost all of these collected during the dry season. During this same period, the carcasses of 50 animals killed by puma and 29 by jaguars were found. Data on prey availability are presented in Table 5.

Puma: The 42 scats contained 12 taxa including livestock. Overall, 17.1% of the prey items were small mammals, 31.7% were medium-size prey and 52.2% were large mammals (Table 6). Large prey represented 70.6% of the biomass consumed (Table 6). Collared-peccary juveniles, deer, capybara and caiman were, in this order, the four most important wild prey items in terms of per cent of occurrence and biomass consumed. The food niche breadth of puma was broader than that of the jaguar (Table 7). Mean weight of vertebrate prey (MWVP) consumed by pumas was 8.36 kg. When livestock was excluded, the MWVP was 4.7 kg. Capybara was the most frequent wild prey in the 50 kills (30%). Domestic stock represented 58% of these kills.

Jaguar: The 42 scats contained a total of 10 species including livestock. Overall, medium-size mammals represented 18.4% of the prey items and contributed 14.1% of the biomass consumed, while large mammals represented 81.6% of the prey items and contributed 85.9% of the biomass consumed (Table 8). Collared peccary, capybara and white-lipped peccary were the most important taxa both in per cent of occurrence and biomass consumed. Without livestock, the food niche breadth of jaguar was 5.41 or 0.55 when standardized. Mean weight of vertebrate prey was 17.2 kg, but without livestock MWVP decreased to 15.9 kg. Jaguar/puma MWVP ratio was 3.38. In 29 jaguar kills, the most frequent wild species were capybara (20.7%), collared peccary (17.2%) and

Table 6. Proportions of prey species in puma *Puma concolor* scats ($n = 42$) and kills ($n = 50$) and relative mammalian and reptilian biomass consumed by pumas (based on scats) at Hato Piñero, Venezuela

Prey size	Prey species	Scats (%)	Kills (%)	% biomass consumed including livestock	% biomass consumed excluding livestock
Large size prey (>15 kg)	<i>T. tajacu</i>	5	2	5	8
	<i>T. pecari</i>	2	0	3	5
	<i>H. hydrochaeris</i>	10	30	12	20
	<i>O. virginianus</i> (adult)	10	8	14	21
	Livestock	24	58	37	0
Subtotal		50	98	71	54
Medium size prey (1–15 kg)	<i>T. tajacu</i> (juvenile)	12	0	12	19
	<i>O. virginianus</i> (juvenile)	0	2	0	0
	<i>S. floridanus</i>	7	0	2	3
	<i>D. agouti</i>	2	0	2	3
	<i>D. novemcinctus</i>	2	0	2	3
	<i>C. crocodilus</i>	10	0	10	16
Subtotal		33	2	28	44
Small size prey (<1 kg)	Small rodents or marsupials (three species represented)	17	0	1	2
Subtotal		17	0	1	2
Total		100	100	100	100

Table 7. Puma *Puma concolor* and jaguar *Panthera onca* food niche breadths^a in Hato Piñero, Venezuela

		With respect to prey size		With respect to taxa	
		Puma	Jaguar	Puma	Jaguar
With livestock	B	2.70	1.32	7.94	6.08
	B _{sta}	0.85	0.32	0.60	0.56
Without livestock	B	2.85	1.35	8.40	5.41
	B _{sta}	0.92	0.35	0.67	0.55

^a B, Niche breadth following Levins (1968); B_{sta}, niche breadth following Colwell & Futuyma (1971).

caiman (17.2%). Domestic animals comprised 38% of these kills.

Puma and jaguar diets were significantly different, both with livestock ($\chi^2 = 27.48$, d.f. = 15, $P = 0.025$) and without livestock ($\chi^2 = 23.25$, d.f. = 14, $P = 0.056$). If collared peccary are separated into adults and juveniles, diets differ even more ($\chi^2 = 35.66$, d.f. = 16, $P = 0.003$ considering livestock; $\chi^2 = 30.90$, d.f. = 15, $P = 0.009$ without livestock), showing that pumas took more young peccaries than did jaguars.

Chesson's selection indices for prey body size for puma are $\alpha_L = 0.32$ for large prey, $\alpha_M = 0.67$ for medium size, and $\alpha_S = 0.006$ for small prey. The selection indices for jaguar are $\alpha_L = 0.98$ and $\alpha_M = 0.023$ for large and medium-size prey, respectively. A χ^2 test indicates that jaguars were taking prey species non-randomly ($\chi^2 = 150.7$, d.f. = 4, $P < 0.0001$). The Bonferroni confidence intervals (Table 9) show that jaguars preyed selectively on capybara and collared peccaries, killed white-lipped peccaries in proportion to availability, and white-tailed deer and caiman were taken less than expected based

on availability. Pumas also were taking their prey non-randomly ($\chi^2 = 37.64$, d.f. = 4, $P < 0.0001$), and the Bonferroni confidence intervals (Table 9) indicate that puma were taking all large prey types in the same proportion as available with the exception of collared peccaries, which were taken selectively. Caiman was taken less than expected based on availability. The Pianka's index for overlap in diet between the two cats was 0.70 with livestock included and 0.83 without livestock.

DISCUSSION

Interspecific spatial interactions

The high degree of interspecific spatial overlap observed in the study area may be indicative of a patchy distribution of prey, with predators moving through the matrix and foraging in places where prey are abundant (Schroder & Rosenzweig, 1975; Schoener, 1982; Rabinowitz & Nottingham, 1986). Furthermore, the analysis of space-use patterns shows that both puma and jaguar intensively used the prey-rich forest-savanna ecotone (for detailed prey distribution see Polisar, 2000). The attraction of carnivores to areas of high prey density has been noted in other studies of sympatric species (Palomares *et al.*, 1996; Durant, 1998).

Differences in habitat use, either temporally or spatially, have been recognized as behavioural characteristics that may promote coexistence (Partridge, 1978). Many studies have found that sympatric carnivores are able to coexist by selecting different habitats (Seidensticker, 1976; Schaller & Crawshaw, 1980; Norton & Lawson, 1985; Konecny, 1989; Johnson, Fuller & Franklin, 1996; Durant, 1998; Fedriani *et al.*, 1999). However, the results of this study

Table 8. Proportions of prey species in jaguar *Panthera onca* scats ($n = 42$) and kills ($n = 30$) and relative mammalian and reptilian biomass consumed by jaguar population (based on scats) at Hato Piñero, Venezuela

Prey size	Prey species	Scats (%)	Kills (%)	% biomass consumed including livestock	% biomass consumed excluding livestock
Large size prey (> 15 kg)	<i>T. tajacu</i>	26	16	24	27
	<i>T. pecari</i>	12	0	14	15
	<i>H. hydrochaeris</i>	21	20	24	26
	<i>O. virginianus</i> (adult)	5	0	6	7
	<i>M. tridactyla</i>	10	0	10	11
	<i>C. crocodilus</i>	0	13	0	0
	Livestock	7	33	10	0
Subtotal		81	83	88	86
Medium size prey (1–15 kg)	<i>T. tajacu</i> (juvenile)	2	0	2	2
	<i>Procyon cancrivorus</i>	5	0	4	4
	<i>S. floridanus</i>	2	0	1	1
	<i>D. agouti</i>	0	7	0	0
	<i>C. crocodilus</i>	7	3	6	7
	<i>Podognemis voglii</i>	0	7	0	0
Subtotal		17	17	13	14
Small size prey (<1 kg)	Unidentified bird	2	0	0	0
Subtotal		2	0	0	0
Total		100	100	100	100

Table 9. Bonferroni confidence intervals (95%) estimated for prey species selectivity in the diet of jaguars *Panthera onca* and pumas *Puma concolor* in Hato Piñero (Estado Cojedes, Venezuela) during 1997–98. Observed, observed frequency of scats; Expected, expected frequency of scats

Prey	Observed	Expected	Lower limit	Upper limit
Jaguar				
<i>H. hydrochaeris</i>	0.29	0.04	0.08	0.50
<i>T. tajacu</i>	0.39	0.08	0.16	0.61
<i>T. pecari</i>	0.16	0.01	-0.01	0.33
<i>O. virginianus</i>	0.06	0.20	-0.05	0.17
<i>C. crocodilus</i>	0.10	0.67	-0.04	0.24
Puma				
<i>H. hydrochaeris</i>	0.20	0.04	0.01	0.38
<i>T. tajacu</i>	0.35	0.08	0.13	0.57
<i>T. pecari</i>	0.05	0.01	-0.05	0.15
<i>O. virginianus</i>	0.20	0.20	0.01	0.38
<i>C. crocodilus</i>	0.20	0.67	0.01	0.38

indicate that habitat selection was not an important factor in promoting the coexistence of jaguar and puma.

The heterogeneity of the landscape in the area may, however, be contributing to the coexistence of these species (P. L. Chesson, 1985; Hanski, 1994). In heterogeneous landscapes the inferior competitor can diminish competition intensity by foraging in a patch at a different time (Fedriani *et al.*, 1999; Karanth & Sunquist, 2000), forage in different patches (Shorrocks, 1991; Johnson, Fuller & Franklin, 1996; Durant, 1998) or even partition each patch (Fierer & Kotler, 2000). The low percentage of overlap (14.6%) of puma locations with jaguar locations may indicate avoidance as well as fine-scale differences

in space use between these two cats. Seidensticker (1976) suggested that fine-scale differences in use of habitat patches by tiger and leopard in Nepal was an important component of their ecological separation. Subtle differences in habitat use, possibly associated with avoidance, have also been documented between jaguar and puma in Peru (Emmons, 1987) and in Mexico (Aranda & Sánchez-Cordero, 1996). Avoidance can also magnify the effect of differential patch use (Ives & Dobson, 1987; Chesson & Rosenzweig, 1991).

The possible spatial avoidance of jaguars by pumas observed at the fine scale in this study, and at other sites by Emmons (1987) and by Aranda & Sánchez-Cordero (1996) seems to contradict observations by Taber *et al.* (1997) in the Paraguayan chaco, where pumas apparently do not avoid jaguars. However, these authors based their affirmations only on the co-occurrence of scats and tracks of these two cats (mainly found on roads and seismic lines). Pumas and jaguars could be using the same travel paths, as observed by Taber *et al.* (1997), but be hunting in different areas.

Temporal separation and activity patterns

Temporal separation has been proposed as a strategy adopted by sympatric predators to allow coexistence (Bertram, 1979; Konecny, 1989; Kitchener, 1991; Mills & Biggs, 1993; Durant, 1998; Karanth & Sunquist, 2000). At Piñero, temporal separation was not observed, at least not in the 3-h periods used for the activity analysis. The higher level of activity at night of pumas and jaguars are probably associated with the activity patterns of their prey (Sunquist, 1981; Emmons, 1987) and that moving

prey are more detectable and/or vulnerable (Sunquist & Sunquist, 1989). The level of detection of a prey changes with its size, with smaller prey being less detectable than large ones (Emmons, 1987; Sunquist & Sunquist, 1989; Dukas & Ellner, 1993; Huggard, 1993). On the other hand, for a predator, the search effort per prey is reduced considerably when the location of a specific prey or patch is predictable (Stephens & Krebs, 1986; O'Brien, Browman & Evans, 1990; Huggard, 1993; Scheel, 1993). Both different detection level of prey and predictability in finding them may result in different search efforts for jaguars and pumas (O'Brien *et al.*, 1990; Dukas & Ellner, 1993; Huggard, 1993; Karanth & Sunquist, 2000). This argument may explain the higher level of nighttime activity of pumas, which probably spend more time searching for smaller and less detectable prey (Griffiths, 1975; O'Brien *et al.*, 1990; Dukas & Ellner, 1993; Huggard, 1993; Karanth & Sunquist, 2000).

High ambient temperatures are thought to have an inverse effect on the activity level of predators (Sunquist, 1981; Crawshaw & Quigley, 1991; Mills & Biggs, 1993). The higher levels of activity of jaguar and puma during the rainy season in Piñero could possibly be related to the lower temperatures registered during that season. The fact that the jaguar is relatively more active than the puma during the daytime in the rainy season may be partially a consequence of a reduction in the search effort by puma resulting from the inclusion of cattle in its diet during that season. Calves are more detectable prey than the medium-sized wild prey that pumas takes during the rest of the year (Cunningham *et al.*, 1995; Linnell *et al.*, 1999) and the location of calves is predictable, both characteristics may be leading to a reduction in search effort. A higher level of daytime activity level in the wet season has also been noted for tigers in Nepal (Sunquist, 1981), where it was thought to be related to prey extending their activity into the early morning hours on overcast, cloudy days.

Diet and prey selectivity

Although jaguars and pumas at Piñero are taking a similar number of prey species, 10 and 12, respectively, the standardized food niche breadth indices indicate that puma ($B_{sta} = 0.62$) are taking their prey in more similar proportions than do jaguar ($B_{sta} = 0.55$). The selectivity of capybara and collared peccary by jaguar may explain this difference.

Collared peccary and capybara are group-living species. It is recognized that preying on group-living species may result in higher risk of injury to the predator (Sunquist & Sunquist, 1989; Huggard, 1993) leading the predators to avoid these species. An example of this risk is the fact that a sub-adult female jaguar (JF3) was killed by collared peccaries. However, the high association of capybara with water holes and collared peccary with particular patches (Polisar, 2000) seems to increase their detection and vulnerability to being selected by jaguars. The selectivity for these two prey species suggests that jaguars are making

foraging decisions on the basis of energy gain and not on injury risk (Sunquist & Sunquist, 1989; Huggard, 1993; Scheel, 1993). The low density of white-lipped peccary (see Polisar, 2000) may be contributing to the difference in the level of predation upon this species.

Capybara are also an important large prey item for pumas. Capybara are large, non-aggressive rodents that live in groups and one would expect pumas to select for them. Capybara kills were always made close to water bodies, but even if water bodies are considered 'open habitats', where pumas could be seen as more efficient predators than in the close structure of the forest (Taber *et al.*, 1997), the fact that there is no selection for these vulnerable prey can be interpreted either that competition with the jaguar partly constrains the availability of capybara or that this prey is less vulnerable to pumas for undetermined reasons (Sunquist & Sunquist, 1989).

It has been suggested that when two sympatric carnivores are closely matched in body size, exploitative competition may occur (Park, 1962) and while the most common response facilitating coexistence is habitat partitioning, some degree of food partitioning may be expected (Johnson *et al.*, 1996). At Piñero, the value of Chesson's indexes indicates that food partitioning does occur, with the larger jaguar preying upon large prey and puma upon medium-sized prey. Note that while both jaguar and puma are selecting for collared peccary, pumas are taking mainly juveniles of this species (see Table 6).

At Hato Piñero caiman are found in both jaguar and puma diets, but less than expected based on availability. Caiman are associated with permanent water sources, and this behaviour probably reduces their vulnerability when compared to other large prey species. Furthermore, given the high abundance of caiman on the ranch, jaguar and puma would have to kill an inordinate number to show selection.

The low frequency of white-tailed deer in the jaguar diet may be a consequence of the low overlap in distribution between these two species. At Piñero, white-tailed deer use mainly open habitats (Table 5) where they are relatively abundant (Polisar, 2000). However, these kinds of habitats are poorly represented in jaguar home ranges (see Table 4) leading to a low probability of encounter between jaguar and white-tailed deer and a low representation of this prey in the jaguar diet.

CONCLUSION

The availability of a prey species for a predator is set by the prey species productivity and the intensity of its use by other predators (Hespenheide, 1975). In this respect theory predicts that among interacting species, space and activity time are more easily subdivided than food (van Valen, 1965; Fretwell, 1972; Hespenheide, 1975). On the other hand, optimal diet theory suggests that when prey are scarce a predator should take items in proportion to their abundance in the environment (Griffiths, 1975), or in other words, feed as a number maximizer. The energy maximizer strategy is favoured when highly

profitable prey is abundant. This reasoning leads to the conclusion that one might expect selectivity for prey species or appropriate body-sized prey when they are abundant.

We suggest that the adequate availability of appropriate medium-sized prey may be an ecological factor that facilitates the coexistence of jaguar and puma at Piñero. Habitat heterogeneity could be considered as another influential ecological factor leading to the coexistence of these species by promoting different patch use and probably fine-scale habitat selection by pumas.

A fine-scale habitat separation between these two predators may benefit both. This separation allows individuals of each species to avoid the cost of interference, and still garner a portion of the profit (Cody, 1974). Case & Gilpin (1974) recognized the benefits of this micro-spatial separation. These authors stated that 'interspecific "microterritoriality" may also allow individuals of each species to better predict the particular nuances of resource microdistribution and renewal rates within their specific home ranges'. Temporal segregation is not a likely strategy because of the generally high ambient temperatures in the region. At Piñero, activity separation can be interpreted as a secondary behavioural factor in the jaguar–puma interaction. Seasonal differences in activity levels of cats probably reflect differences in the size and species of prey taken.

Acknowledgments

This study was funded by the Wildlife Conservation Society, the National Geographic Society, International Union for Conservation of Nature and Natural Resources (IUCN) Cat Specialist Group, the Katherine Ordway Foundation, the Department of Wildlife Ecology and Conservation (University of Florida), the Branger Foundation, and the British Embassy to Venezuela's Cooperation Fund. Laura Farrell is thanked for her cooperation and information. Dr Edgardo Mondolfi was the perfect go-between when we needed him. Rocky and Roy McBride shared with us their invaluable experience in the field during the captures. Mr Antonio Branger and the llaneros (cowboys) of Piñero contributed with their knowledge about jaguars and pumas. Francisco Bisbal, Carlos A. Iudica and the Florida Museum of Natural History provided help during scat analysis. We are grateful to Dr John Eisenberg, Dr Lyn Branch, Dr Samuel Wu and Fiona Sunquist for helpful comments. Dr J. A. J. Nel and an anonymous referee are thanked for their comments during the final stages of the manuscript development.

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