

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest

Fernando Cesar Cascelli de Azevedo^{a,b,*}, Dennis Lewis Murray^c

^aDepartment of Fish and Wildlife, College of Natural Resources, University of Idaho, Moscow, ID 83843, USA

^bInstituto Pró-Carnívoros, Caixa Postal 10, Atibaia, SP 12940-970, Brazil

^cDepartment of Biology, Trent University, Peterborough, ON, Canada K9J 7B8

ARTICLE INFO

Article history:

Received 23 November 2006

Received in revised form

26 February 2007

Accepted 28 February 2007

Available online 1 May 2007

Keywords:

Territoriality

Home-range

Predation

Food-base

Pantanal

Brazil

ABSTRACT

For most carnivore populations, territoriality is the regulating social system ultimately determined by food abundance and/or strife. However, in some food-based territorial felid species such as the jaguar (*Panthera onca*), the influence of food availability on territoriality remains unclear and may be lessened because of a tendency for individuals to occur at high densities across the landscape. We examined spatial organization and use of food in a population of jaguars in the southern region of the Pantanal, Brazil (2003–04). We predicted that if territoriality plays an important role in determining jaguar population dynamics, exclusive use of territories should be observed and thereby influence prey selection patterns. We determined that home range sizes were comparable between sexes and overlapped little at the core area level. Line transect surveys revealed that large mammals comprised the bulk of available wild prey for jaguars, and scat analysis indicated that jaguars relied mostly on large mammalian prey. The most common wild species killed by jaguars were capybara (*Hydrochaeris hydrochaeris*) and caiman (*Caiman yacare*). We estimated that the wild prey base was adequate to support the jaguar population. Larger wild prey species were considerably more likely to die from predation than from other causes, and predation was more likely to occur in jaguar core areas than in areas of home range overlap. Modest cattle depredation rates had little demographic importance to the local jaguar population. We conclude that spacing patterns in the local jaguar population were likely based on exclusion through territoriality rather than food limitation.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Several basic questions in ecology focus on understanding how animals are organized in space and time, and the factors affecting spatial arrangement and movement of individuals (Kernohan et al., 2001). Variations in social organization of several carnivore species have been related to availability of key resources (Litvaitis et al., 1986; Kissui and Packer, 2004). However, when resources are not limited, carnivore popula-

tions seem to regulate themselves by social interactions manifested through territoriality and aggression (Lindzey et al., 1994; Pierce et al., 1999; Adams, 2001). Territorial behavior is observed through the exclusion of conspecifics from areas containing key resources, and the defense of such areas through various behaviors including agonistic interactions (Maher and Lott, 2000). For instance, since defense of areas may be difficult to observe in several carnivore species, many studies have characterized carnivore populations as

* Corresponding author. Address: Instituto Pró-Carnívoros, Caixa Postal 10, Atibaia, SP 12940-970, Brazil. Tel.: +55 11 44116966; fax: +55 11 44116633.

E-mail addresses: oncaf@yahoo.com (F.C.C. Azevedo), dennismurray@trentu.ca (D.L. Murray).

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.02.022

territorial due to their exclusive use of areas inferred by low degrees of overlap (e.g., <25%) between conspecifics of the same sex (Maher and Lott, 1995; Poole, 1995; Ferreras et al., 1997). For several carnivore species, the ultimate determinant of territoriality pertains to food abundance, such that food limitation promotes increased exploitative competition, aggression, and territorial disputes (Fuller, 1989; Poole, 1995; Pierce et al., 2000). It follows that, competition for food should be less pronounced in areas where individuals overlap, such that fewer prey would be killed in those areas than would be expected based on the availability of resources (Mech, 1977; Pierce et al., 2000). Thus, under this scenario a carnivore population may experience increased territoriality and spatial exclusion. The social ecology of many felids is purported to be governed by such dynamics (Poole, 1995; Pierce et al., 2000; Benson et al., 2004, 2006).

Few data are available on the spatial dynamics of jaguar populations (*Panthera onca*) (Rabinowitz and Nottingham, 1986; Crawshaw and Quigley, 1991; Crawshaw, 1995) and the influence of food availability on territory dynamics (Taber et al., 1997; Farrell et al., 2000; Nuñez et al., 2000; Polisar et al., 2003; Scognamillo et al., 2003). Considered opportunistic feeders, jaguars can subsist on a wide variety of prey, but preference toward medium and large-size prey species has been suggested (Seymour, 1989; Gonzalez and Miller, 2002; Scognamillo et al., 2003), particularly in areas where prey abundance is not limited (Polisar et al., 2003). In the Pantanal region of Brazil, the annual flooding regime and the relative availability of prey species, including cattle, may influence home range size and prey selection patterns by jaguars (Schaller and Crawshaw, 1980; Crawshaw and Quigley, 1991). However, there has been no empirical assessment of the importance of prey species availability and prey biomass on the spatial distribution of jaguars and patterns of prey selectivity.

In the present study we examined spatial organization and use of food resources in a population of jaguars. If territoriality plays an important role in determining jaguar population dynamics, exclusive use of territories should be observed and influence prey selection patterns. More specifically, we expected: (i) limited intra-sexual home range overlap, especially among core areas (<25% of overlap) and (ii) heavier prey use in core areas of the home range. In addition, the importance of large prey in the jaguar diet was examined with the expectation jaguars would exhibit non-selective behavior towards wild prey species and thus (iii) consume wild prey in accordance to their availability in the study area.

2. Methods

2.1. Study area

The study was conducted in the southern part of the Pantanal region of the Mato Grosso do Sul state in Brazil (20° 05'S and 56° 36'W), during February 2003 to December 2004. The Pantanal is a floodplain covering approximately 140,000 km² of land on the borders of Bolivia and Paraguay. The Pantanal is characterized by an annual regime of flooding and low land relief, with the landscape being comprised of wetlands habitats, seasonally inundated grasslands and woodlands, and

non-flooding forests. The study site is a working 150 km² cattle ranch/wildlife reserve, located in the southern region of the state. Three major habitat types occur on the ranch: (1) open areas, with grasslands composed mainly of grass species interspersed with palm trees such as the carandá (*Copernicia australis*) and acuri palms (*Attalea phalerata*) and commercial rice fields; (2) closed woodlands constituting a one-story forest with trees such as the ipê (*Tabebuia* sp.) lacking clear vertical stratification and a grass understory that is flooded during wet season; and (3) semi-deciduous forests having vertical differentiation including ipê and acuri palms (Dubs, 1994). Average annual precipitation at the study site between 1988 and 2004 was 1336.3 mm, with most of the rainfall occurring between April and October.

2.2. Sampling

We captured jaguars and pumas (*Puma concolor*) with trained hounds and/or steel box-traps. Captured animals were immobilized with the use of Tiletamine hydrochloride and Zolazepam hydrochloride (Zoletil[®], Virbac do Brazil) administered at 10 mg/kg body weight. Once immobilized, animals were sexed, weighed, reproductive condition was evaluated, and age class (adult >2 years; subadult) was determined based on tooth wear. Animal handling procedures were approved by IBAMA, the Brazilian Environment Institute (permit #02027.007013/03-81). Immobilized animals were fitted with VHF radio-collars (ATS/Advanced Telemetry Systems, Isanti, MN, USA and Telonics Inc., Mesa, AZ, USA). Radio-collared animals were monitored during March 2003 to December 2004 and locations were obtained three times per week from the ground using standard triangulation techniques (Samuel and Fuller, 1996), and weekly via fixed-wing aircraft. Only locations >24 h apart were considered independent and used in analyses (Grassman et al., 2005). A total of 570 radio-locations (60.3% aerial, 39.7% ground) were obtained from eight collared jaguars (five females and three males) after excluding locations with error and animals with <30 locations recorded (three males). Accuracy of ground and aerial telemetry was determined by location by 'blind' observation of transmitters placed throughout the study area; mean error associated with ground and aerial telemetry was 206 ± 168 m ($n = 10$) and 131 ± 47 m ($n = 10$), respectively; we considered that such error was acceptable for our rather coarse spatial distribution analysis.

2.3. Estimation of prey density

Prey density of wild species was estimated using the line transect method (Burnham et al., 1980; Buckland et al., 2001); this method has been widely used to estimate vertebrate prey densities in tropical environments (Karanth and Sunquist, 1992, 1995; Varman and Sukumar, 1995; Khan et al., 1996; Peres, 1996; Biswas and Sankar, 2002). Eighteen transects varying in length from 0.5 km to 5.3 km were established throughout the study area (Fig. 1). We attempted to cover all habitat types available within the ranch. However, because of the flooding regime in the Pantanal, some transects had to be established in areas not subject to the influence of the water, which could bias our results toward wild prey abun-

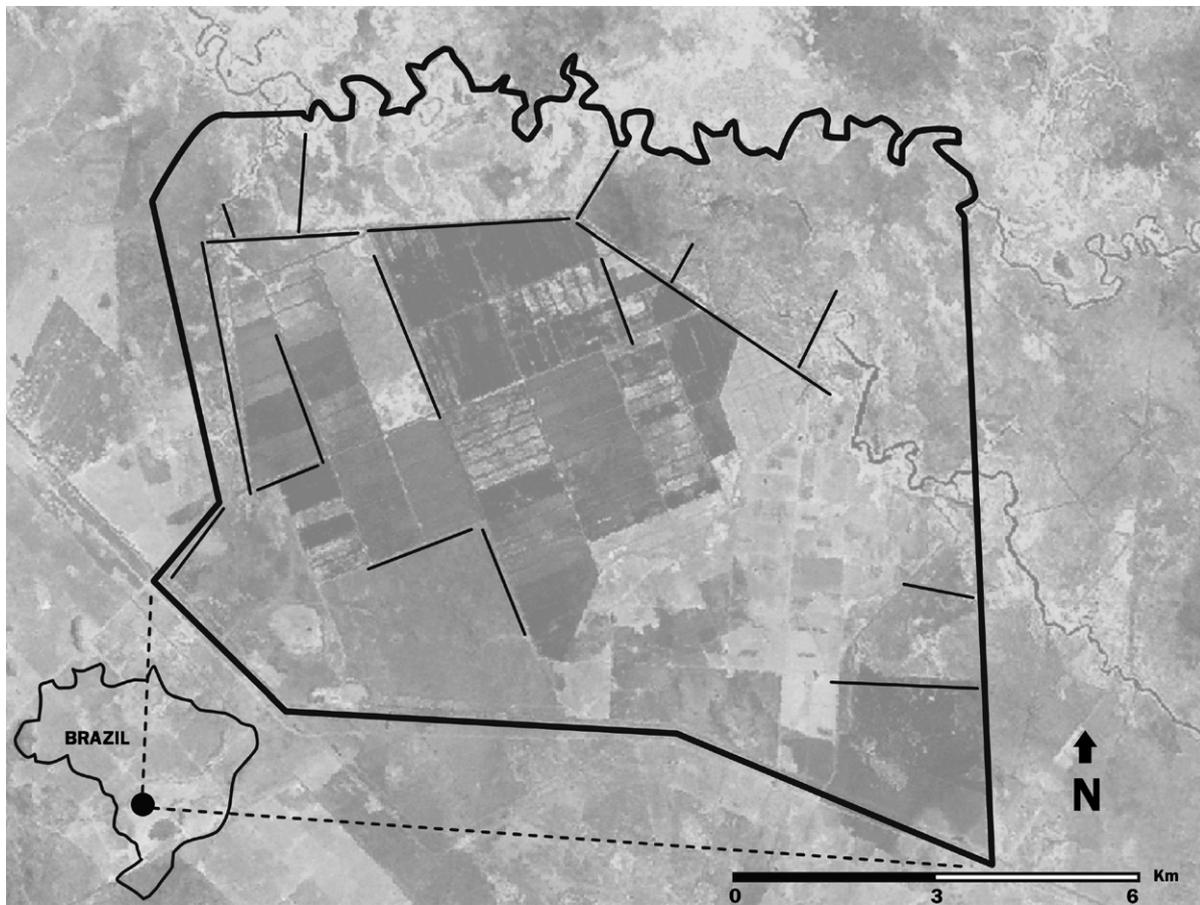


Fig. 1 – Study site and line transects ($n = 18$) surveyed during 2003–2004 within San Francisco ranch, Brazil.

dance in drier areas. Transects were visited from 06:00 to 10:00 a.m. daily ($n = 12$) on 140 different occasions (total of 214 km), and using vehicles with spotlights from 07:00 to 09:00 p.m. at night ($n = 6$) on 57 occasions (total of 1845 km). Daily transects were conducted along established trails. Night transects were conducted along abandoned roads. Transects covered an approximated perimeter of 67 km within the study area (approximately 0.09% of the total ranch area), with the closest transects being 1.0 km apart and furthest being 13.0 km apart. We combined data from daily and night transects. However, night transects were mainly used to estimate density of caiman (*Caiman yacare*). Density of caiman was estimated through systematic counts of individuals occurring in permanent rice irrigation canals and swamps. We used the average number of sighted individuals/night/transect to generate density estimates of caiman within the ranch. White-lipped peccary (*Tayassu pecari*) density was estimated based on the average number of individuals sighted from one major herd occupying a specific dry and isolated area within the ranch. This herd was recorded through counts along night transects during 2004.

2.4. Predator diet

Predator diet was determined from combined analyses of scats and kills found in the study area (Schaller, 1972; Kruuk, 1972; Sunquist, 1981; Johnsingh, 1983; Karanth and Sunquist,

1995, 2000; Scognamillo et al., 2003). Scat collection occurred opportunistically on trails and roads within the ranch and its borders. Collection of scats may have been biased toward proximity to unpaved roads. To minimize this influence we focused our collection of scats on line transects surveyed during collection of prey density estimates. Jaguar scats were differentiated from those of pumas based on tracks found close to the collection site; scats not associated with recognizable tracks were excluded from the analyses (Nuñez et al., 2000; Scognamillo et al., 2003). Scats were dried at 72 °C for 24 h and contents were separated under running water. Food contents were identified to species using hair, skull fragments, teeth, scales, as well as via comparison with reference material available at the ranch. Carcasses of wild prey were found opportunistically while checking transects or by using presence of vultures. We estimated the probability to detect carcasses of wild prey by comparing the number of times daily transects were conducted and the total number of carcasses recovered while collecting data on transects. Predation by jaguars and pumas was determined if ≥ 2 of the following were observed: signs of bites on carcasses, presence of scats near kill sites, presence of fresh tracks near the site, cached remains, or signs of a trail where the prey had been carried or dragged. The presence of such signs indicated death due to predation as opposed to alternate causes of death. We attempted to find signs of predator attack on the head/neck of carcasses to confirm predation and reduce chances of finding

scavenging carcasses of animals dying of other reasons. The estimated area where carcasses could be reasonably found due to habitat accessibility represented 60% of the total area of the ranch (approximately 90 km²).

2.5. Data analysis

Home ranges were calculated using the Animal Movement Extension (Version 2.04) in the program ArcView GIS 3.2 (Hooge et al., 1999; ESRI®, 2000). The fixed kernel estimator with contours of 95% and 50% was used to estimate home and core range areas respectively, using least squares cross validation (Worton, 1995). For all analyses of home range and spatial organization we included only data on resident collared jaguars occurring in the area during the 2 years of study. We estimated density of jaguars in the study area by dividing the number of resident individuals by the area encompassing all jaguar telemetry locations for the period of study (Benson et al., 2006). Home ranges were found to reach an area asymptote with a minimum of 30 locations and this constituted our minimum for inclusion in home range analysis (Seaman et al., 1999). Data on home range sizes and spatial organization were checked for normality and analyzed using ANOVA.

Static and dynamic interactions among jaguars were calculated as described by Poole (1995). The spatial overlap of individual animals (the static interaction according to Macdonald et al., 1980) was calculated by determining the percent of inter and intra-sexual home-range overlap and percent overlap among individuals, irrespective of gender (Poole, 1995). To determine whether adjacent individuals moved independently of each other, we also examined dynamic interactions among jaguars. Defined as the degree at which two animals attract, ignore or avoid each other (Macdonald et al., 1980), dynamic interactions were examined by determining mean observed distance between locations (D_o) and mean expected distance (D_e) of each location from animal A to all locations from animal B (Kenward et al., 1993); this provided the coefficient of sociality, $\{S_c = (D_e - D_o)/D_e + D_o\}$. Positive and negative values indicate attraction and repulsion of two individuals, respectively. Independent movement is indicated by 0 values.

In order to determine the biomass of prey species, density estimates derived from line transects were used. For those prey species sighted yielding a minimum of 30 independent observations (26%, $n = 10$) to estimate densities (Peres, 1996), transect data were analyzed with the program Distance (Version 5.0, Laake et al., 2005) using the Hazard Rate model (Buckland et al., 1993). Because tourism activities have taken place in the ranch for more than 5 years prior to our study, prey species seemed to be indifferent to human presence. Line transects were periodically cleared of visual obstruction to avoid missing detection of prey species. Therefore, we believe the first two assumptions required for reliable estimation of prey density using the line-transect method were met (Buckland et al., 1993). We estimated sighting distances on transects via visual means and estimated densities for ungrouped data. To correct for potential bias due to heaping, we conducted a second analysis by grouping counts in different distance class intervals (5–7) (Buckland et al., 2001). Because

the goal of the analysis was to estimate prey densities for the entire study area, we pooled all survey sites to provide an average value for the entire area (Peres, 1996). This procedure was utilized only when within-transect variances in perpendicular distances from the sampling transect to the sighted animal were greater than between-transect variances (ANOVA, $P > 0.05$). The lowest Akaike information criterion values were chosen in order to select for the best model of prey density (Burnham and Anderson, 2002) using the program Distance. Prey live weight estimates were based on published references (Ackerman et al., 1984; Robinson and Redford, 1986; Emmons, 1987; Crawshaw, 1995), and livestock biomass was estimated based on data from annual cattle counts available for the study area (San Francisco ranch, unpublished data).

Scat collection complemented carcass recovery in our assessment of jaguar diet. Our detection of carcasses of prey killed may have been biased in favor of larger prey; to minimize this influence, we focused on the scat sample analysis (Karanth and Sunquist, 2000; Vos, 2000; Biswas and Sankar, 2002). Frequency of occurrence of food items in scats was determined by calculating percent composition based on relative frequency of occurrence (Ackerman et al., 1984; Hidalgo-Mihart et al., 2001; Neale and Sacks, 2001). To account for potential bias due to overestimation of small prey (Ackerman et al., 1984) and underestimation of large prey (Weaver, 1993), we converted estimates of relative biomass and relative number of prey consumed through the use of a correction algorithm $Y = 1.98 + 0.035X$, where Y is the mass of prey consumed per scat and X is the live body mass (Ackerman et al., 1984). Dietary breadth of jaguars was determined by calculating niche breadth (Levins, 1968) using the relative frequency of occurrence of food items (where $B = 1/\sum p^2_j$, where B is the Levin's measure of niche breadth and p_j is the fraction of items in the diet that are of food category j), and standardized dietary breadth on a scale from 0 to 1.0, using Hulbert's measure (1978): $B_A = B - 1/n - 1$, where B_A is the Levin's standardized niche breadth; B the Levin's measure of niche breadth; n is the number of possible resource states (see Krebs, 1999). Values approaching 0 mean high frequency of occurrence of few prey items and low frequency of occurrence of many prey items in the diet, while values approaching 1 mean equal frequency of occurrence of all prey items. This approach enabled us to assess the extent to which carnivore-specific food selection patterns focused on particular food categories.

We estimated the minimum annual requirement of killed prey necessary to sustain the jaguar population in the study area by multiplying the number of jaguars (three adults resident and one adult transient male; five adult resident females and two cubs) by the average weight of captured animals. Eight jaguars (five females and three males) were deemed to be residents based on their long-term occupation of the study area. In addition, one transient collared jaguar was also known to be present on the study area during the first 6 months of study. Despite intensive capture efforts and monitoring of trails and roads, no other signs of jaguars occurring in the study area were recorded. For analysis, we used 9 as the total number of adult jaguars present on the study area in the context of prey consumption. For our calculations, we used consumption requirements of 34 g/day kg of cat for jaguars

(Emmons, 1987) assuming that 70% of prey carcass mass was consumed and digested by jaguars (Polisar et al., 2003). Cub requirements during their first year of age were estimated as 25% that of adult females, whereas subadult requirements were assumed to be equal to those estimated for adult females (Sunquist, 1981; Polisar et al., 2003). Confidence intervals for jaguar minimum annual requirements of food were estimated based on the sex-specific variability in body mass among captured jaguars. In order to analyze selection for prey sizes, we calculated the mean weight of vertebrate prey in jaguar diets (MWVP) as described in Iriarte et al. (1990) and determined prey biomass consumed by classifying prey in three size categories according to their mean mass. The three major groups are: small = <1 kg, medium = 1–15 kg, and large = >15 kg prey. Prey selectivity was evaluated by comparing observed versus expected counts of scats containing each prey item. To minimize bias towards larger prey species and provide correct estimates of proportions of young animals and smaller species in predator diets, we determined the average number of collectable scats produced by a given predator from an individual animal of each prey species ($\lambda_i = X/Y$) using the same correction algorithm described above (Ackerman et al., 1984).

Factors affecting wild prey mortality were examined from recovered carcasses (predation vs. non-predation mortality) and using logistic regression (Proc Logistic SAS Institute, 1999). Causes of wild prey mortality were compared using data collected at the site where prey were found dead, including jaguar use level (categorical data: core areas at 50% Fixed Kernel, overlap areas) and size of prey species (categorical data: large prey: >15 kg; medium/small prey: <15 kg). The fit of regression models were compared using Akaike's Information Criterion, with the sum of Akaike weights (w_i) for each variable serving to rank each by importance (Burnham and Anderson, 1998). We used Pearson χ^2 analysis to test for differences between the number of animals preyed inside jaguar core areas and in overlap areas. Based on the total number of wild prey found dead in the study area, we also performed a χ^2 analysis to further test the hypothesis of jaguar non-selective behavior towards larger prey species.

We used a multinomial likelihood ratio test (see Link and Karanth, 1994) to test the null hypothesis of non-selective predation. The expected proportion of prey species in scats was calculated using the program Scatman (Link and Karanth, 1994). The program compares the observed and expected proportions of prey species in the scats through a Person χ^2 statistic to evaluate selective predation. In case

two items occurred in a single scat, those were counted each as 0.5. This minimizes the effect of potential source of inflation of type I error caused by the variability in density estimates of each prey species and number of scats produced from a particular kill. A parametric bootstrap procedure with 1000 replicates served to estimate significance levels (Link and Karanth, 1994). To further investigate the selectivity for each prey species, we conducted analyses of deviance using results of the simultaneous 1 df likelihood ratio tests from the overall pattern of prey use generated from the bootstrap simulations (Link and Karanth, 1994). All analyses were considered statistically significant when $P < 0.05$. Probability levels were two-tailed in all analyses of determinants of prey mortality and jaguar prey selectivity.

3. Results

3.1. Home ranges

Eleven adult jaguars were captured and body mass averaged 61.5 ± 6.2 kg (\pm SD) ($n = 5$) and 99.7 ± 13.0 kg ($n = 6$) for females and males, respectively, differing significantly between sexes ($t_1 = 12.24$, $P = 0.0001$). The total home range size area for five females and three males jaguars in the study area was 112.2 km² (95% FK), which translated to a density of 0.07 adult resident jaguars per square kilometer on the ranch. We found that home-range size was comparable between sexes at 95% FK ($F = 1.28$, $P = 0.30$) and at 50% FK ($F = 0.03$, $P = 0.86$). The mean size averaged 49.15 ± 36.02 km² and 11.58 ± 12.44 km² at the 95% and 50% levels, respectively (Table 1). Jaguars shared similarly almost half of their home range areas with conspecifics of the same sex at 95% FK (pooled mean sizes for both sexes averaged 51.73%; Mann-Whitney test, $U = 8.0$, $P = 0.88$). However, little overlap was observed at core areas (mean size averaged 8.24%; $U = 8$, $P = 0.87$), suggesting that same-sex resident individuals established exclusive core areas. Intersexual overlap was extensive at both 95% and 50% FK areas (Table 1). For male jaguars occupying adjacent or overlapping areas, dynamic interactions approached neutral (0.04 ± 0.08 ; mean \pm SD), indicating neither attraction nor avoidance between individuals. Low positive attraction was observed only between a single pair ($+0.13$). Intrasexual interaction for most pairs of female jaguars ($n = 10$) exhibit neither avoidance nor attraction (0.007 ± 0.04). This pattern was supported by the results of home range overlap for female pairs (Table 2). Strong intersexual attraction was observed for three of fifteen intersexual pairs of jaguars (Table 2).

Table 1 – Mean home-range sizes (km²) using 95% and 50%

Sex	n	Range size					
		FK 95% (Mean \pm SD)	FK 50% (Mean \pm SD)	Overlap within sex		Overlap between sexes	
				95% FK	50% FK	95% FK	50% FK
Male	3	67.38 (50.54)	10.47 (8.24)	49.72 (44.64)	3.26 (5.65)	66.27 (12.55)	39.75 (32.96)
Female	5	38.20 (24.37)	12.25 (15.34)	52.93 (24.74)	11.22 (20.28)	84.22 (14.99)	48.07 (41.09)

Fixed Kernel (FK) contours and 95% mean percent home-range overlap at 95% and 50% FK (\pm SD) levels are reported.

Table 2 – Percent coefficient of overlap at 95% and 50%

Type of interaction	Jaguar pairs	95% FK	50% FK	S _c (number of paired locations)
Males overlapping	M01–M02	48.80	22.97	0.13 (10)
	M01–M03	6.75	0.00	–0.01 (18)
Males adjacent	M02–M03	0.00	0.00	0.00 (08)
Females overlapping	F01–F02	13.69	0.00	0.00 (68)
	F01–F03	8.29	0.00	0.03 (41)
	F01–F04	10.57	0.00	–0.06 (31)
	F01–F05	37.71	5.70	0.00 (41)
	F02–F03	50.28	0.00	0.01 (44)
	F04–F05	3.57	0.00	0.00 (22)
	F02–F05	16.63	0.00	0.01 (43)
	F03–F05	13.05	0.00	0.00 (27)
Females adjacent	F02–F04	0.00	0.00	0.00 (28)
	F03–F04	0.00	0.00	–0.01 (21)
M–F overlapping	M01–F01	48.23	4.88	0.08 (37)
	M01–F02	10.52	0.00	0.00 (34)
	M01–F03	11.00	0.00	+0.67 (22)
	M01–F04	19.56	0.00	–0.06 (16)
	M01–F05	30.10	18.20	–0.02 (20)
	M02–F01	62.70	13.29	+0.86 (26)
	M02–F04	18.22	0.00	0.09 (14)
	M02–F05	25.38	31.18	0.01 (18)
	M03–F01	6.63	0.00	0.00 (27)
	M03–F02	68.37	35.91	0.07 (38)
	M03–F03	51.60	50.97	–0.04 (27)
	M03–F05	4.55	0.00	+0.47 (21)
	M–F adjacent	M02–F02	0.06	0.00
M02–F03		0.00	0.00	0.00 (10)
M03–F04		0.00	0.00	0.09 (14)

Fixed Kernel contours and coefficient of sociality (S_c) for jaguar pairs with adjacent or overlapping home ranges.

Table 3 – Density and biomass estimates for principal prey species within the study area between February 2003 and December 2004

Species	Common name	Mean animal density (individuals/km ² ± SE)	C.V. (%)	95% C.I.	Weight (kg)	Biomass (kg)	Biomass (kg/km ²)
<i>Sylvilagus brasiliensis</i>	Rabbit	0.87 ± 0.17	19.63	0.59–1.28	1.1	143.28	0.96
<i>Procyon cancrivorus</i>	Raccon	0.09 ± 0.04	44.16	0.04–0.22	10.1	135.00	0.90
<i>Cerdocyon thous</i>	Crab-eating fox	0.23 ± 0.08	34.21	0.12–0.45	5.0	173.25	1.16
<i>Myrmecophaga tridactyla</i>	Giant anteater	0.27 ± 0.05	17.02	0.19–0.37	20.0	801.00	5.34
<i>Mazama americana</i>	Red-brocket deer	0.08 ± 0.02	27.76	0.05–0.14	35.0	430.50	2.87
<i>Tayassu pecari</i>	White-lipped peccary	0.25 ± 0.06	66.00	0.24–0.27	35.0	1330.00	8.87
<i>Hydrochaeris hydrochaeris</i>	Capybara	5.89 ± 0.49	8.35	5.00–6.94	45.0	39,757.50	265.05
<i>Blastocerus dichotomus</i>	Marsh deer	0.36 ± 0.03	8.93	0.30–0.42	100.0	5325.00	35.50
<i>Tapirus terrestris</i>	Tapir	0.15 ± 0.04	29.37	0.08–0.27	177.0	3955.95	26.37
<i>Caiman yacare</i>	Caiman	16.36 ± 2.12	67.36	14.30–18.42	50.0	49,100.00	327.33
Total native						101,812.80	678.75
Livestock		42.66 ± 0.71	1.01	29.94–55.36	291.6	1,865,948.40	12,439.66
Total						1,967,761.20	13,118.41

3.2. Prey density estimates and biomass

Estimates of densities of ten potential wild prey species for jaguars are described in Table 3. Biomass for all species was estimated at approximately 101,812 kg (95% C.I. 85,944–124,933 kg) which translated to 6,787.5 kg/km². Mammalian biomass represented 52%, while reptilian (caiman) biomass comprised 48%. The most important available prey species

by density were caiman, capybara (*Hydrochaeris hydrochaeris*), rabbit (*Sylvilagus brasiliensis*), marsh deer (*Blastocerus dichotomus*), and giant anteater (*Myrmecophaga tridactyla*). Among mammals, capybara, marsh deer, tapir and white-lipped peccary represented the most important prey biomass, constituting 49% of all prey biomass. These results suggest that, in addition to caiman, large mammals comprised the bulk of available food for jaguar. Annual cattle standing crop biomass

for the entire ranch was estimated at 1,865,948 kg (95% C.I. 1,309,575–2,421,446 kg) which translated to 12,439.7 kg/km². The most vulnerable cattle age class, calves <1 year, represented 8.5% of cattle biomass on the ranch. Annual prey biomass requirements for survival of individual jaguars in the study population was estimated at 9634 kg (95% C.I. 8524–10,935 kg), which represented 9.5% (95% C.I. 9.3–9.7%) of the standing crop biomass based on availability of wild prey species.

3.3. Predator diet analysis

We identified 209 separate prey items (mean per scat: 1.41 ± 0.67 (±SD), n = 149) from 19 taxa in jaguar scats, and we were able to correctly relate 25 scats (16.7%) to six out of eight known resident individual jaguars in the study area. Scat analysis revealed that jaguars relied mostly on large mammalian prey (61% of prey items and 77% of biomass, including livestock) (Table 4). The most important prey items for jaguars were large prey species such as capybara and caiman, but in terms of biomass, livestock was the second most important prey (Table 4). Jaguar standardized niche breadth was estimated at 0.453 and increased to 0.480 when livestock was included, indicating intermediate levels of dietary breadth. The mean weight of vertebrate prey for jaguars was estimated as 14.0 kg. We found 114 carcasses of wildlife and cattle killed by jaguars in the ranch. The most common wild species killed was capybara (31%, n = 35) followed by caiman (20%, n = 23). Livestock represented 28% (n = 32) of all kills found within the study area (Table 4). The percentage of livestock kills was probably overestimated because of high detectability of livestock over wild prey species.

3.4. Determinants of prey mortality

We found a total of 151 carcasses of wild prey species in the study region. Of those, 87% (n = 131) comprised large, and the remainder medium/small (13%, n = 20), prey species. Our rate of success in finding carcasses of wild prey was estimated at 0.41 during the period of study. Our analysis revealed that the percent of prey mortality due to predation (60%, n = 90) was higher than that from non-predation causes (40%, n = 61) ($\chi^2 = 5.57$; df = 1, P = 0.02). Jaguars were responsible for most of wildlife predation incidents (91%, n = 82), while pumas were occasionally involved (5%, n = 6) and the remaining incidents the predator was not identified (3%, n = 3). The sum of Akaike weights for models containing the variable for size of prey species equaled 0.94, suggesting that the model that was truly the best had a high likelihood of containing this variable. The odds-ratio for the model (4.17; 95% C.I. 1.502–11.574) indicated that larger prey species were considerably more likely to die from predation than from other causes, with 64% (n = 84) of large prey species recovered dying of predation ($\chi^2 = 7.03$; df = 1, P = 0.008). When the variable jaguar use level was included in the analysis, the odds-ratio for the full model (1.64; 95% C.I. 0.812–3.314) indicated mortality due to predation was more likely to occur in jaguar core areas than in areas of overlap (Table 5). Although the proportion of prey mortality due to predation versus non-predation causes inside core areas was similar (47%, n = 42 and 53%, n = 48, respectively), more carcasses were found dead from non-predation causes in regions of overlap (69%, n = 42). These results indicate mortality by predation was more intense in regions of exclusivity. However, we failed to find that larger prey species were sub-

Table 4 – Relative frequency of occurrence and biomass of prey consumed assessed from scats (n = 149) and kills (n = 114) collected within the study area during February 2003 to December 2004

Prey species size		Scats (%)	Kills (%)	Biomass (%) without livestock	Biomass (%) with livestock
Small prey size (<1 kg)	Birds	6.2	0.0	1.6	1.3
	Small rodents	1.9	0.0	0.2	0.1
Medium size prey (1–15 kg)	<i>Dasypus novemcinctus</i>	0.0	1.8	0.0	0.0
	<i>Cerdocyon thous</i>	4.0	0.0	1.9	1.7
	<i>Hydrochaeris hydrochaeris</i> (young)	6.4	0.9	4.1	3.3
	<i>Tayassu tajacu</i> (young)	0.8	0.0	0.4	0.3
	<i>Procyon cancrivorus</i>	4.0	0.0	2.4	2.0
	<i>Nasua nasua</i>	4.8	0.9	6.5	5.2
	<i>Tamandua tetradactyla</i>	2.4	1.5	4.5	3.6
	<i>Sylvilagus brasiliensis</i>	0.8	0.0	0.3	0.3
	<i>Mazama rufina</i>	7.2	0.0	5.2	4.2
	<i>Mazama americana</i> (young)	0.8	0.0	0.4	0.3
Large prey size (>15 kg)	<i>Tapirus terrestris</i>	0.0	0.0	1.4	1.2
	<i>Hydrochaeris hydrochaeris</i>	14.4	30.7	24.3	19.5
	<i>Tayassu tajacu</i>	4.8	0.9	6.5	5.2
	<i>Blastocercus dichotomus</i>	7.2	10.5	9.6	7.7
	<i>Rhea Americana</i>	0.8	1.7	0.5	0.4
	<i>Tayassu pecari</i>	0.0	0.9	1.1	0.9
	<i>Myrmecophaga tridactyla</i>	2.4	1.7	1.4	1.1
	<i>Mazama americana</i>	11.2	0.0	8.4	6.8
	<i>Caiman yacare</i>	6.4	20.2	19.3	15.5
	Livestock	11.2	28.1	0.0	19.4

Table 5 – Logistic regression models of variables found to be significant in predicting the likelihood of wild prey being killed by jaguars or dying from reasons other than depredation

Model i	K_i	AIC	Δ_i	w_i	O.R. ₁	O.R. ₂	C.I. ₁	C.I. ₂	Model P-value
Constant + species size	2	199.44	0.00	0.48	4.17	–	1.502–11.574	–	0.006
Constant + cat use level + species size	3	199.52	0.08	0.46	1.64	3.66	0.812–3.314	1.296–10.336	0.014
Constant + cat use level	2	204.04	4.60	0.05	1.93	–	0.978–3.825	–	0.058
Constant only	1	205.73	6.29	0.02	–	–	–	–	0.019

For each model i, K_i is the number of parameters in the model, Δ_i is the change in AIC between the model and the model with the lowest AIC (best model), and w_i is the Akaike weight. Models are ranked by AIC values. Odds ratios (O.R.) and corresponding 95% confidence intervals (C.I.) are provided. Model significance was determined via the likelihood ratio test.

Table 6 – Results of prey selectivity test from scat data

	Wild prey species ^a									
	ANT	CDM	CAP	CER	JAC	MPL	QUE	TMB	TPT	VMA
Scat freq	1.00	2.50	37.00	9.50	18.00	3.80	0.50	2.00	0.30	9.90
Exp freq	0.93	0.38	15.97	1.48	59.39	0.16	0.61	0.55	1.34	0.20
χ^2 Adjusted P value	0.941	0.001	0.000	0.001	0.000	0.000	0.889	0.050	0.374	0.000
(SE)	0.001	0.000	0.000	0.001	0.000	0.000	0.001	0.000	0.000	0.000
λ_i	8.17	2.15	3.55	5.48	4.08	2.33	3.20	2.68	2.02	3.20
SD(λ_i)	3.27	0.86	1.42	2.19	1.63	0.93	0.14	1.07	0.81	1.28
d_i	0.15	0.23	5.89	0.35	19.09	0.09	0.25	0.27	0.87	0.08
SD(d_i)	0.04	0.08	0.49	0.03	11.02	0.04	0.16	0.04	0.17	0.02

'Scat freq' denotes the observed number of scats related to each of the 10 wild prey species. 'Exp freq' denotes the expected frequencies under the null hypothesis of non-selective prey killing by jaguars and was calculated using point estimates of scat production rates (λ_i) and prey density (d_i). Adjusted P values are the significance levels of χ^2 statistics based on 1000 bootstrap replicates with correction for overdispersion. a Wild prey species: ANT: Tapir (*Tapirus terrestris*); CDM: Crab-eating fox (*Cerdocyon thous*), CAP: Capybara (*Hydrochaeris hydrochaeris*), CER: Marsh deer (*Blastocerus dichotomus*); JAC: Caiman (*Caiman yacare*); MPL: Raccoon (*Procyon cancrivorus*); QUE: White-lipped peccary (*Tayassu pecari*); TMB: Giant anteater (*Myrmecophaga tridactyla*); TPT: hare (*Sylvilagus brasiliensis*); and VMA: Red brocket deer (*Mazama americana*). Standard deviation of λ_i is assumed to be 40% of λ_i values (Link and Karanth, 1994).

ject to higher predation rates inside jaguar core areas, because size of prey species predated was independent of the location where carcasses were found ($\chi^2 = 1.21$; $df = 1$, $P = 0.271$). Similar numbers of large prey species were found predated in jaguar core areas and in areas of overlap (49%, $n = 41$, and 51%, $n = 43$, respectively).

3.5. Prey selectivity

We compared proportions of wild prey species found in jaguar scats to our estimates of prey availability through the multinomial likelihood ratio tests and concluded that prey were not killed randomly ($\chi^2 = 668.83$, $df = 9$; $P = 0.000$) (Table 6). This provides significant evidence for predator selectivity among all prey species. In general, jaguars consumed larger prey species more than available, including capybara ($P = 0.000$), marsh deer ($P = 0.000$), giant anteater ($P = 0.05$) and red-brocket deer ($P = 0.000$). In addition, two medium sized prey species were also found to be consumed more than available, the crab-eating fox ($P = 0.001$) and the raccoon ($P < 0.001$). Tapir, white-lipped peccary and rabbit were taken in proportion to their availability ($P > 0.400$), whereas caiman were taken less than available ($P < 0.001$).

4. Discussion

Jaguars in our study were characterized by having distinct territories with low degree of spatial overlap, which indicated the presence of regions of exclusivity inside home ranges. These regions of exclusivity were apparently maintained passively, since intra-sexual dynamic interactions in both sexes approached neutral, indicating little or no active avoidance or overt defense of areas between pairs of jaguars with overlapping or adjacent home ranges. In contrast, high degree of intersexual static interaction was observed, suggesting that male spacing patterns were apparently affected by the distribution of females (Sandell, 1989). Although dynamic interactions might vary temporally, our results support our first prediction of limited intra-sexual home range overlap among resident jaguars, especially among core areas during the period of our study. Our results contrast with other studies where resident male felids do not exhibit home range overlap and show strong aggression and territorial defense against conspecifics (Sunquist, 1981; Ross and Jalkotzy, 1992; Logan and Sweanor, 2001) whereas female ranges show a higher degree of overlap (Seidensticker et al., 1973; Ross and Jalkotzy, 1992; Logan and Sweanor, 2001).

The interpretation of our results of social interactions among jaguars could be confounded by the potential presence of uncollared animals in the studied population. However, evidence from tracks, scats, and intensive monitoring of trails and roads indicate that, with the exception of one adult transient collared male, only two young (<2 years) cubs and two adult males occupying marginal areas farther away from the studied population were present in addition to all collared jaguars with enough locations to be included in our analysis. These results strengthen our assessment that sampling bias was minimal. Although exclusiveness may be a function of degree, where some overlap may occur at 95% contour but little may occur at 50% contour core areas (Poole, 1995), the presence of individuals with their own distinct distributions encompassing regions of exclusivity is indicative of the influence of a territorial system on the spacing pattern of the population herein analyzed (Pierce et al., 2000).

Territoriality may also have affected interactions of jaguar and puma in the region. Coexistence between these predator species has been reported to occur in heterogeneous landscapes with high abundance of medium sized-prey species (Scognamillo et al., 2003). Poaching of wild species is rare in the Pantanal region and jaguar and puma are the most frequently species poached as a retaliation for livestock depredation incidents (Quigley and Crawshaw, 1992). High abundance of large-sized prey species and jaguar prey selection patterns within regions of jaguar exclusivity may have contributed to the low abundance of resident pumas within the study area and hence reduced potential interactions between these two predators. In addition, homogeneity of habitats may have influenced coexistence between jaguars and pumas (Scognamillo et al., 2003). Higher abundance of forested areas inside the ranch seems to favor the presence of jaguars. However, our lack of information on differences in use of habitat patches by jaguars and pumas may preclude further conclusions regarding jaguar competitive exclusion of pumas within the study area.

Regions of exclusivity are expected to occur in populations of solitary carnivores when food resources are uniformly distributed and abundant and when the cost of defense is less than the benefit of having exclusive use of a resource (Sandell, 1989; Poole, 1995; Feldhamer et al., 1999). Although we were not able to determine the specific distribution of principal prey species, our results indicate prey base was sufficiently abundant to influence patterns of exclusivity in the spatial distribution of resident jaguars and hence prey selection patterns. Our analysis indicates that jaguars consumed approximately 10% of the biomass of available wild prey. These results are similar to predator requirements in other tropical environments (Schaller, 1972; Emmons, 1987; Sunquist, 1981; Polis et al., 2003). Moreover, although abundance of livestock was approximately 18 times higher than wild prey in the study area, livestock represented <20% of the biomass consumed (Table 3). This consumption rate was qualitatively less pronounced than what we would expect based on high abundance of cattle in the Pantanal (Schaller and Crawshaw, 1980). Our results suggest the wild prey base was sufficient to sustain the population of jaguars. Resident jaguars did not require a subsidy of livestock to survive (Polis et al., 2003; Scognamillo et al., 2003).

The most important cause of wild prey mortality in our study area was predation by jaguars. Our results from model selection indicate that predation was the most common mortality cause for large prey species. Jaguar's preference for available large prey species appears to corroborate the hypothesis that in prey-rich habitats, predators should be selective in maximizing available energy (Griffiths, 1975). Using the average weight of captured jaguars and principal prey, the average predator: prey body weight ratio was 1:0.6, whereas using the maximum weight of a captured jaguar and the estimated weight of the larger prey species, predator-prey weight ratio was 1:1.6. Thus, as reported for other similar body-sized large felids, jaguars killed an array of available larger prey species, although consumption was more strongly focused on prey smaller than jaguars (Packer, 1986; Karanth and Sunquist, 1995; Seidensticker and McDougal, 1993).

We found that predation was more intense in regions of exclusivity. However, despite the preference for large prey species, locations of carcasses indicated predation of large prey species was not heavier inside jaguar core areas, although our sample size of carcasses of small and medium sized prey was low. Given the difficulties finding small and medium prey species before they were totally consumed by jaguars or vultures, we cannot rule out the possibility that predation upon these prey types was higher than reported. Our results on the MWVP based on scat analysis indicate that in average jaguars consumed prey species weighting slightly <15 kg. This result is mainly due to the inclusion of juvenile large prey species in these estimates. Thus, we suspect that predation rates upon medium/small prey species may have influenced jaguar predation patterns and minimized potential higher rates of predation upon large-bodied prey species inside regions of exclusivity.

Considering food resources were not a limiting factor, selection for preferred prey species was expected (Emlen, 1966; MacArthur and Pianka, 1966; Sunquist and Sunquist, 1989). Our results from diet analysis indicate the diversity of prey consumed by jaguars was relatively high ($n = 19$ taxa). However, when comparing our results to other studied jaguar populations (Scognamillo et al., 2003), analysis of dietary breadth from the present study was relatively narrow and suggestive of feeding specialization. Selective feeding was most prominent toward large-bodied prey such as capybara and marsh deer. Capybara are group-living and the cost of predation toward group-living species may be high due to potential injury (Sunquist and Sunquist, 1989; Huggard, 1993; Scognamillo et al., 2003). In contrast, marsh deer are solitary, and can reach large size, but may be associated with lower injury risk to jaguars. However, both species are closely related to water, they prefer dense vegetation for cover, and are abundant on the study area. These factors may increase their vulnerability to predation by jaguars, especially considering jaguars show preference toward forested habitats that are associated with water (Schaller and Crawshaw, 1980; Quigley, 1987; Crawshaw and Quigley, 1991). Capybara and marsh deer were primary prey, which supports the contention of prey selection in this jaguar population. In contrast, the most abundant solitary large species in the study area was taken less than expected based on availability. Caiman is a species

closely related to permanent water courses. In addition to permanent water courses, they were year-round residents of canals located in rice fields on the ranch. Despite being a frequent item in jaguar's diet, jaguars did not show selective behavior toward caiman. Their abundance was so high that a substantial number of caiman would be necessary to be consumed by predators in order to show selection (Scognamiglio et al., 2003). Therefore, although jaguars consumed a high variety of prey, specialization toward certain species occurred, hence limiting our prediction of non-selective predation pattern.

5. Conservation implications

While prey availability seems to be the predominant factor affecting large felid populations (Pierce et al., 2000), spacing patterns of the studied jaguar population seemed to be influenced by a territorial system, governed by regions of exclusivity despite prey abundance. However, our limited data on the consistency in home-range tenure in the system prevent further conclusions related to the role of transient jaguars in population dynamics. In addition, more efforts determining densities of a broader array of wild prey species as well as their distributions and long term population fluctuations are needed for a comprehensive understanding of the predator-prey relationship and its consequences on the shaping of spacing patterns of the jaguar population herein studied.

Our findings may help improve human-predator conflicts in the Pantanal region. The Pantanal is rich in wildlife diversity, yet more than 95% of its area is privately owned, with livestock being the main economic activity (Quigley and Crawshaw, 1992; Soisalo and Cavalcanti, 2006). Illegal jaguar control in response to livestock depredation is a significant source of jaguar mortality (Schaller and Crawshaw, 1980). The real impact of jaguars on livestock is usually exaggerated because of the lack of consistent and reliable data on predation factors. Because cattle are raised in close proximity to jaguars, retaliation from ranchers following predation incidents is a primary cause of jaguar decline in the region (Crawshaw and Quigley, 1991). Our study provides the type of data that could be used to improve management decisions in order to minimize cattle predation by jaguars. Placing cattle allotments away from jaguar core areas where predation on large bodied prey is less intense could reduce livestock-predator conflicts and thus contribute to the survivorship of jaguar populations in the Pantanal and elsewhere.

Acknowledgements

Financial support for this work was provided by The Institute for the Conservation of Neotropical Carnivores (PRÓ-CARNÍVOROS), Eucatex Company, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil. In Brazil the permission to conduct this research was granted by the Brazilian Environment Institute (IBAMA) through the IBAMA's National Center for the Conservation of Predators (CENAP). We thank all people from San Francisco ranch, in special H. Coelho, R. Coelho, E. Coelho, and C. Coelho for their support and for letting us establish a research project on their land in

the Pantanal region. Their encouragement during the 2-year field work at the ranch was much appreciated. In the field we thank J. Batista, A. Mello, E. Sicoli, and R. Fernandez for their invaluable assistance. We also thank C. Azevedo for help preparation of Fig. 1. We thank H. Quigley, K. Steinhorst and L. Waits for critiques and comments on the first drafts of this paper.

REFERENCES

- Ackerman, B.B., Lindzey, F.G., Hemker, T.P., 1984. Cougar food habits in southern Utah. *Journal of Wildlife Management* 48, 147–155.
- Adams, E.S., 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32, 277–303.
- Benson, J.F., Chamberlain, M.J., Leopold, B.D., 2004. Land tenure and occupation of vacant home ranges by bobcats (*Lynx rufus*). *Journal of Mammalogy* 85, 983–988.
- Benson, J.F., Chamberlain, M.J., Leopold, B.D., 2006. Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour* 71, 685–693.
- Biswas, S., Sankar, K., 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. *Journal of Zoology* 256, 411–420.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Lake, J.L., 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Lake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press.
- Burnham, K.P., Anderson, A.R., Laake, J.L., 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72, 1–202.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*, second ed. Springer-Verlag, NY.
- Crawshaw Jr., P.G., Quigley, H., 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology* 223, 357–370.
- Crawshaw Jr., P.G., 1995. Comparative ecology of ocelot (*Felis pardalis*) and jaguar (*Panthera onca*) in a protected subtropical forest in Brazil and Argentina. Ph.D. Dissertation, University of Florida, Gainesville, Florida.
- Dubs, B., 1994. Differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. Ph.D. Thesis, University of Zürich, Edinburgh.
- Emlen, J.M., 1966. The role of time and energy in food preference. *The American Naturalist* 100, 611–617.
- Emmons, L.H., 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology* 20, 271–283.
- Environmental Systems Research Institute (ESRI), 2000. Arcview, Version 3.2. ESRI, Redlands, California, USA.
- Farrell, L., Roman, J., Sunquist, M.E., 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology* 9, 1583–1590.
- Feldhamer, G.A., Drickamer, L.C., Vessey, S.H., Merritt, J.F., 1999. *Mammalogy: Adaptation, Diversity and Ecology*. WCB/McGraw-Hill.
- Ferreras, P., Beltrán, J.F., Aldama, J.J., Delibes, M., 1997. Social organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology* 243, 163–189.

- Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105, 1–41.
- Gonzalez, C.A.L., Miller, B.J., 2002. Do jaguars (*Panthera onca*) depend on large Prey? *Western North American Naturalist* 62, 218–222.
- Grassman, L.I., Tewes, M.E., Silvy, N.J., Kreetiyutanont, K., 2005. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in the north-central Thailand. *Journal of Zoology* 266, 45–54.
- Griffiths, D., 1975. Prey availability and the food of predators. *Ecology* 56, 1209–1214.
- Hidalgo-Mihart, M.G., Cantu-Salazar, L., Lopez-Gonzalez, C.A., Martinez-Meyer, E., Gonzalez-Romero, A., 2001. Coyote (*Canis latrans*) food habits in a tropical deciduous forest of Western Mexico. *American Midland Naturalist* 146, 210–216.
- Hooge, P.N., Eichenlaub, W., Solomon, E., 1999. The animal movement program. USGS. Alaska Biological Center.
- Huggard, D.J., 1993. Prey selectivity of wolves in Banff National Park. I. Prey species. *Canadian Journal of Zoology* 71, 130–139.
- Iriarte, J.A., Franklin, W.L., Johnson, W.E., Redford, K.H., 1990. Biogeographic variation of food habits and body size of the American puma. *Oecologia* 85, 185–190.
- Johnsingh, A.J.T., 1983. Prey selection in three large sympatric carnivores in Bandipur. *Mammalia* 56, 517–526.
- Karanth, K.U., Sunquist, M.E., 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. *Journal of Tropical Ecology* 8, 21–35.
- Karanth, K.U., Sunquist, M.E., 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64, 439–450.
- Karanth, K.U., Sunquist, M.E., 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology* 250, 255–265.
- Kenward, R.E., Marcstrom, V., Karlbom, M., 1993. Post nestling behaviour in Goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. *Animal Behaviour* 46, 371–378.
- Kernohan, B.J., Gitzen, R.A., Millsbaugh, J.J., 2001. Analysis of animal space use and movements. In: Millsbaugh, J.J., Marzluff, J.M. (Eds.), *Radio Tracking and Animal Populations*. Academic Press, pp. 125–166.
- Kissui, B.M., Packer, C., 2004. Top-down regulation of a top predator: lions in the Ngorongoro Crater. *Proceeding of the Royal Society B: Biological Sciences* 271, 1867–1874.
- Khan, J.A., Chellam, R., Rodgers, W.A., Johnsingh, A.J.T., 1996. Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujrat, India. *Journal of Tropical Ecology* 12, 149–162.
- Krebs, C.J., 1999. *Ecological Methodology*. Benjamin/Cummings, California.
- Kruuk, H., 1972. *The Spotted Hyena*. University of Chicago Press, Chicago.
- Laake, T.L., Strindberg, J.L., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., Marques, T.A., 2005. Distance 5.0 Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available from <<http://www.ruwpa.st-and.ac.uk/distance/>>.
- Levins, R., 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, New Jersey.
- Lindzey, F.G., Sickle, V., Ackerman, B.B., Barnhurst, D., Hemker, T.P., Laing, S.P., 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management* 58, 619–624.
- Link, W.A., Karanth, K.U., 1994. Correcting for overdispersion in tests of prey selectivity. *Ecology* 75, 2456–2459.
- Litvaitis, J.A., Sherburn, J.A., Bissonette, J.A., 1986. Bobcat habitat use and home range size in relation to prey density. *Journal of Wildlife Management* 50, 110–117.
- Logan, K.A., Sweanor, L.L., 2001. *Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore*. Island Press, Washington, DC.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *The American Naturalist* 100, 603–609.
- Macdonald, D.W., Ball, F.G., Hough, N.G., 1980. The evaluation of home range size and configuration using radio-tracking data. In: Amlaner, C.J., Jr., Macdonald, D.W. (Eds.), *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, Oxford, England, pp. 405–424.
- Maher, C.R., Lott, D.F., 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behavior* 49, 1581–1597.
- Maher, C.R., Lott, D.F., 2000. A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist* 143, 1–29.
- Mech, L.D., 1977. Wolf pack buffer zones as prey reservoirs. *Science* 198, 320–321.
- Neale, J.C.C., Sacks, B.N., 2001. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. *Canadian Journal of Zoology* 79, 1794–1800.
- Núñez, R., Miller, B., Lindzey, F., 2000. Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology* 252, 373–379.
- Packer, C., 1986. The ecology of sociality in felids. In: Rubenstein, D.I., Wrangham, R.W. (Eds.), *Ecological Aspects of Social Evolution*. Princeton University Press, Princeton, pp. 429–451.
- Peres, C.A., 1996. Population status of white-lipped and collared peccaries in hunted and nonhunted Amazonian forests. *Biological Conservation* 77, 115–123.
- Pierce, B.M., Bleich, V.C., Wehausen, J.D., Bowyer, R.T., 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy* 80, 986–992.
- Pierce, B.M., Bleich, V.C., Bowyer, R.T., 2000. Social organization of mountain lions: Does a Land-Tenure system regulate population size? *Ecology* 91, 1533–1543.
- Polisar, J., Maxit, I., Scognamillo, D., Farrel, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base and cattle ranching: ecological interpretations of a management problem. *Biological Conservation* 109, 297–310.
- Poole, K.G., 1995. Spatial organization of a lynx population. *Canadian Journal of Zoology* 73, 632–641.
- Quigley, H., 1987. *Ecology and conservation of the jaguar in the Pantanal region, Mato Grosso do Sul, Brazil*. Ph.D. Thesis, University of Idaho, Moscow, Idaho.
- Quigley, H., Crawshaw Jr., P.G., 1992. A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. *Biological Conservation* 61, 149–157.
- Rabinowitz, A.R., Nottingham, B.G., 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology* 210, 149–159.
- Robinson, J.G., Redford, K.H., 1986. Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. *Oecologia* 68, 516–520.
- Ross, P.J., Jalkotzy, M.G., 1992. Characteristics of a hunted population of cougars in Southwestern Alberta. *Journal of Wildlife Management* 56, 417–426.
- Samuel, M.D., Fuller, M.R., 1996. *Wildlife telemetry*. In: Bookhout, T.A. (Ed.), *Research and Management Techniques for Wildlife and Habitats*, fifth ed., revised. The Wildlife Society, Bethesda, MD, pp. 370–418.
- Sandell, M., 1989. The mating tactics and spacing patterns of solitary carnivores. In: Gittleman, J.L. (Ed.), *Carnivore*

- Behaviour, Ecology and Evolution. Chapman & Hall, London, pp. 164–182.
- SAS Institute, 1999. SAS/STAT User's Guide: Statistics. SAS Institute, Cary, North Carolina, USA.
- Schaller, G.B., 1972. The Serengeti Lion: A Study of Predator–Prey Relations. The University of Chicago Press, Chicago.
- Schaller, G.B., Crawshaw Jr., P.G., 1980. Movement patterns of jaguar. *Biotropica* 12, 161–168.
- Scognamillo, D.G., Maxit, I.E., Sunquist, M.S., Polisar, J., 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology* 259, 269–279.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63, 739–747.
- Seidensticker, J.C., Hornocker, M.G., Wiles, W.V., Messick, J.P., 1973. Mountain lion social organization in the Idaho primitive area. *Wildlife Monographs* 35, 1–60.
- Seidensticker, J.C., McDougal, C., 1993. Tiger predatory behaviour, ecology and conservation. *Symposium of the Zoological Society of London* 65, 105–125.
- Seymour, K.L., 1989. *Panthera onca*. *Mammalian Species* 340, 1–9.
- Soisalo, M.K., Cavalcanti, S.M.C., 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* 129, 487–496.
- Sunquist, M.E., 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithsonian Contributions to Zoology* 336, 1–98.
- Sunquist, M.E., Sunquist, F.C., 1989. Ecological constraints on predation by large felids. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology and Evolution*. Cornell University Press, New York, pp. 283–381.
- Taber, A.B., Novaro, A.J., Neris, N., Colman, N.N., 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* 29, 204–213.
- Varman, K.S., Sukumar, R., 1995. The line transect method for estimating densities of large mammals in a tropical deciduous forest: An evaluation of methods and field experiments. *Journal of Bioscience* 20, 273–287.
- Vos, J., 2000. Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *Journal of Zoology* 251, 457–462.
- Weaver, J.L., 1993. Refining the equation for interpreting prey occurrence in wolf scats. *Journal of Wildlife Management* 57, 534–538.
- Worton, B.J., 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59, 794–800.