

**PREDATION PATTERNS OF JAGUARS (*PANTHERA ONCA*) IN A
SEASONALLY FLOODED FOREST IN THE SOUTHERN REGION OF
PANTANAL, BRAZIL**

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AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Fernando Cesar Cascelli de Azevedo, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled “Predation Patterns of Jaguars (*Panthera onca*) in a Seasonally Flooded Forest in the Southern Region of Pantanal, Brazil,” has been reviewed in the final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Jaguar predation patterns and spatial organization were studied from 2003 to 2004 in a ranch/wildlife reserve located in the southern region of the Pantanal, Brazil. Through radio-tracking we found that jaguar home-range sizes were comparable between sexes and little overlap was observed between core areas. Jaguars relied mostly on mammalian prey species (61% of prey items and 77% of biomass) and selected large-sized prey species. The most common prey consumed were capybara (*Hydrochaeris hydrochaeris*) and caiman (*Caiman crocodilus*). We estimated the wild prey base was adequate to support the resident jaguar population and therefore that jaguars did not require a livestock subsidy to survive. Large prey species were considerably more likely to die from jaguars predation than from other causes, and predation was more likely to occur in jaguar home range core areas than in areas of home range overlap. Spacing patterns seemed to be influenced by a territorial system because regions of exclusiveness occurred for both sexes and predation was more likely in core areas.

Despite the appearance jaguars did not require a livestock subsidy, livestock depredation was one of the most important sources of carnivore-human conflict in the region. We examined patterns of livestock depredation by jaguars to assess the factors contributing to mortality risk. Interactions between jaguars and domestic cattle were examined by recording each death event for the entire ranch and estimating survival and mortality causes of livestock through daily visits to 15 allotments, comprising one third of all livestock holdings in the ranch. Predation mortality was less common than non-predation mortality, and survival in allotments was lower for calves. Forest was the only significant explanatory

variable found to explain cause of mortality, because predation increased as distance to forest declined. Cattle movement patterns and grouping behavior did not vary relative to the level of spatial overlap with jaguars. The overall effect of jaguars on cattle was low and cattle likely constitute an alternative prey killed opportunistically. However, despite the higher abundance of non-calves, our results indicate a preponderance of jaguar predation toward calves within a limited range of distance from forest, a pattern that may be explained through selection of substandard individuals.

The importance of food resources on the dynamics of carnivore populations was further investigated through the study of dietary breadth and overlap of sympatric small and medium-sized carnivores from a prairie habitat in central North America. We performed a stomach content analysis of carcasses salvaged as part of a predator control program in southern Saskatchewan, Canada (2000-2001). American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) consumed a total of 25 separate food items. Dietary breadth varied among the 5 carnivore species, and was narrowest for raccoons and widest for skunks. Overall, dietary overlap tended to be highest for species pairings associated with the highest level of presumed niche similarity, which included raccoon-skunk and coyote-fox dyads. The assessment of a larger assemblage of carnivores within a North American prairie community showed that marked interspecific and temporal variation in dietary breadth and overlap may characterize a guild of sympatric species occupying similar habitat.

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DEDICATION

This dissertation is dedicated to my parents and family.

'And to man He said: Behold, the fear of the Lord is wisdom; and avoiding evil is understanding'.

Job 28, 28.

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PREFACE

This dissertation is divided into four chapters and written in the form of three manuscripts intended for submission to peer-reviewed journals or already accepted for publication. The first chapter provides a brief description of the major objectives and general approaches of each one of the following chapters. Chapter II, entitled “Spatial Organization and Food Habits of Jaguars in a Floodplain Forest” examines the importance of prey species availability and size on the spatial distribution of jaguars. Chapter III, “Evaluation of Potential Factors Predisposing Livestock to Predation by Jaguars” examines patterns of livestock depredation by jaguars to assess the main factors contributing to mortality risk. Chapters II and III were part of an extensive field study investigating predation patterns of jaguars in the Pantanal region of Brazil, and comprised the bulk of my doctoral research. The fourth chapter, “Dietary Overlap Among Five Sympatric Prairie Carnivores” examines resource partitioning in a community of five sympatric prairie carnivores in an effort to determine the patterns of diet overlap and niche breadth among prairie carnivores. This chapter has been accepted and published in the *Journal of Zoology, London*. 2006 (269: 127 – 135) and was part of a study developed at the University of Idaho, USA, during my first two years as a Ph.D. student at the Department of Fish and Wildlife Resources. The common theme through the three empirical chapters is an assessment of prey selection and food habits in carnivores. The chapters comprising this dissertation are part of a cooperative research and co-authors names are listed at the beginning of each chapter.

CHAPTER 1

General Introduction

The spatial organization of carnivore species has been intrinsically related to the availability of resources (Litvaitis et al. 1986, Kissui and Packer 2004). When carnivores exclude conspecifics from areas containing key resources and defend those areas, territorial behavior is manifested (Maher and Lott 2000). For most populations of large solitary felids, territoriality has been described as the regulating social system (Lindzey et al. 1994, Pierce et al. 1999, Adams 2001), yet the paucity of information on spatial dynamics of jaguar populations is a major obstacle to understanding the influence of food availability on patterns of space use and, extension, social tolerance for conspecifics. To evaluate the spatial organization and use of food resources in a population of jaguars, I conducted a two-year study (2003-4) in the world's largest naturally-flooded environment, the Pantanal region of Brazil, where populations of jaguars still persist in relatively high numbers. The study was conducted in a working 150 km² cattle ranch/wildlife reserve, located in the southern region of the Pantanal. Through monitoring of collared jaguars, estimation of prey densities, and examination of prey carcasses and jaguar scats, jaguar spatial interactions and prey selection patterns were evaluated to determine the importance of territoriality in the dynamics of the studied population. This study comprises Chapter II of the dissertation.

In the Pantanal region of Brazil, the annual flooding regime and the availability of large prey species including cattle have been described as factors affecting home range size and selection of prey by jaguars (Schaller 1980, Crawshaw and Quigley 1991). Rudimentary cattle management and close proximity with jaguars contribute to high levels of jaguar

predation on livestock, which recently has become an important source of carnivore-human conflict in the Pantanal. Historically, the consequences of this conflict, such as human persecution and direct killing, constituted the main source of jaguar decline in the region (Quigley and Crawshaw 1992). The assessment of factors causing direct livestock depredation and potential sublethal effects of predation on livestock therefore should be vital for understanding the impact of jaguars on livestock, and thus contribute to minimizing their decline through the implementation of management strategies. In order to assess the main factors contributing to mortality risk of domestic cattle, I examined the patterns of livestock depredation by monitoring cattle survival and evaluating how predator space use affected mortality risk. I also measured livestock behavioral responses to predation risk. This study comprises Chapter III of the dissertation.

The structure and function of ecological communities is influenced by patterns of resource use. Sympatric species occupying a common trophic level tend to exhibit niche differentiation and partitioning of resources (Pianka 1969; Schoener 1974, 1986). A clear deficiency of most studies investigating the importance of food resources for carnivore populations is the lack of community-level analysis involving more than two or three species. In order to better understand the structure of a community of carnivores and the role of carnivores, a collaborative study was conducted from 2000 to 2002 as part of a predator control program in southern Saskatchewan, Canada. Through stomach content analysis, the dietary breadth and overlap of sympatric American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) were determined. Differences in diet preference and whether species with similar ecological niches showed greater dietary overlap were examined. This study comprises Chapter IV of the dissertation.

CHAPTER 2

Spatial Organization and Food Habits of Jaguars in a Floodplain Forest

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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 a seasonally-flooded environment in the southern region of 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. Through radio-tracking of 8 jaguars, 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 food for jaguars, and scat analysis indicated that jaguars relied mostly on large mammalian prey (61% of prey items and 77% of biomass, including livestock). Of the 114 prey carcasses found to have been killed by jaguars, the most common wild species were capybara (*Hydrochaeris hydrochaeris*) followed by caiman (*Caiman crocodilus*). We estimated that the wild prey base was adequate to support the jaguar population even in the absence of livestock, implying that modest cattle depredation rates had little demographic importance to the local jaguar population. This point logically follows the observation that larger prey species were considerably more likely to die from predation than from other causes, and that predation was more likely to occur in jaguar core areas than in areas of home range overlap. We conclude that spacing patterns in the local jaguar population were likely based on exclusion through territoriality rather than food limitation.

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 populations 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 territorial due to their exclusive use of areas inferred by low degrees of overlap (i.g., less than 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 2004, Benson et al. 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, Farrel 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, González 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 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 (less than 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.

METHODS

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-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.

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, U.S.A. and Telonics, Inc., Mesa, AZ, U.S.A). Radio-collared animals were monitored during March 2003-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 hours 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 8 collared jaguars (five females and three males) after excluding locations with error and animals with less than 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.

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 randomly throughout the study area. 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 abundance in

drier areas. Transects were visited from 06:00 to 10:00 am daily ($n = 12$) on 140 different occasions (total of 214 km), and using vehicles with spotlights from 07:00 to 09:00 pm at night ($n = 6$) on 57 occasions (total of 1845 km). Transects were conducted along established trails and abandoned roads covering 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. Density of caiman (*Caiman crocodilus*) 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.

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 1993, 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 (Núñez et al. 2000, Scognamillo et al. 2003). Scats were dried at 72°C for 24 hours 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).

Data analysis

Home range

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 two 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.

Interactions

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, $\{Sc = (De - Do)/De + Do\}$. Positive and negative values indicate attraction and repulsion of two individuals, respectively. Independent movement is indicated by 0 values.

Prey density and biomass estimates

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 five 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, unpubl. data).

Jaguar diet

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 $Y = 1.98 + 0.035 X$, where Y is 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 $B = 1 / \sum p_j^2$, where B = Levin's measure of niche breadth; p_j = 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 = Levin's standardized niche breadth; B = Levin's measure of niche breadth; n = 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.

Jaguar prey consumption

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 (3 adult resident and 1 adult transient male; 5 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 six 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).

Determinants of wild prey mortality

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: > 15kg; medium/small prey: < 15kg). 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 chi-square 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 chi-square analysis to further test the hypothesis of jaguar non-selective behavior towards larger prey species.

Jaguar prey selectivity

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 chi-square 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.

RESULTS

Home ranges

Eleven adult jaguars were captured and body mass averaged 61.5 ± 6.2 kg (\pm S.D.) ($n = 5$) 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 5 female and 3 male 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 II-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 II-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 II-2). Strong

intersexual attraction was observed for three of fifteen intersexual pairs of jaguars (Table II-2).

Prey density estimates and biomass

Estimates of densities of ten potential wild prey species for jaguars are described in Table II-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 species, constituting 49% of all 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 9,634 kg (95% C.I. 8,524 – 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.

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 6 out of 8 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 II-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 II-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 II-4). The percentage of livestock kills was probably overestimated because of higher detectability of livestock over wild prey species.

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 II-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 subject 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).

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 II-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 ($P < 0.001$).

DISCUSSION

Home ranges and interactions

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 intrasexual 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 intrasexual 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). Since 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 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 seem 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.

Prey density estimates and jaguar consumption

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 less than 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). This result suggests the wild prey base was sufficient to sustain the population herein studied. In addition, our results indicate that resident jaguars did not require a livestock subsidy (Polis et al. 2003, Scognamillo et al. 2003).

Determinants of wild prey mortality

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 MacDougal 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 less than 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.

Jaguar prey selectivity

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 is 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). Thus, the fact that capybara and marsh deer were primary prey most supports the contention of prey selection in this jaguar population. Similar results reported for predation of capybara by jaguars in similar environment further substantiated the argument of selective behavior (Scognamillo et al. 2003). 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 (Scognamillo et al. 2003). Therefore, although jaguars consumed a high variety of prey, specialization toward certain species occurred, thus not supporting the prediction of non-selective predation pattern.

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 locations and use for periods beyond two years prevent further conclusions that possible transient jaguars could become permanent members of the population through displacement of resident individuals

or occupancy of vacant territories. 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 the complete understanding of the predator-prey relationship and its consequences on the shaping of spacing patterns of the jaguar population herein studied.

LITERATURE CITED

- Ackerman, B.B., Lindzey, F.G. and 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. *Ann. Rev. Ecol. Syst.* 32:277-303.
- Benson, J.F., Chamberlain, M.J., and Leopold, B.D. 2004. Land tenure and occupation of vacant home ranges by bobcats (*Lynx Rufus*). *Journal of Mammalogy* 85: 983-988.
- _____, Chamberlain, M.J., and Leopold, B.D. 2006. Regulation of space use in a solitary felid: population density or prey availability?
- Biswas, S., and 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., and Lake, J.L. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London.
- _____, Anderson, D.R., Burnham, K.P., Lake, J.L., Borchers, D.L., and Thomas, L. 2001. Introduction to Distance Sampling: estimating abundance of biological populations. Oxford University Press.
- Burnham, K.P., Anderson, A.R., and Laake, J.L. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, 72: 1- 202.
- _____, and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, NY, USA.
- Crawshaw, P.G., Jr., and Quigley, H. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology* 223:357-370.

- _____. 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, FL: 195 pp.
- Dubs, B. 1994. Differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. PhD 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. *Behav. Ecol. Sociobiol.* 20: 271-283.
- Environmental Systems Research Institute (ESRI). 2000. Arcview, version 3.2. ESRI, Redlands, California, USA.
- Farrell, L., Roman, J., and 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., and Merritt, J.F. 1999. *Mammalogy: adaption, diversity and Ecology*. WCB/McGraw-Hill.
- Ferreras, P., Beltrán, J.F., Aldama, J.J., and 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., and Miller, B.J. 2002. Do jaguars (*Panthera onca*) depend on large Prey?
- Grassman, L.I., Tewes, M.E., Silvy, N.J., and 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., and 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., and 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., and 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., and Sunquist, M.E. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. *Journal of Tropical Ecology* 8: 21-35.
- _____, and Sunquist, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64: 439-450.
- _____, and Sunquist, M.E. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. *Journal of Zoology* 250: 255-265.
- Kenward, R.E., Marcstrom, V., and Karlbom, M. 1993. Post nestling behavioru in Goshawks, *Accipiter gentiles*:II. Sex differences in sociality and nest-switching. *Animal Behaviour* 46:371-378.

- Kernohan, B.J., Gitzen, R.A., and Millspaugh, J.J. 2001. Analysis of animal space use and movements. In: Radio tracking and animal populations: 125-166. Millspaugh, J.J. and Marzluff, J.M.(Eds.). Academic Press.
- Kissui, B.M., and Packer, C. 2004. Top-down regulation of a top predator: lions in the Ngorongoro Crater. *Proc. Roy. Soc. Series B.* 271, 1867-1874.
- Khan, J.A., Chellam, R., Rodgers, W.A., and 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., and Marques, T.A. 2005. Distance 5.0 Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <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., and Laing, S.P. 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management* 58: 619-624.
- Link, W.A., and Karanth, K.U. 1994. Correcting for overdispersion in tests of prey selectivity. *Ecology* 75: 2456-2459.

- Litvaitis, J.A., Sherburn, J.A., and 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., and Sweanor, L.L. 2001. *Desert Puma: Evolutionary ecology and conservation of an enduring carnivore*. Washington, D.C. Island Press.
- MacArthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603-609.
- Macdonald, D.W., Ball, F.G., and Hough, N.G. 1980. The evaluation of home range size and configuration using radio-tracking data. In: *A handbook on biotelemetry and radio tracking*. Amlaner C. J. Jr, Macdonald, D.W (Eds.). Pergamon Press, Oxford, England.
- Maher, C.R., and Lott, D.F. 2000. A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist* 143:1-29.
- Neale, J. C. C., and 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., and 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: *Ecological aspects of Social Evolution*: 429-451. Rubenstein, D.I., and Wrangham, R.W. (Eds.). Princeton: Princeton Univ. Press.
- 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., and Bowyer, R.T. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy* 80:986-992.

- ____, Bleich, V.C., and 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., and 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. PhD thesis, University of Idaho, Moscow, Idaho.
- Rabinowitz, A.R., and 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., and 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., and Jalkotzy, M.G. 1992. Characteristics of a hunted population of cougars in Southwestern Alberta. *Journal of Wildlife Management* 56: 417-426.
- Samuel, M.D., and 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: *Carnivore behaviour, ecology and evolution*: 164-182. Gittleman, J.L. (Ed.). London: Chapman and Hall.
- 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.
- _____, and Crawshaw, P.G. Jr. 1980. Movement patterns of jaguar. *Biotropica* 12: 161-168.
- Scognamillo, D.G. 2001. Ecological separation between jaguar and puma in a mosaic landscape in the Venezuelan Llanos. MS thesis, University of Florida, Gainesville.
- _____, Maxit, I.E., Sunquist, M.S., and 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., and 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., and Messick, J.P. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildl. Monogr.* 35:1-60.
- _____, and McDougal, C. 1993. Tiger predatory behaviour, ecology and conservation. *Symposia of the Zoological Society of London*, 65:105-125.
- Seymour, K.L. 1989. *Panthera onca*. *Mammalian Species* 340: 1-9.
- Sunquist, M.E. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithsonian Contributions to Zoology* 336: 1-98.
- _____, and Sunquist, F.C. 1989. Ecological Constraints on predation by large felids. In: *Carnivore behavior, ecology and evolution*. 283-381. Gittleman, J.L. (Ed.) Cornell University Press, NY, USA.
- Swank, W.G., and Teer, J.G. 1989. Status of the jaguar-1987. *Oryx* 23: 14-21.

- Taber, A.B., Novaro, A.J., Neris, N., and Colman, N.N. 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* 29: 204-213.
- Varman, K.S., and 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.

Table II-1. Mean home-range sizes (km²) using 95% and 50% Fixed Kernel (FK) contours and 95% mean percent home-range overlap at 95 and 50% FK (\pm SD) levels are reported.

Sex	n	FK 95%	FK 50%	<u>Overlap within sex</u>		<u>Overlap between sexes</u>		Metabolic Range Size
		(Mean \pm SD)	(Mean \pm SD)	95% FK	50% FK	95% FK	50% FK	(Mean \pm SD)
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)	56.28 (5.57)
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)	36.18 (2.28)

Table II-2. Percent coefficient of overlap at 95% and 50% Fixed Kernel contours and coefficient of sociality (Sc) for jaguar pairs with adjacent or overlapping home ranges.

Type of interaction	Jaguar pairs	95% FK	50% FK	Sc (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	0.00 (18)
	M02 – F03	0.00	0.00	0.00 (10)
	M03 – F04	0.00	0.00	0.09 (14)

Table II-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	1,330.00	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	5,325.00	35.50
<i>Tapirus terrestris</i>	Tapir	0.15 ± 0.04	29.37	0.08-0.27	177.0	3,955.95	26.37
<i>Caiman crocodilus</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

Table II-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 - 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>Dasybus 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 crocodilus</i>	6.4	20.2	19.3	15.5
	Livestock	11.2	28.1	0.0	19.4

Table II-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. 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.

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

Table II-6. Results of prey selectivity test from scat data. ‘Scat freq’ denotes the observed number of scats related to each of the ten 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_i statistics based on 1000 bootstrap replicates with correction for overdispersion.

	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_i 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
$SD(\lambda_i)$	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

^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 crocodilus*); 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).

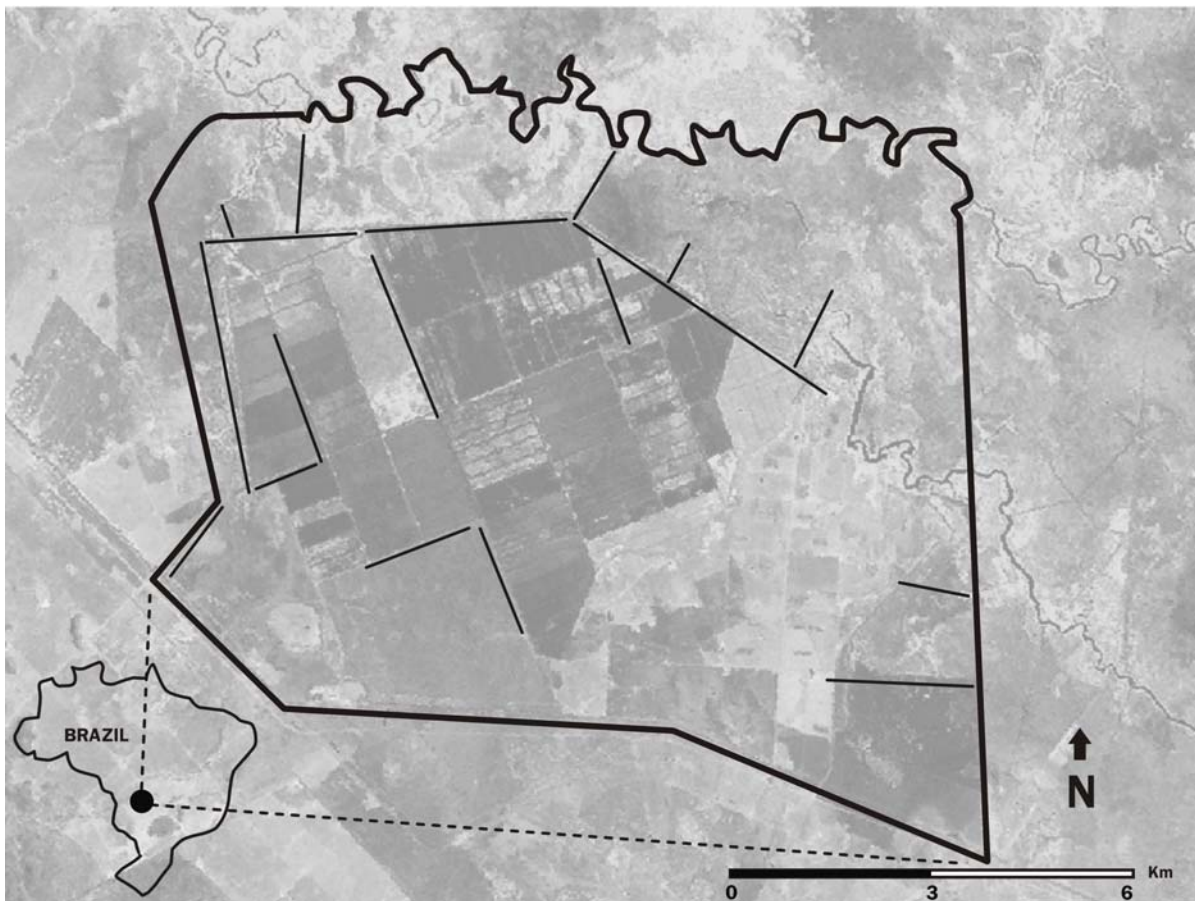


Figure II-1. Study site and line transects ($n = 18$) surveyed during 2003- 2004 within San Francisco ranch, Brazil

CHAPTER 3**Evaluation of Potential Factors Predisposing Livestock to Predation by
Jaguars (*Panthera onca*)**

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ABSTRACT

Depredation of livestock by large carnivores is one of the most important sources of human-carnivore conflicts. Livestock depredation rates may vary considerably depending on environmental and socio-ecological factors. However, predators may also impose sublethal effects through increased perceived predation risk. We examined patterns of livestock depredation by jaguars (*Panthera onca*) to assess the factors contributing to prey mortality risk. We predicted jaguars would kill a greater proportion of calves and that proximity to suitable habitat would increase mortality rates. We further inferred that exposure to predation risk would promote livestock grouping and increased movement distances. Interactions between jaguars and domestic cattle in a ranch/wildlife reserve were examined by recording each death event for the entire ranch. We estimated survival and mortality causes of livestock through daily visits to 15 allotments, representing one third of all livestock holdings in the ranch. Overall, we recorded 169 cattle mortality incidents, with predation (19%) being less common than other sources of mortality (81%). Jaguars and pumas (*Puma concolor*) killed a total of 32 cattle, which represented 0.2% and 0.3% of the total livestock holdings for 2003 and 2004, respectively. Jaguars were responsible for most (68.8%) of cattle predation events, and survival in allotments was lower for calves than other age classes. Forest was the only variable found to explain patterns of livestock mortality, with predation risk increasing as distance to forest declined. Due to low predation risk, cattle movement patterns and grouping behavior did not vary relative to the level of spatial overlap with jaguars. The overall effect of jaguars on cattle was low and cattle likely constitute an alternative prey, killed opportunistically. However, despite the higher abundance of non-calves, our results indicate

jaguar prey selection toward calves within a limited range of distance from forest, a pattern that may be explained through selection of substandard individuals.

INTRODUCTION

Conflict with humans is arguably the primary proximate cause of mortality and population decline among many large carnivore species (Woodroffe and Ginsberg 1998). Declines in most large carnivore populations contrast with recent dramatic increases in human populations and associated anthropogenic effects in areas where humans and large carnivores co-occur (Woodroffe 2000, Treves and Karanth 2003). Consequent to human encroachment, large carnivores can face habitat destruction and alteration, decline of natural prey, exotic disease, and direct exploitation (Woodroffe 2001, Graham et al. 2005, Kolowski and Holekamp 2006). In addition, actual or perceived threat to humans and their livestock can lead to active persecution of carnivores by humans and constitutes the most significant factor in causing decline of many large carnivore populations worldwide (Woodroffe, 2001, Kolowski and Holekamp 2006). Indeed, global livestock depredation by large carnivores is one the most important sources of human-carnivore conflicts (Linnell et al. 1999, Mazzoli et al. 2002, Graham et al. 2005).

Rates of depredation of livestock by large carnivores vary considerably, depending on environmental and socio-ecological factors (Kolowski and Holekamp 2006). For instance, abundance and distribution of natural prey, habitat characteristics, and husbandry practices may increase vulnerability of livestock and thus influence depredation by large carnivores (Meriggi and Lovari 1996, Mizutani 1999, Mech et al. 2000, Ogada et al. 2003, Polisar et al., 2003, Kolowski and Holekamp 2006). In theory, under opportunistic predation, species that

are attacked less than in proportion to their abundance should not show anti-predator responses and thus be more vulnerable to predators (Fernández-Juricic et al. 2004). Vulnerability should be more pronounced on substandard individuals (for instance the young, sick, weak, small, aged) because they are conspicuous and less able to escape or repel predators (Lima and Dill 1990, Curio 1993). It follows that, predators should take a disproportionate number of substandard individuals of a particular prey species, for instance calves, when individuals of that species are more difficult to capture and kill (Temple 1987). However, predators may also impose sublethal effects through increased perceived predation risk. Indeed, when carnivores harass, chase, or otherwise stress prospective prey by their presence or activities, general changes in prey social behavior, feeding or movement patterns may be expected (Boonstra et al. 1998, Berger et al. 2001, Creel et al. 2005). Clearly, the assessment of potential sublethal effects of predation on livestock, concurrent with the study of the factors causing direct livestock depredation, are important for understanding the full impact of large carnivores on livestock.

The jaguar (*Panthera onca*) is the largest felid occupying the Americas. In recent decades, extensive fragmentation of jaguar habitat and the expansion of human activities into such areas has increased jaguar depredation on livestock and thus conflict with humans (Rabinowitz and Nottingham 1986, Weber and Rabinowitz 1996). However, there has been limited assessment of the magnitude of jaguar use of livestock as prey, or factors predisposing livestock to depredation by jaguars. With wild ungulate prey, factors such as habitat type, prey abundance and relative vulnerability due to age, gender, or body condition are important determinants (Ramakrishnan et al. 1999, Husseman et al. 2003, White and Garrott 2005). For instance, the demonstrated preference by jaguars for forested habitats in close association with standing water is attributed to increased prey vulnerability to predation

in such habitats (Crawshaw and Quigley 1991, Quigley and Crawshaw 1992). Alternatively, jaguars may simply select the largest available prey type, irrespective of the availability of specific habitat types (Scognamillo et al. 2003). Similar patterns may apply to jaguar selection of domestic prey. Inappropriate husbandry practices and wild prey availability and vulnerability, are factors reported to influence vulnerability of livestock to depredation by jaguars, particularly among calves (Quigley and Crawshaw 1992, Hoogesteijn et al. 1993, Polisar et al. 2003). It follows that the development of general models of livestock predation by jaguars will remain incomplete in the absence of more detailed empirical work examining how the above factors affect livestock vulnerability to predation.

In the present study, we examined patterns of livestock depredation by jaguars to assess the main factors contributing to mortality risk. Specifically, jaguar-livestock interactions were assessed by monitoring survival of domestic cattle and evaluating how predator space use affected mortality risk as well as by measuring livestock behavioral responses to predation risk. Consistent with the hypothesis that close contact with jaguars within suitable habitat favors increased, albeit non-random, depredation, we predicted: (i) jaguars would kill a greater proportion of livestock calves relative to yearlings and adult cattle; and (ii) proximity to suitable habitat, such as forest and permanent water sources, would increase overall mortality rates. Furthermore, we speculated increased exposure to predation risk would promote livestock grouping and increase movement distances.

METHODS

Study area

The study was undertaken in the southern part of the Pantanal region of the Mato Grosso do Sul state in Brazil from February 2003 to December 2004. The Pantanal is a floodplain covering approximately 140,000 km² of land in Brazil, on the borders of Bolivia and Paraguay. The Pantanal is characterized by an annual regime of flooding and low land relief. The landscape in the region is characterized by a mosaic of rivers, ponds, swamps, seasonally inundated grasslands and woodlands, and non-flooding forests. The study site is a 150 km² cattle ranch/wildlife reserve, San Francisco ranch, located in the southern region of the state (20° 05' S and 56° 36' W). 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, the cerradão, constituting a one-storey forest with trees such as the ipê (*Tabebuia sp.*) lacking clear vertical stratification and a grass understorey that is flooded during wet season; 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 rain falling between April and October.

The ranch has approximately 5,000 head of cattle that include mainly *Bos indicus* cebú race (nelore) and the breed Montana. Cattle are kept in fenced allotments in elevated areas of permanent pastures and routinely rotated between allotments to avoid overgrazing. Vegetation inside allotments is mostly comprised of introduced grass species with few patches of semi-deciduous forests left inside allotments to provide shade. After the rice season (February-June), part of the herd is left to feed on rice fields. In addition, some lowland areas of cerradão are used for livestock grazing during the dry season. Calving

period occurs from September to December. Data on livestock causes of death at the ranch have been recorded between 1991- 2002, with annual depredation by large felids (jaguar and puma *Puma concolor*) estimated at 11% (n = 667) of all livestock mortality (San Francisco ranch 2004). In relation to total livestock holdings for the period (n = 56,408 head; mean = $4,700 \pm 495.39$ (\pm SD) head per year) the average annual rate of livestock depredation by cats in the ranch was $0.13 \pm 0.11\%$ and death by other causes (e.g. accident, snake, disease, parturition problems, flood and unknown natural causes) was $1.06 \pm 0.25\%$ (San Francisco ranch 2004).

Sampling

During March 2003-October 2004, we captured 11 jaguars (five females and six males) and three pumas (two females and one male) and fitted them with radio-collars. Eight jaguars (five females and three males) were deemed to be residents based on their long-term occupation of the study area, the female pumas had territories adjacent to the intensive study area, whereas the male puma was never relocated post-capture and thus was a transient. In addition, 1-2 transient pumas and two young uncollared jaguars were also known to be present on the study area. Thus, in our study we monitored 8 collared jaguars in the context of predation on livestock. Note that, although predation incidents attributed to transient pumas were recorded during the study, for all analysis of space use we included only data on collared jaguars. Jaguars were monitored every 3-4 days via ground telemetry, as well as weekly via aerial telemetry. Ninety-five percent and 50% kernel home range sizes were calculated using the Animal Movement Extension in the program ARCVIEW GIS 3.2 (Hooge et al. 1999, ESRI® 2000), using least squares cross validation (Worton 1995). This allowed

us to determine home and core areas, respectively. Only home ranges that were found to reach an asymptote at a minimum of 30 locations were included in our analysis. Accuracy of ground and aerial telemetry was determined by location by 'blind' observation of transmitters placed throughout the study area; mean error associated with aerial telemetry was 131 ± 47 meters ($n = 10$) and from the ground was 206 ± 168 meters ($n = 10$).

To survey depredation events or other mortality, we recorded each death event for the entire ranch during 2003-4. In order to estimate survival and mortality causes of livestock we conducted daily visits of 15 allotments where animals had been held intensively for most of year 2004. These allotments contained one third of all livestock holdings in the ranch (approximately 2000 head), and comprised an area of 7.24 square kilometers, with individual allotments averaging 0.72 ± 0.46 km². Allotments were adjacent to each other and separated by wire fences. The distance of allotment fences to permanent forest averaged 211 ± 371 meters ($n = 15$; \pm SD). Allotments contained roughly similar amounts of patches of forest. Each allotment contained a herd comprised of a single age/sex class, and a total of 12 age/sex classes herds were rotated among allotments. Three different classes of herds separated by sexes were studied: weaned calves from 6 – 12 months, yearlings from 13 to 24 months, and adult animals older than 25 months. During the study, all dead cattle were recovered within 48 hours of death, with the exception of one newborn calf in 2004. For the purpose of our survival analysis, each cattle herd (or allotment) was considered the experimental unit, and herds were observed during several time intervals of unequal lengths. Therefore, for each herd we recorded information on time in the allotment (days), survival status (number of deaths), and habitat type where the herd was located (pasture, cerradão, rice field).

Livestock found dead were necropsied and we collected information on gender, age, and precise location using a GPS unit; GPS locations were later used to estimate proximity to nearest forest and water source, and habitat type. Predation by cats was determined if ≥ 2 of the following were observed: signs of bites on carcasses of cattle, the presence of tracks and scats near kill sites, or signs of a trail where the prey had been carried or dragged. In order to determine cause of death for non-predation mortality, a veterinarian at the ranch examined animals within 2 days of recovery. Because it was not always possible to perform necropsies on carcasses, we classified mortalities into 2 proximate causes: cat predation (jaguar and puma), and other (accident, snake, disease, poison, parturition problems, flood and unknown natural causes). Previous field observations of cattle moving and staying away from the interface between allotment fences and permanent forest up to five days after a jaguar attack (Azevedo, pers. obs.) suggested potential influence of predation risk by jaguars on cattle movement and gregarious behavior. Thus, to evaluate cattle location relative to known locations among collared cats, each cattle herd was located weekly inside each allotment within 2 days after collared cats had been located. We determined cattle locations based on the position of the majority of the herd using a GPS unit. For each cattle location, information on habitat type, grouping behavior (grouped or ungrouped) and size of allotment were recorded.

Data analysis

Predation impact

To assess the impact of predation for the entire ranch, we compared the frequency of predation to non-predation incidents using a chi-square goodness of fit test, including all

events of mortality recorded during 2003-04. To assess predator selectivity for cattle for the entire ranch, including allotments not visited daily by research personnel, we performed a chi-square goodness of fit test, using each predation event during 2003-04 as the experimental unit. We investigated whether the recorded frequency of predation on different livestock age-classes deviated significantly from their known availability. We also investigated whether livestock depredation varied between jaguars and pumas. For these analyses, cattle were divided into four age class groups not separated by sexes: (i) calves < 4 months; (ii) calves 4-12 months; (iii) yearlings 13-24 months; and (iv) adults >24 months. Expected numbers of livestock were based on the known number and age distribution of cattle within the entire ranch. All analyses of predation impact were considered statistically significant when $p < 0.05$ and probability levels were two-tailed.

Survival

Survival and cause-specific mortality rates of cattle within allotments were estimated based on two main assumptions: 1) within each interval daily survival and age-specific mortality rates were constant; 2) all animals within an age/sex-class had the same probability of survival and mortality (Heisey and Fuller 1985). We recorded cattle survival for a cumulative total of 9,200 animals (213.1 ± 71.0 cattle per allotment). We calculated annual survival and cause-specific mortality rates for each cattle age-class using program MICROMORT (Heisey and Fuller 1985). Tracking days were defined as the total number of tagged animals within each allotment multiplied by the number of days of observation of each time interval. Unless otherwise noted, estimates of survival rates are accompanied by 95% confidence intervals. Note that cattle of different ages and genders were kept in different

allotments at different times, therefore potentially influencing predation risk exposure among groups. However, given that all allotments were located in the same general vicinity, we assumed that cattle were exposed to essentially the same predator cohort and thus that differences in mortality patterns between groups were reflective of differential predation risk.

In order to assess relationships between survival and selected explanatory variables, models of cattle mortality were generated using Poisson regression (Zar 1999, Proc Genmod: SAS Institute 1999). Using this procedure, the dependent variable is a rate and a Poisson distribution is the basis for statistical inference (Selvin 1995). We evaluated the relationship between daily predation rate and independent variables including age class and sex. In our predation risk models, the dependent variable was calculated from observations of cattle inside each allotment during different time intervals; thus each sample unit in our regression analysis was the number of deaths offset by the number of tracking days for each cattle herd during the interval. The parameters of each model were estimated using maximum likelihoods, and the fit of regression models was compared using Akaike's Information Criterion with small-sample correction (AIC_C) (Anderson et al. 2000). In addition we described the influence of variables on predation rates using rate ratios (rate ratio = $e^{\text{coefficient}}$) representing the ratio of predation rates as a function of variation in independent variables (Hosmer and Lemeshow 2000).

Vulnerability to predation

We used logistic regression to investigate the importance of habitat factors such as water courses and forest patches on cattle mortality risk. Cause of mortality (predation vs. other causes) was used as dependent variable. Distance of locations of cattle dead in relation to nearest forest and water courses were compared. To assess to what extent proximity to

suitable habitat affected livestock vulnerability to predation, we performed a series of simple correlation analyses using distance of locations of depredated cattle versus nearest forest and water sources. For comparison, we also examined the similar relationship with cattle dead from other causes. Data were tested for normality using the Kolmogorov-Smirnov test for goodness of fit (Dytham 2003). When variances were comparable, we used *t*-tests, otherwise non-parametric Mann-Whitney tests were used.

Space use

To describe spatial distribution of livestock relative to collared cats, cattle locations were used to construct home ranges (95% fixed kernel – FK) and core use areas (50% FK), using the animal movement extension in program ARCVIEW GIS 3.2 (Hooge et al. 1999, ESRI® 2000). For this analysis, locations of separate allotments were pooled. Jaguar home ranges for the entire period of study were transposed onto a grid (Fixed Kernel) and specific levels of utilization were assigned to each area within the home range (Roloff et al. 2001, Oakleaf et al. 2003). We then overlaid cattle locations and determined levels of overlap to infer potential jaguar predation risk at each cattle location. To determine cattle movement patterns and grouping behavior in relation to jaguar home range areas, livestock locations at various predation risk levels were assessed (Oakleaf et al. 2003). Predation risk was assumed to increase with proximity to core jaguar use areas.

Cattle gregarious behavior and movement

We used logistic regression (Hosmer and Lemeshow 2000) to identify factors influencing cattle grouping behavior relative to proximity to jaguars. Grouping behavior (grouped, ungrouped) was the dependent variable, with cattle considered as being grouped

whenever the majority of animals from a herd were located moving or standing in close (i.e., <2 m) proximity during visual observations. Each observation trial lasted a minimum of thirty minutes, and because food resources inside each allotment were equally spaced we assumed that grouping was a response to increased perceived predation risk (Hebblewhite and Pletscher 2002). As independent variables we used habitat type (categorical variables: open areas (pastures and rice fields) versus closed woodland (cerradão)) and jaguar use level (categorical variable: no jaguar use, 1 – 50 % Fixed Kernel use, 51 – 80% FK; 81 – 95% FK).

Cattle movement in relation to proximity to jaguars was analyzed using linear regression, with cattle daily movement distance as the dependent variable. Independent variables included days between locations, jaguar use level (continuous variable, 1 – 100% FK) at the initial cattle location, jaguar use level at the final cattle location, and the amount of jaguar use change between locations (continuous variable, 1 -100% FK; Oakleaf et al. 2003). Models for cattle grouping and movement were selected using Akaike's Information Criterion (AICc). The relative strength of each model was assessed through the use of Akaike's weights (w_i) and the change in AIC between models (ΔAIC) (Burnham and Anderson 1998, Anderson et al. 2000). We did not include interaction terms in our models because we wanted to limit the number of models under examination and because interactions between variables were not presumed a priori (Anderson et al. 2000).

RESULTS

Predation and cattle populations

For the entire study period and total ranch area, we recorded 169 cattle mortality incidents. Predation mortality was less common than non-predation mortality ($\chi^2 = 8.91$, $df =$

3, $P = 0.03$). Jaguars and pumas killed a total of 32 cattle, which represented 0.2% and 0.3% of the total livestock holdings for 2003 and 2004 respectively. Mortality due to other causes represented 0.7% and 1.5% of total livestock holding for each year of study, respectively. Depredation by cats represented 18.9% of all causes of livestock death. Based on the number of cattle killed by cats during period of study, livestock depredation rates differed significantly between jaguars and pumas ($\chi^2 = 11.73$, $df = 3$, $P < 0.01$), with jaguars being responsible for most 68.8% ($n = 22$) cattle predation. While jaguars preyed upon all cattle age-classes, pumas selected only calves aged <12 months. Among all cattle killed by cats, selectivity was observed towards the two younger cattle age classes ($\chi^2 = 40.01$, $df = 3$, $P < 0.001$); cattle that were older than 12 months were preyed less than expected (Table III-1).

Survival

We recorded cattle survival during 43 different time intervals (40.4 ± 47.4 (\pm SD) days per interval). The annual survival rate was 0.86 (0.80 – 0.93; 95% CI), 0.97 (0.94 – 0.99) and 0.96 (0.94 – 0.99), for calves, yearlings and adults, respectively. We recorded 34 cattle deaths inside the 15 allotments, representing 20.1% of all cases of mortality on the ranch during the study period (2003-4). We found that 8 deaths (23.5%) were due to predation, with jaguars being proximally responsible for most kills ($n = 7$), and puma the additional kill. For all three age classes, mortality rates due to non-predation causes were higher than due to depredation by cats (Table III-2). The predation risk model that best explained patterns of cattle mortality due to predation included only the variable for age class, and model-averaged coefficient estimate and unconditional standard error for the variable age (-9.806 ± 0.452) indicated a strong age effect on livestock mortality risk (Table

III-3). The rate ratio for the age variable indicated that yearling predation risk declined by 89% ($e^{-2.23} = 0.11$) in comparison with calves, whereas adults were 79% lower ($e^{-1.549} = 0.21$) than calves.

Habitat and vulnerability to predation

Our analysis of the importance of habitat factors in cattle mortality suggested that forest was the prevalent variable explaining cause of mortality (Table III-4). The odds-ratio for the best model (0.997; 95% C.I. 0.995 – 0.999) indicated that the probability of a death occurring due to predation by jaguars increased as distances to forest declined. Correlation analyses further indicated that the number of locations of cattle killed by cats decreased with increased distances from both forest ($r = -0.82$, $P < 0.0003$) and water ($r = -0.89$, $P = 0.0001$). The same pattern was observed for locations of cattle dying of non-predation causes in relation to either forest ($r = -0.80$, $P = 0.049$) and water ($r = -0.83$, $P = 0.003$). However, when comparing the average distances to forest, locations of cattle killed by cats (213.3 ± 188.5 m, $n = 32$) were closer to forest ($t_1 = 2.68$, $P = 0.008$) than were non-predation mortalities (318.2 ± 204.5 m, $n = 157$). In contrast, distances between depredated (348.8 ± 292.0 m, $n = 32$) and non-depredated (320.2 ± 207.6 m, $n = 157$) deaths were similar relative to distance to water (Mann-Whitney $U = 2498.5$, $P = 0.962$).

Space use

Our spatial analysis suggested the degree of cattle-to-jaguar static interaction was low within the study area. Considering the total estimated home range size for resident jaguars within the ranch (112.2 km^2 , 95% FK) and our study area, the percent overlap with cattle

home range was only 16.4 %. When analyzing the overlap between jaguar core areas (50% FK) and cattle space use within allotments (95% FK), overlap was only 2.4%. No overlap was observed between cattle core areas (50% FK) and jaguar home range areas (95% FK).

Our analysis of cattle gregarious behavior suggested habitat type was the prevalent variable explaining grouping behavior (Table III-5). Of all cattle locations recorded during the study ($n = 278$), 69.8% were from ungrouped animals in open habitat. The odds-ratio for the model (0.404; 95% C.I. 0.317 – 0.515) indicated that cattle grouping in open habitats was 60% less likely to occur than in closed habitats. Our results showed that among the factors influencing cattle movement, the best model included only the variable amount of jaguar use change between cattle locations ($F = 6.38$, $P = 0.012$). The model-averaged coefficient estimate (1.15 ± 1.03) suggested that the effect of this variable on cattle movement was substantive (Table III-6). Variables representing days between locations, jaguar use level at initial location, and jaguar use level at final location of cattle, were not predominant factors affecting cattle movement patterns. The average movement distance of cattle during the period of tracking was 1213.4 ± 1482.5 m per day.

DISCUSSION

Predation and survival of cattle populations

Our results of depredation for the entire ranch indicate that the overall impact of large felid predation on cattle was low. We found that predators killed 0.5% of the total number of livestock in the study area. This rate is lower than most annual livestock predation rates by large felids reported elsewhere (Mizutani 1993, Butler 2000, Madhusudan 2003, Patterson et al. 2004). Considering the estimated daily energetic needs of the jaguar population in our area

(34g/day/kg of cat; Emmons 1987, Polisar et al. 2003), depredated livestock represented only 0.56% (9,634 kg) of the standing crop of cattle (approximately 1,865,000 kg) (Azevedo and Murray in prep.). Therefore cattle predation rate was very low, indicating that cats did not subsist on cattle during the period of study. Similar conclusions were suggested for other studies on carnivores (Mizutani 1993, 1999, Polisar et al. 2003, Patterson et al. 2004). In contrast, losses due to non-predation causes were 4 times higher (2.14% of total livestock holdings). These results suggest that, although the overall mortality rate for cattle in the study area was low (2.64% of total livestock holdings), non-predation causes constituted a more important factor of cattle mortality (Mizutani 1993, Cozza et al. 1996, Patterson et al. 2004, Graham et al. 2005). Our results strongly suggest that cattle likely constitute an alternative prey, which are killed opportunistically by predators in the study area (Oakleaf et al. 2003, Polisar et al. 2003, Patterson et al. 2004). Thus, cattle depredation is likely an additive source of food.

Similarly to patterns of mortality for the entire ranch, cattle survival rates within allotments indicate that livestock mortality was low and mortality risk from non-predation causes was higher than predation risk. In support of our first prediction, predation risk was highest among the younger age class, and these results are consistent with those from several other studies of large carnivore depredations on livestock (Hoogesteijn et al. 1993, Anderson 1998, Oakleaf et al. 2003, Polisar et al. 2003). However, overall predation rates were likely not high enough to cause anti-predator responses in cattle so that it could be argued that predation should be equally distributed among all cattle age classes. However, selective calf predation may suggest that jaguar predation was limited by prey size and that selection for young/small individuals reflected the difficulties to capture larger-bodied cattle (e.g., see Temple 1987).

Habitat affecting vulnerability to predation

Under the assumption of non-selective predation behavior within suitable habitat, higher predation of cattle should occur closer to forest and water courses. Indeed, our results indicate that more cattle died due to predation by jaguars than due to other causes when close to forest. However, our data indicate that a higher proportion of the most vulnerable age class calves was killed by jaguars in proximity to forest, therefore suggesting that proximity to suitable habitat should affect livestock vulnerability. Despite the higher abundance of non-calves in the allotments area, our data indicate jaguar prey selection towards calves within a limited range of distance from forest, a pattern that may be explained through selection of individuals that are more vulnerable due to their weak defense capabilities and smaller size (Berger 2001, Oakleaf et al 2003). Although the overall number of cattle predated was low, forested habitats were important in increasing vulnerability of calves to predation by jaguars (Quigley 1987, Quigley and Crawshaw 1992). In contrast, our results do not conform with the prediction that proximity to water sources would increase cattle vulnerability to predation. The landscape in the Pantanal is characterized by an annual flooding regime in a low terrain, which favors the occurrence of ephemeral water bodies that persist throughout the first months of the dry season. The availability of these water bodies likely reflected the lack of influence of permanent water sources on the vulnerability of cattle to predation by jaguars.

Space use

Habitat overlap can influence predator selectivity of prey (Meriggi and Lovari 1996). In our study, the lack of spatial overlap of cats and cattle herds, particularly at core-areas, suggests that predation risk was low in the allotments. In general, grouping behavior in ungulates is a defense response to predation risk (Bertram 1978, Pulliam and Caraco 1984,

Carbyn and Trottier 1987, Oakleaf et al. 2003) and the benefits of grouping are dilution of predation risk (Bertram 1978, Hebblewhite and Pletscher 2002) and/or reduction in individual vigilance necessary to detect potential predators (Pulliam and Caraco 1984). Our results indicate a lack of influence of jaguar use levels on cattle grouping and also low tendency of cattle grouping in open habitats. These results suggest that the number of cattle depredated and cattle-carnivore interactions were not sufficient to promote cattle grouping behavior. The low predation risk may also explain the lack of cattle movement in response to exposure to higher predation risk. Similar justification has been offered to explain cattle behavior in ranges occupied by other large carnivores (Oakleaf et al. 2003). Note, however, that our movement models had low predictive power and therefore predation risk likely was not sufficient to influence cattle movement patterns or grouping behavior.

Despite the extensive data gathered on livestock depredation for most carnivore species, most studies have been limited by the lack of information on prey availability, predator densities and factors promoting depredation (Graham et al. 2005, Kolowski and Holekamp 2006). To our knowledge, our study is the first to assess comprehensively the effects of potential factors predisposing livestock to predation by jaguars and pumas. While our information on predator density is temporally limited (two years), the long-term depredation dataset from the study area (San Francisco ranch 2004) indicate that large felids seem to respond to fluctuations in the availability of cattle (Figure 1), but predation does not have a regulatory effect. In our study, cattle were checked daily and rotated periodically among allotments. This management system seems to have been effective at reducing depredation risk of cattle. In addition, a better management of cattle inside allotments seems to decrease the need to clear more forest to expand available areas for cattle ranching. This system seems also to secure the availability of wild prey for jaguars in the study area, because

livestock-free areas are used to enhance local tourism activities through sightings of wildlife (Mishra et al. 2003). Clearly, additional efforts are needed to further evaluate how sublethal effects associated with different intensities of perceived predation risk might influence predator's prey selection in the study area. Furthermore, a continuous monitoring of jaguar and puma densities and their selection of habitats will contribute to a better understanding of the patterns of livestock depredation by jaguars and pumas and how these cats respond to variations in the availability of cattle within the studied area.

LITERATURE CITED

- Anderson, C.R., Ternent, M.A., Moody, D.S., Bruscano, M.T., and Miller, D.F. 1998. Grizzly bear-cattle interactions on two cattle allotments in Northwest Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence and an alternative. *Journal of Wildlife Management* 64:912-923.
- Azevedo, F.C.C., and Murray, D.M. Spatial organization and food habits of jaguars in the southern region of Pantanal, Brazil. In prep.
- Berger, J., Swenson, J. E., and Persson, I. 2001. Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science* 291:1036-1039.
- Bertram, B.C.R. 1978. Living in groups: predators and prey. In: *Behavioral ecology: an evolutionary approach*. Krebs, J.R., Davies, N.B. (eds.). Blackwell Scientific Publications, Oxford. Pp. 64-96.
- Boonstra, R., Hik, D., Singleton, G.R., and Tinnikov, A. 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs* 68:371-394.
- Burnham, K.P., and Anderson, D.R. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, NY, USA.
- _____, and Anderson, D.R. 2002. *Model selection and multimodal inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, NY, USA.
- Butler, J.R.A. 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38:23-30.

- Carbyn, L.N., and Trottier, T. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Canadian Journal of Zoology* 65:2072-2078.
- Cozza, K., Fico, R., Battistini, M.L., and Rogers, E. 1996. The damage-conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation* 78:329-336.
- Crawshaw, P.G., Jr., and Quigley, H. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology* 223:357-370.
- Creel, S., Winnie, Jr. J., Maxwell, B., Hamlin, K., Michael, C. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387-3397.
- Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. *Advances in the Study of Behavior* 22:135-238.
- Dubs, B. 1994. Differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. PhD thesis, University of Zürich, Edinburgh.
- Dytham, C. 2003. *Choosing and Using Statistics: A Biologist's guide*. Blackwell publishing.
- Emmons, L.H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* 20: 271-283.
- Environmental Systems Research Institute (ESRI). 2000. Arcview, version 3.2. ESRI, Redlands, California, USA.
- Fernández-Juricic E., Jokimäki, J., McDonald, J.C., Melado, F., Toledano, A., Mayo, C., Martín, B., Fresneda, I., and Martín, V. 2004. Effects of opportunistic predation on anti-predator behavioural responses in a guild of ground foragers. *Oecologia* 140:183-190.
- Graham, K., Beckerman, A.P., and Thirgood, S. 2005. Human-predator correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.

- Hebblewhite, M., and Pletscher, D.H. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800-809.
- Heisey, D.M., and Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wild. Manage.* 49:668-674.
- Hooge, P.N., Eichenlaub, W., and Solomon, E. 1999. The animal movement program. USGS. Alaska Biological Center.
- Hoogesteijn, R., Hoogesteijn, A., and Mondolfi E. 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. *Symp. Zool. Soc. Lond* 65:391-407
- Hosmer, D.W., and Lemeshow, S. 2000. Applied logistic regression. – John Wiley and Sons, Inc.
- Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., and Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101: 591-601.
- Kolowski, J.M., and Holekamp, K.E. 2006. Spatial, temporal, and physical characteristics of livestock depredation by large carnivores along a Kenyan reserve border. *Biological Conservation* 128:529-541.
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 69:619-640.
- Linnell, J.D.C., Olden, J., Smith, M.E., Aanes, R., and Swenson, J.E. 1999. Large carnivores that kill livestock: do problem individuals really exist? *Wildlife Society Bulletin* 27: 698-705.

- Madhusudan, M.D. 2003. Living amidst large wildlife: Livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, South India. *Environmental Management* 31, 466-475.
- Mazzoli, M., Graipel, M.E., and Dunstone, N. 2002. Mountain Lion depredation in southern Brazil. *Biological Conservation* 105: 43-51.
- Mech, L.D. 1977. Wolf-pack buffer zones as prey reservoirs. *Science* 198: 320-321.
- _____, Harper, E.K., Meier, T.J., and Paul, W.J. 2000. Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. *Wildlife Society Bulletin* 28: 623-629.
- Meriggi, A., and Lovari S., 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33:1561-1571.
- Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., and Prins, H.H.T. 2003. The role of incentive programs in conserving the snow leopard. *Conservation Biology* 17: 1512-1520.
- Mizutani, F. 1993. Home range of leopards and their impact on livestock on Kenyan ranches. *Symp. Zool. Soc. Lond.* 65:425-439.
- _____. 1999. Impacts of leopards on a working ranch in Laikipia, Kenya. *African Journal of Zoology* 37: 211-225.
- Oakleaf, J.K., Mack, C., and Murray, D.L. 2003. Effects of wolves on livestock calf survival and movements in central Idaho. *Journal of Wildlife Management* 67: 299-306.
- Ogada, M.O., Woodroffe, R., Oguge, N.O., and Frank, L.G. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology* 17: 1521-1530.

- Patterson, B.D., Kasiki, S.M., Selempo, E., and Kays, R.W. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119: 507-516.
- Polisar, J., Maxit, I., Scognamillo, D., Farrel, L., Sunquist, M.E., and Eisenberg, J.F. 2003. Jaguars, pumas, their prey base and cattle ranching: ecological interpretations of a management problem. *Biological Conservation* 109:297-310.
- Pulliam, H.R., and Caraco, T. 1984. Living in groups: is there an optimal group size? In: *Behavioral ecology: an evolutionary approach*. 2nd edition. Krebs, J.R., Davies, N.B. (eds.). Blackwell Scientific Publications, Oxford. pp. 122-147.
- Quigley, H. 1987. Ecology and conservation of the jaguar in the Pantanal region, Mato Grosso do Sul, Brazil. PhD thesis, University of Idaho, Moscow, Idaho.
- _____, and Crawshaw, P.G., Jr. 1992. A conservation plan for the jaguar (*Panthera onca*) in the Pantanal region of Brazil. *Biological Conservation*. 61: 149-157.
- Rabinowitz, A.R., and Nottingham, B.G. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology* 210:149-159.
- Ramakrishnan, U., Coss, R.G., and Pelkey, N.W. 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation* 89:113-120.
- Roloff, G.J., Millspaugh, J.J., Gitzen, R.A., and Brundige, G.C. 2001. Validation tests of a spatially explicit habitat effectiveness model for rocky mountain elk. *Journal of Wildlife Management* 65: 889-914.
- San Francisco ranch. 2004. Relatório de mortes bovinas 2003-2004. Fazenda San Francisco.
- SAS Institute. 1999. SAS/STAT user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

- Scognamillo, D., Maxit, I.E., Sunkuist, M.S., and 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.
- Selvin, S. 1995. *Practical biostatistical methods*. Duxbury Press, Belmont, California, USA. (Eds.). Univ. Montana, Missoula.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology* 68:116-125.
- Treves, A., and Karanth, K.U. 2003. Human-carnivore conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* 17: 1491-1499.
- Weber, W., and Rabinowitz, A. 1996. A global perspective on large carnivore conservation. *Conservation Biology* 10:1046-1054
- White, P.J., and Garrott, R.A. 2005. Yellowstone's ungulates after wolves – expectations, realizations, and predictions. *Biological Conservation* 125: 141-152.
- Woodroffe, R., and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.
- _____. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165-173.
- _____. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. In: Gittleman, J., Funk, K., Macdonald, D., Wayne, R. (Eds.), *Carnivore Conservation, Conservation Biology Series 5*. Cambridge University Press, Cambridge, pp. 282-312.
- Worton, B.J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.
- Zar, J.Z. 1999. *Biostatistical analysis*. Prentice-Hall, Inc.

Table III-1. Livestock availability and number of mortality incidents on San Francisco ranch during 2003-04.

Livestock age class	Availability average \pm SD (% of total)	Cause of death (n = 169)	
		Predation (% of class)	Other (% of class)
Adults (> 2 years old)	3414 \pm 205.7 (53.3)	4 (0.1)	44 (1.2)
Yearlings (13 – 24 months)	1522 \pm 41.0 (23.7)	6 (0.3)	37 (2.4)
Calves (4 – 12 months)	753 \pm 230.5 (11.7)	12 (1.5)	27 (3.5)
Calves (0 – 3 months)	709 \pm 166.8 (11.0)	10 (1.4)	29 (4.0)
Total	6398 \pm 150.6	32 (0.5)	137 (2.1)

Table III-2. Survival and cause-specific mortality rates of cattle tracked inside allotments on San Francisco ranch, Brazil, during January-December 2004. Relative rates difference indicates the ratio between depredation versus non-predation mortality.

Age class	Cumulative number of animals (mean \pm SD)	Deaths (%)	Annual cause-specific mortality rate			
			Predation	95% C.I.	Other	95% C.I.
Calves	1261 (180 \pm 75)	20 (1.58)	0.047	0.005 – 0.089	0.087	0.037 – 0.137
Yearlings	6421 (229 \pm 68)	6 (0.09)	0.004	0.000 – 0.011	0.029	0.002 – 0.057
Adults	1518 (190 \pm 69)	8 (0.53)	0.004	0.000 – 0.012	0.030	0.008 – 0.052

Table III-3. Factors influencing mortality of cattle in allotments on San Francisco ranch, Brazil, during January-December 2004. For each model i , K_i is the number of parameters in the model, Δ_i is the change in AICc between the model and the model with the lowest AICc (best model), and w_i is the Akaike weight.

Model $_i$	Coefficient	K_i	Δ_i	w_i	95% C.I.	Model P -value
age	-9.7658	3	0.00	0.609	-10.566 - -8.966	0.000
age + sex	-9.8245	4	1.08	0.356	-10.845 - -8.804	0.000
sex	-10.5910	2	5.84	0.003	-11.571 - -9.611	0.000

Table III-4. Logistic regression models of variables found to be significant in predicting causes of cattle mortality (predated vs other causes) on San Francisco ranch, Brazil, during January-December 2004 as ranked by AICc, where other causes is the reference cell. For each model i , K_i is the number of parameters in the model, Δ_i is the change in AICc between the model and the model with the lowest AICc (best model), and w_i is the Akaike weight. Odds ratios and corresponding 95% confidence intervals are provided. Model significance was determined by the likelihood ratio test.

Model _{<i>i</i>} <i>value</i>	O.R. ₁	O.R. ₂	C.I. ₁	C.I. ₂	K_i	Δ_i	w_i	Model <i>P</i> - value
Constant + forest	0.997	-	0.995 - 0.999	-	2	0.00	0.61	0.006
Constant + forest + water	1.000	0.997	0.999 - 1.002	0.995 - 0.999	3	1.42	0.30	0.017
Constant only	0.411	-	0.150 - 0.67	-	1	5.47	0.04	0.000
Constant + water	1.012	-	1.000 - 1.02	-	2	7.08	0.02	0.513

Table III-5. Logistic regression models of variables found to be significant in predicting cattle grouping behavior (grouping vs ungrouping) on San Francisco ranch, Brazil, during January-December 2004 as ranked by AICc, where grouping are the reference cell. For each model i , K_i is the number of parameters in the model, Δ_i is the change in AICc between the model and the model with the lowest AICc (best model), and w_i is the Akaike weight. Odds ratios and corresponding 95% confidence intervals are provided. Model significance was determined by the likelihood ratio test.

Model _{<i>i</i>} <i>value</i>	O.R. ₁	O.R. ₂	C.I. ₁	C.I. ₂	K_i	Δ_i	w_i	Model <i>P</i> - <i>value</i>
Constant + habitat ^a	0.404	-	-0.28 - 1.09	-	2	0.00	0.77	0.006
Constant + habitat ^a + cat use level	0.428	1.011	-0.27 - 1.13	1.00 - 1.02	5	3.24	0.15	0.033
Constant only	0.411	-	0.15 - 0.67	-	2	4.98	0.06	0.000
Constant + cat use level	1.012	-	1.00 - 1.02	-	4	8.23	0.01	0.392

^a Design coded with open habitats as reference (i.e. – cattle are 0.40 times more likely to be ungrouped in closed habitats than in open habitats).

Table III-6. Factors influencing cattle movement, as ranked by AIC on San Francisco ranch, Brazil, during January-December 2004. 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. Model jaguar change refers to the amount of change in jaguar use levels between cattle locations; model days refers to days between locations; model use final refers to cat use level at final location; model use initial refers to cat use level at initial location.

Model i	K_i	AIC	Δ_i	w_i	R^2	Model P -value
jaguar change	2	166.09	0.00	0.169	0.031	0.012
days + jaguar change	3	166.43	0.34	0.143	0.039	0.019
use final + jaguar change	3	167.03	0.94	0.106	0.036	0.026
days + use final + jaguar change	4	167.42	1.33	0.087	0.044	0.031
use initial + jaguar change	3	167.82	1.73	0.071	0.033	0.039
days + use initial + jaguar change	4	168.17	2.08	0.060	0.041	0.044
use initial + use final + jaguar change	4	168.97	2.88	0.040	0.037	0.062
use final	2	169.32	3.23	0.034	0.015	0.079
days + use initial + use final + jaguar change	5	169.36	3.27	0.033	0.044	0.064
days + use final	3	169.49	3.40	0.031	0.024	0.183
days	2	170.46	4.37	0.019	0.009	0.163
use initial	2	171.00	4.91	0.015	0.007	0.235
days + use initial	3	171.09	5.00	0.014	0.017	0.193
use initial + use final	3	171.32	5.23	0.012	0.015	0.216
days + use initial + use final	4	171.49	5.40	0.011	0.024	0.183

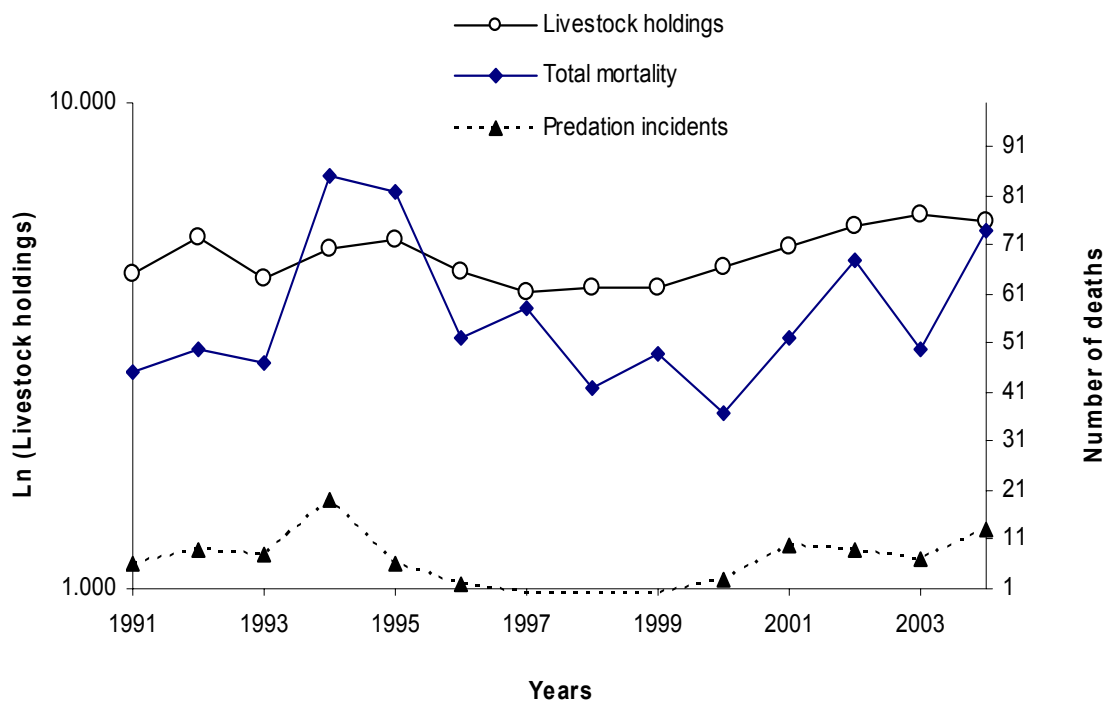


Figure III-1. Fluctuations in livestock holdings and mortality incidents on San Francisco ranch, Brazil, during 1991-2004. Mortality refers to total number of livestock dead and predation incidents refer to the number of livestock killed by jaguars and pumas.

CHAPTER 4**Dietary Breadth and Overlap Among Five Sympatric Prairie Carnivores**

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ABSTRACT

Ecological communities are shaped, in part, by the manner in which similar species consume and partition food resources. To better understand the structure of a mammalian carnivore community from prairie habitat in central North America, we determined the dietary breadth and overlap of sympatric American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*), via stomach content analysis of 411 carcasses salvaged as part of a predator control program in southern Saskatchewan, Canada (2000-2001). Carnivores consumed a total of 25 separate food items; for all species except raccoons, the majority of stomachs contained mammals, whereas other foods such as amphibians, bird remains, and insects were also recovered. Raccoon stomachs tended to contain wheat seed, eggshells and birds. Dietary breadth varied among the 5 carnivore species, being narrowest for raccoons and widest for skunks. Overall, dietary overlap tended to be highest for species pairings associated with the highest level of presumed niche similarity, which included raccoon-skunk and coyote-fox dyads. Yet, levels of dietary overlap exhibited notable interannual variability for most species pairings. The assessment of a larger assemblage of carnivores within a North American prairie community shows that marked interspecific and temporal variation in dietary breadth and overlap may characterize a guild of sympatric species occupying similar habitat.

INTRODUCTION

One of the basic tenets of community ecology is that sympatric species occupying a common trophic level tend to exhibit niche differentiation and resource partitioning (Pianka 1969, Schoener 1974, 1986). Among the most important modes of resource partitioning in ecological communities is the differentiation of food resources, such that cases of extensive dietary overlap between similar species are limited. Questions concerning dietary breadth and overlap among carnivore guilds may be especially problematic, however, given the inconsistency in the distribution and abundance associated with many of their prey species, temporal or demographic variability in prey vulnerability to predation, the influence of intra- as well as interspecific competition on carnivore food habits, and even the potentially strong individual-based variability in carnivore food preference (Maddock and Perrin 1993, Wu 1999). Accordingly, patterns of resource partitioning characterizing resident carnivore populations within particular ecological communities may be complex and dynamic.

For North American carnivores, the literature is replete with analyses of dietary breadth and overlap between species pairs or triads (e.g., Witmer and DeCalesta 1986, Major and Sherburne 1987, Litvaitis and Harrison 1989, White et al. 1995, Kitchen et al. 1999, Neale and Sacks 2001 *a*). Many of these studies have explained dietary differences within the context of alternative feeding strategies (i.e., generalist versus specialist foraging), or intrinsic niche differentiation (i.e., disparity in habitat requirements or body size) (Schoener 1974, Rosenzweig 1966, Brown 1975, Tokeshi 1999). However, not all species fall into such discrete categories (Fox and Morrow 1981). Indeed, within a given community, the relative breadth of a particular carnivore's diet (and by extension levels of interspecific dietary overlap) is arguably best defined in relation to the feeding habits manifested by its trophic

counterparts. Thus, insofar as many previous analyses have likely painted an incomplete picture of dietary relationships among carnivores, future studies should seek to monitor more complete assemblages of these species in order to better understand patterns of community structure and function.

The prairies of North America are characterized by a diverse array of resident mammalian carnivore species. Among these, badgers (*Taxidea taxus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), striped-skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*) are known to coexist along the prairie-agricultural interface, where they can occur at relatively high densities (Messick 1987, Rosatte 1987, Sanderson 1987, Sargeant and Arnold 1984, Voigt 1987, Voigt and Berg 1987). Most prairie carnivores conventionally have been considered to be opportunistic or generalist feeders (Bekoff 1977, Wade-Smith and Verts 1982, Larivière and Pasitschniak-Arts 1996, Sovada et al. 1999, Chamberlain et al. 2002). However, the five aforementioned predators are known to (i) exhibit disparate prey choice patterns (e.g., Dion et al. 1999, Greenwood et al. 1999) and (ii) rely upon a prey base that is both diverse and spatio-temporally variable. Thus, differences in their specific feeding patterns, and in particular interspecific variability with respect to dietary breadth and niche overlap, are likely to exist.

We studied the dietary breadth and overlap among the above five species of carnivores as part of a larger effort to determine the role of carnivores on nesting success of prairie waterfowl. Specifically, we used stomach content analysis to determine diet composition and evaluate if prairie carnivore species: (i) differed in their dietary breadth, and (ii) showed greater dietary overlap among pairs of species occupying presumably similar ecological niches (e.g., coyote-fox, skunk-raccoon). From a community perspective, we also

predicted that any temporal changes in dietary breadth of carnivores would be associated with corresponding changes in dietary overlap between pairs of species.

METHODS

Study area

The study was conducted ca. 75 km southwest of Weyburn, SK, Canada (49° 24'N, 104° 39'). This area is in the Canadian Prairie Pothole Region, which includes about 480 km² of combined parklands, grasslands and wetlands (Johnson et al. 1989). Primary land use in the study area includes cultivation of cereal and oil seed crops, and livestock production. Most of the area is cultivated, although small parcels of native grassland pasture and hay production are present (< 20% of entire area). The area is typified by rolling hills with a high density of semi-permanent, seasonal, and ephemeral wetlands. Common native grassland plant species in the area include several grasses (*Agropyron sp.*, *Bouteloua sp.*, *Festuca sp.*, *Hordeum sp.*, *Koeleria sp.*, *Poa sp.*, *Stipa sp.*) and shrubs (*Symphoricarpos occidentalis*, *Rosa sp.*, *Elaeagnus communtata*). During each year of study (2000 and 2001), predators were harvested in two randomly selected 41 km² sampling zones, spaced roughly 10 km apart. New sampling zones were chosen in 2001 that were > 6 km from those used during the previous year. Importantly, we sought to ensure that general habitat characteristics remained consistent across the sampling zones for both years of the investigation.

Collection of specimens

During April-June 2000 and 2001, carnivores in the study area were collected as part of a predator control effort initiated by the Delta Waterfowl Foundation. On each sampling

zone, badgers, coyotes, raccoons, red foxes, and skunks were harvested by professional trappers using a combination of snares (primarily), foothold traps, cage-type live traps, and opportunistic shooting. Upon capture, carnivore species, capture date, and animal sex were recorded. The stomachs and intestinal tracts of all harvested animals were extracted and frozen prior to laboratory analysis. All predator removal procedures conformed to standard protocols and were approved by the University of Saskatchewan Animal Care Committee (UCACS protocol #20010055). Note that carcasses used in the present analysis were salvaged following the predator control program, and thus no animals were killed specifically for the purpose of this research.

Laboratory analysis of food habits

Samples were thawed and intestinal tracts were sectioned (duodenum, ileum, jejunum) and opened longitudinally. Stomachs and intestinal walls were rinsed under running water whereas food contents were collected in a 600 μm sieve and placed in petri dishes to be air-dried. Examination of the contents of dried food items was performed using dissecting and compound scopes. Food contents were separated and identified to genus and species using general morphologic features of hair (for mammals; see Adorjan and Kolenosky 1969), as well as via comparison with reference material (for seeds, invertebrates, and amphibians; see Martin and Barkley 1961, Fromm 1982, Arnett 1993, Conant and Collins 1998, Acorn 2000).

Traps used to capture raccoons and skunks sometimes were baited with fish or infertile chicken eggs. Clearly, the consumption of such bait by carnivores captured in livetraps (i.e., about 50% of raccoons and skunks) could have biased our diet composition

results. However, because fish are absent from the study area (V. Lester, pers. obs.), the modest occurrence of this food item in raccoon and skunk stomachs was interpreted as bait consumption and therefore not included in our analyses. For eggshells, we did not differentiate between those from chicken versus native birds, but because <5% of all traps were baited with chicken eggs in either year of study (S. Lariviere, pers. obs), we retained eggs as a food item in analyses. Yet, it is important to note that because our analysis was restricted to determining presence/absence of food items in carnivore stomachs (see below), it is unlikely that bait consumption would have substantially affected our estimation of the relative importance of the remaining food types in carnivores.

Data analysis

To compare the relative consumption of prey among species and between years, we determined the frequency of occurrence of food items in stomachs (Kitchen et al. 1999, Sovada et al. 2001). To account for instances where multiple items were recovered from a single stomach, we calculated the relative frequency of occurrence of each food item (i.e., Hidalgo-Mihart et al. 2001, Neale and Sacks 2001 *a*). Initially, we classified food items into 10 major categories; mammals, birds, amphibians, insects, wheat, eggshells, fish, leaves/fiber, grass, and other (bones, sand, wood material, non-insect invertebrates, plastic, and seeds/crops other than wheat). Ultimately, we limited our statistical analysis to prey items that occurred in ≥ 2 % of samples for each species in both years combined, which comprised 6 major categories (mammals, birds, amphibians, insects, wheat, and eggshells). From these categories, we selected 25 food items to analyze dietary breadth and overlap. We used chi-square analyses to compare frequency of occurrence of food items between years and among species, and Fisher's exact tests when expected values were < 5. Note that sample

sizes were low for some species/year combinations and thus statistical power is reported for analyses of interannual variability in diet. When performing multiple comparisons of food consumption among mammals, we used Bonferroni's correction to minimize the likelihood of Type I statistical error (Oehlert 2000). All tests were performed using SYSTAT software (SYSTAT 2000).

We calculated measures of niche breadth (Smith 1982) using the relative frequency of occurrence of food items (where $FT = \sum(\sqrt{p_j a_j})$), where FT = Smith's measure of niche breadth; p_j = fraction of items in the diet that are of food category j ; a_j = proportion of total resources comprised by resource j). Smith's measure of niche breadth is a standardized measure varying from 0 (minimal) to 1.0 (maximal) that is relatively insensitive to selectivity for rare resources (Franzreb 1984, Krebs 1999, Hofer et al. 2003). Use of this index enabled us to (i) quantify the extent to which carnivore-specific food selection patterns focused on particular food categories, (ii) assess the consistency of these food selection patterns between the two years of study, and (iii) evaluate the uncertainty of our estimates using 95 % confidence intervals. Importantly, we obtained results qualitatively similar to those presented herein when using Levin's index (Levins 1968). To analyze the overlap in food use among the five species and between years, we used the Renkonnen index ($P = \sum \text{minimum}(p1_i, p2_i)$), where P = percentage similarity between sample 1 and 2; $p1_i$ = percentage of species i in community sample 1; $p2_i$ = percentage of species i in community sample 2) of percentage overlap (see Krebs 1999), using the relative frequency of occurrence of food items in our samples. To further investigate the similarity between carnivore species and evaluate diet overlap in the context of the relative abundance of the 6 major food groups, we correlated overall frequency of occurrence of food categories between species pairs (see Neale and

Sacks 2001 *a*). The correlation coefficient (r) was considered an index of overall dietary similarity.

RESULTS

We analyzed 411 intestinal tracts during the course of the study, with 186 animals being taken in 2000 and 228 in 2001. Among the carcasses examined, 42.8% were striped skunks ($n = 176$), 27.7% raccoons ($n = 114$), 12.4% badgers ($n = 51$), 9.7% foxes ($n = 40$), and 7.3% coyotes ($n = 30$).

Occurrence and abundance of food items

The five carnivore species consumed a total of 25 separate food items, constituting the six major food categories (mammals, insects, eggshells, birds, wheat, and amphibians) which were used in subsequent analyses. The overall mean percent frequency of occurrence for the five most common carnivore food categories (carnivore species and years combined) was $54.7 \pm 18.6\%$ (\pm SE) for mammals, $34.0 \pm 29.7\%$ for insects, $30.5 \pm 13.0\%$ for eggshells, $29.2 \pm 14.1\%$ for birds, and $12.2 \pm 18.2\%$ for wheat (Table IV-1). Combined, eggshells and birds were recovered from $59.8 \pm 13.9\%$ of stomachs, and across predator species this percentage ranged from 43.1% for badgers to 78.9% for raccoons.

A total of thirteen mammal species were recovered from carnivore stomachs. In general consumption of mammals was different among the five carnivore species ($\chi^2 = 53.2$, $df = 4$, $P < 0.001$), mostly due to the low use of this food item by raccoon (Table IV-1). Badgers relied most heavily on mammalian prey, followed by coyote, fox, skunk, and raccoon (overall two-year consumption = 68.6% of all stomachs contained mammals; Table

IV-1). For badger, fox, and raccoon, meadow voles (*Microtus pennsylvanicus*) were the most commonly recovered species in 2000 and 2001; coyotes consumed deer most frequently in 2000 and meadow voles most often in 2001, whereas skunks consumed meadow jumping mouse (*Zapus hudsonius*) most frequently in 2000 and red-backed voles (*Clethrionomys gapperi*) most often during 2001 (Table IV-2). Although all carnivores consumed a number of small mammals other than voles, skunks and foxes appeared to have the greatest diversity of rodent species in their diet (Table IV-2). The frequency of mammal occurrence increased between years only for badgers ($\chi^2 = 7.56$, $P = 0.006$; power = 0.51). When carnivore species were compared collectively, interannual variability in the consumption of mammals existed only for badgers.

Consumption of insects was different among carnivores ($\chi^2 = 149.3$, $df = 4.0$, $P < 0.001$), with skunks consuming insects with greater frequency than the remaining carnivores (overall 2-year consumption = 82.9%; Table IV-1). Insects belonging to the taxonomic families Orthoptera and Coleoptera were most commonly encountered, especially among skunk and raccoon (Table IV-2). Although insects occurred more frequently during 2001 for four of the five predator species (Table IV-1), no interannual differences in the consumption of insects were observed (all $P > 0.58$).

Consumption of birds differed among carnivores ($\chi^2 = 18.1$, $df = 4.0$, $P = 0.001$). Bird remains were more common in foxes than for the remaining carnivore species (overall 2-year consumption = 47.5 %; Table IV-1). Although raccoons and skunks had a higher frequency of bird feathers in the second year ($p < 0.05$), power of the tests was low (power < 0.20). For the remaining three species there was no interannual variability in the occurrence of bird feathers (all $P > 0.61$, Tables IV-1, IV-2).

Carnivore species also differed in their consumption of eggs ($\chi^2 = 17.6$, $df = 4.0$, $P = 0.001$). Eggshell fragments were most commonly found in raccoon stomachs (overall 2-year consumption = 47.4%; Table IV-1). In contrast, such fragments rarely were recovered from fox and coyote stomachs (Table IV-1), and interannual variability in the occurrence of eggshells was observed only for skunks ($\chi^2 = 18.81$, $P < 0.001$, power = 0.69).

Wheat seeds were clearly most prevalent in raccoon stomachs (overall 2-year consumption = 44.7%; Table IV-1), compared with other carnivores ($\chi^2 = 108.5$, $df = 4.0$, $P < 0.001$). Raccoons exhibited substantive variation in wheat consumption between years (Tables IV-1, IV-2; $\chi^2 = 3.62$, $P < 0.057$, all other $P > 0.12$), however, the power of the test was low (power = 0.25).

Amphibians were present in the diets of badgers, raccoons, and skunks during both years, with skunks apparently consuming amphibians to the greatest extent and coyotes and foxes not consuming them at all (Table IV-1). The absence of amphibians from coyote and fox diets contributed to the observed difference in this food between carnivores ($\chi^2 = 40.95$, $df = 4.0$, $P < 0.001$). Chorus frog (*Pseudacris triseriata*) was the most commonly encountered amphibian in skunk stomachs, whereas badgers consumed tiger salamanders (*Ambystoma tigrinum*) and raccoons ate a greater diversity of amphibian species including treefrogs (*Hyla* spp.) and wood frogs (*Rana sylvatica*) (Table IV-2). Interannual differences in amphibian consumption were detected only for skunks ($\chi^2 = 22.92$, $P < 0.001$, power = 0.40; Table IV-2).

Dietary breadth and overlap

Smith's (1982) niche breadth index, using the suite of 25 separate food items, indicated that dietary breadth was narrower for coyotes, foxes, and raccoons than for the

remaining two carnivore species in 2000 (Table IV-3). This pattern was not repeated during 2001, when only foxes and raccoons manifested restricted dietary patterns (Table IV-3). During 2000, badgers and then skunks were characterized by the broadest diet, whereas in 2001, coyotes, badgers and skunks, showed the most generalized diet (Table IV-3). When the two years of the study were combined, skunks and then badgers were characterized by the greatest dietary breadth (Table IV-3). Coyotes were the only species to manifest a temporal shift in dietary breadth, primarily because of increased consumption of mammals during spring of 2001 (Tables IV-2, IV-3). Notably, our sample for coyotes was small during spring 2000, which might have influenced our observation of greater dietary breadth for this carnivore species for spring 2001.

With both years of the study pooled, the extent of dietary overlap (measured using the Renkonnen index) characterizing all possible carnivore pairings ranged from 44.7 % for the fox-skunk pairing to 66.9 % for the coyote-fox pairing (Table IV-3). The highest levels of dietary overlap were recorded for coyote-fox, raccoon-skunk, and badger-fox pairings; the lowest values were associated with the fox-skunk, fox-raccoon and coyote-skunk pairings (Table IV-3). Percent dietary overlap was lower among most carnivore pairings in 2000 (seven pairs) than in 2001; however, levels of overlap characterizing the badger-fox, badger-raccoon, and fox-raccoon pairings were higher in the study's first year. Pairings featuring the highest levels of percent overlap also varied temporally: in spring 2000, percent overlap values were highest for badger-fox, badger-raccoon, and raccoon-skunk pairings; the following year, percent overlap values were highest for the coyote-fox, raccoon-skunk and badger-skunk pairings (Table IV-3).

Our index of overall dietary similarity with respect to use of the six designated food categories (expressed using a correlation coefficient [r]) indicated slightly different trends in

carnivore dietary overlap. Specifically, this index revealed close dietary correlation for only coyote-fox (both years), badger-coyote and badger-fox (spring 2001) pairings (all $P < 0.1$) (Table IV-4).

DISCUSSION

The results of this analysis generally support the contention that assemblages of sympatric carnivore species should exhibit variability in dietary breadth and overlap that is consistent with general principles of resource partitioning and niche delineation within ecological communities. Among the five carnivores studied, interspecific differences were observed; specifically, overall dietary breadth values were relatively high for skunks and badgers, intermediate for coyote and fox, and low for raccoons (Table IV-3). Moreover, as predicted, two of the three species pairs presumably sharing ecological niches (coyote-fox, skunk-raccoon) manifested the highest recorded degree of dietary overlap as measured using the Renkonen index; similarly, two of the three pairs ostensibly characterized by high niche overlap (badger-coyote, coyote-fox) were the only pairs to show significant overlap when analyzed using the correlative index.

Occurrence and abundance of food items

Among the carnivores assessed, four species (badgers, coyotes, foxes, and skunks) preyed heavily on a wide variety of mammals. By contrast, raccoon stomachs contained mammal remains infrequently, and instead this carnivore appeared to commonly ingest birds, eggs (presumably as a result of nest predation), and plant material (in particular wheat seeds).

Skunks, and to a lesser extent badgers and foxes, often included insects in their diet, whereas skunks also appeared to prey heavily on amphibians. These findings generally are consistent with previous reports concerning dietary composition of the five study species in central North America (e.g., Messick 1987, Rosatte 1987, Sanderson 1987, Sargeant and Arnold 1984, Voigt 1987, Voigt and Berg 1987). Interestingly, we rarely documented interannual fluctuation in the use of particular food categories, suggesting that patterns of prey availability for the carnivores assessed may have been relatively stationary over the two years of the investigation. For example, a closer look at the interannual variation in use of mammals by the four carnivore species other than coyotes (Table IV-2) fails to reveal evidence for substantive temporal changes in small mammal occurrence. In particular, consumption of voles, a small mammal species for which dramatic numerical fluctuations across much of North America have been documented (Johnson and Johnson 1982), was remarkably consistent during the study.

Dietary breadth and overlap

Feeding specialization has been described as ‘use of a relatively narrow portion of the resource spectrum’ (Cody 1974), or ‘the stable use of a particular food type irrespective of fluctuations in the availability of that food type’ (Kruuk and Parish 1981). With these traditional definitions providing a conceptual framework, several carnivore species have been shown to exhibit rather pronounced feeding specialization (e.g., Martin et al. 1995, Fedriani et al. 1998). However, when prey abundance fluctuates dramatically over a period of time, even alleged specialist species may exhibit more generalist feeding patterns (e.g., O’Donoghue et al. 1998). Moreover, a review of dietary breadth among herbivorous insects

revealed that while generalization characterized the diet of many insect species, the dietary choices of individuals within particular populations often were specialized (according to the traditional framework described above), suggesting that in many cases dietary breadth may be a local (i.e., system-specific) phenomenon, rather than an immutable species characteristic (see Fox and Morrow 1981).

Although spatio-temporal patterns of prey availability were not assessed, our results show that analyses involving multiple sympatric carnivore species (occupying a similar trophic level within an ecological community) can provide insights that would be missed by simpler dietary investigations focusing on species pairs or triads. The five carnivores studied are believed to be generalists (according to the traditional framework), and accordingly each manifested intermediate levels of dietary breadth. Thus, studies of these carnivores in isolation or as pairs would be likely to underestimate actual levels of variability characterizing their dietary breadth. For example, when analyzed individually, the Eurasian badger (*Meles meles*) has been characterized extensively as opportunistic feeder (Kruuk and de Kock 1981, Martín et al. 1995, Fedriani et al. 1998) acting locally as a specialist based on the availability of prey resources, even though variations in temperature and food resources can force this carnivore to diversify its diet and therefore behave more as a generalist carnivore (Sidorovich et al. 2000). Here, in evaluating them simultaneously, we show that a range in diet breadth does exist; namely, over the course of our investigation, skunks and badgers manifested similar generalized feeding patterns relative to other species in the community, while raccoons and foxes were characterized by the most specialized diet. Frequency estimates for occurrence of food in stomachs do not account for relative biomass, and we acknowledge that use of an index incorporating biomass information may have led the five carnivores under investigation to be rated differently in terms of niche breadth.

Nevertheless, it is clear that the interpretation of diet breadth analyses can be subject to influence from the feeding behaviour of other species in the analysis, and thus should be considered as context-specific.

In addition to notable diet breadth variability, we found large interspecific differences in dietary overlap that in many cases coincided with presumed levels of niche similarity. Based upon a review of the literature (Scott-Brown et al. 1987, Kitchen et al. 1999, Neale and Sacks 2001 *a*), we predicted that coyotes would compete strongly with foxes and perhaps badgers for mammalian prey, and consequently that the coyote-fox and coyote-badger pairings would be characterized by high levels of dietary overlap. We predicted that high dietary overlap would characterize the raccoon-skunk pairing as well, given that these species have been shown in the past to rely on similar prey items (e.g., waterfowl nests, see Lokemoen et al. 1982, Greenwood 1986, LaGrange et al. 1995). Accordingly, using two different indices, we found that the majority of pairings (four of five, years pooled) associated with significant dietary overlap were in fact those sharing similar niches. The considerable overlap characterizing the diets of coyotes and foxes, due primarily to heavy mutual reliance on small mammals, indicates that resource competition between these two species may be severe. However, coyotes relied more heavily on ungulates and lagomorphs, while foxes preyed more heavily on small rodents; these dietary specializations may have alleviated overall levels of competition between canid species. This pattern of exclusive use of particular prey items despite overall dietary similarity also characterizes the relationships between sympatric coyotes and both gray foxes (*Vulpes velox*; Kitchen et al. 1999) or bobcats (*Lynx rufus*; Neale and Sacks 2001*b*). Interestingly, the raccoon-skunk pairing was found to have the second highest overlap using Renkonen's index, but no overlap when using the correlative index of overall dietary similarity. A thorough examination of the diets of these

two species over the course of this analysis (Table IV-2) shows apparently different patterns of prey selection: skunks used insects, amphibians, and small mammals more extensively whereas raccoons were more reliant upon wheat seeds and eggs. Thus, our finding that these two carnivores manifested closely overlapping diets using Renkonnen's index may be suspect. More importantly, perhaps, this disparity underscores the variability that can typify different approaches to measuring dietary overlap, and suggests that future analyses of diet breadth should use multiple methods of measurement to reduce the likelihood of model-specific bias.

Measures of niche (i.e., diet) overlap should be used to determine, in a descriptive manner, the way an ecological community is organized (Abrams 1980), and niche theory predicts that as species become more reliant on a limited number of food types (i.e., undergo a reduction in dietary breadth), their dietary overlap with other species in the community should decline (Tokeshi 1999). Accordingly, we anticipated that dietary overlap between carnivores would be related to their dietary breadth during a given year. It is notable that, although badgers did not exhibit a significant temporal shift in diet breadth, a qualitative reduction in its usage of the food items analyzed in this study from 2000 to 2001 was associated with concomitant reductions in dietary overlap with two of its four counterparts.

A clear shortcoming of previous studies of diet breadth and overlap in carnivores is the lack of community-level analyses involving more than two or three species. This deficiency has led to a restricted view of the structure and function of ecological communities, and how these community attributes may be influenced by particular resource use patterns. By virtue of our assessment of a larger assemblage of carnivores within a North American prairie community, we were able to show that notable interspecific and temporal

variation in dietary breadth and overlap may characterize a group of sympatric species occupying similar habitat. Yet, our work also highlighted, by its absence, the need to monitor prey abundance concurrently with predator diet studies. Future work on this topic should be conducted extensively, both in terms of space and time, so that spatio-temporal changes in dietary habits can be assessed in the context of prey population change. Such multi-faceted research will further elucidate general patterns of resource partitioning and niche differentiation in ecological communities, and thus help improve our understanding of the mechanisms underlying species coexistence and community structure.

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REFERENCES

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44-49.
- Acorn, J. 2000. *Bugs of Alberta*. Lone Pine Publishing, Canada.
- Adorjan, A.S., and Kolenosky, G.B. 1969. *A manual for the identification of hair of selected Ontario mammals*. Department of Lands and Forests Research Report (Wildlife) No. 90.
- Arnett, R.H., Jr. 1993. *American Insects. A handbook of the insects of America North of Mexico*. The SandHill Crane Press, Inc. Gainesville, Florida.
- Bekoff, M. 1977. Coyote. *Mammalian Species*. 79:1-9.
- Brown, J.H. 1975. Geographical ecology of desert rodents. In: *Ecology and Evolution of Communities*. M.L. Cody & J.M. Diamond (Eds.), pp. 315-341. Belknap Press, Cambridge, MA.
- Chamberlain, M.J., Conner, L.M., and Leopold, B.D. 2002. Seasonal habitat selection by raccoons (*Procyon lotor*) in intensively managed Pine Forests of central Mississippi. *American Midland Naturalist* 147:102-108.
- Cody, M.L. 1974. *Competition and the structure of bird communities*. Princeton University Press, Princeton.
- Connant, R., and Collins, J. T. 1998. *A field guide to reptiles and amphibians of eastern and central North America*. Third Edition, Expanded. Houghton Mifflin Company. New York, NY.
- Dion, N., Hobson, K.A., and Larivière, S. 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. *Canadian Journal of Zoology* 77: 1801-1806.

- Fedriani, J.M., Ferras, P., and Delibes, M. 1998. Dietary response of the Eurasian badger, *Meles meles*, to a decline of its main prey in Doñana National Park. *Journal of Zoology* 245: 214-218.
- Froom, B. 1982. *Amphibians of Canada*. The Canadian Publishers, Toronto Canada.
- Fox, L.R., and Morrow, P.A. 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.
- Franzreb, K. E. 1984. Foraging habits of the ruby-crowned and golden-crowned kinglets in an Arizona montane forest. *The Condor* 86: 139-145.
- Greenwood, R.J. 1986. Influence of striped skunk removal on upland duck nest success in North Dakota. *Wildlife Society Bulletin* 14: 6-11.
- ___, Sargeant, A.B., Piehl, J.L., Buhl, D.A., and Hanson, B.A. 1999. Foods and foraging of prairie striped skunks during the avian nesting season. *Wildlife Society Bulletin* 27: 823-832.
- Hidalgo-Mihart, M.G., Cantu-Salazar, L., Lopez-Gonzalez, C.A., Martinez-Meyer, E., and Gonzalez-Romero, A. 2001. Coyote (*Canis latrans*) food habits in a tropical deciduous forest of Western Mexico. *American Midland Naturalist* 146:210-216.
- Hofer U., Baur H., and Bersier, L-F. 2003. Ecology of three sympatric species of the Genus *Chamaeleo* in a tropical upland forest in Cameroon. *Journal of Herpetology* 37: 203-207
- Johnson, M. L., and Johnson, S. 1982. Voles. In J. A. Chapman and G. A. Feldhamer, eds. *Wild Mammals of North America: Biology, Management, Economics*. Baltimore: Johns Hopkins Univ. Press. pp. 326-354.

- Johnson, D. H., Sargeant, A.B., and Greenwood, R. J. 1989. Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. *Canadian Journal of Zoology* 67:291-297.
- Kitchen, A.M., Gese, E.M., and Schauster, E.R. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Canadian Journal of Zoology* 77: 1645-1656.
- Krebs, C.J. (1999). *Ecological Methodology*. Benjamin/Cummings, California.
- Kruuk, H., and de Kock, L. 1981. Food and habitat of badgers (*Meles meles* L.) on the Monte Baldo, northern Italy. *Z. Säugetierkd.* 46: 295-301.
- _____, and Parish, T. 1981. Feeding specialization of the European badger *Meles meles* in Scotland. *Journal of Animal Ecology* 50:773-788.
- LaGrange, T.G., Hansen J.L., Andrews, R.D., Hancock, A.L., and Kienzler, J.M. 1995. Electric fence predator enclosure to enhance duck nestling: a long-term case study in Iowa. *Wildlife Society Bulletin* 23:261-266.
- Larivière, S., and Pasitschniak-Arts, M. 1996. *Vulpes vulpes*. *Mammalian Species* 537:1-11.
- Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, New Jersey.
- Litvaitis, J. A. and Harrison, D. J. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. *Canadian Journal of Zoology* 67:1180-1188.
- Lokemoen, J.T., Doty, H.A., Sharp, D.E., and Neaville, J.E. 1982. Electric fences to reduce mammalian predation on waterfowl nests. *Wildlife Society Bulletin* 10: 318-323.

- Maddock, A.H., and Perrin, M.R. 1993. Spatial and temporal ecology of southern river otter (*Lutra provocax*) and mink (*Mustela vison*) in southern Chile. *Journal of Zoology* 229: 227-287.
- Major, J.T., and Sherburne, J.A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *Journal of Wildlife Management* 51:606-616.
- Martin, A.C., and Barkley, W. D. 1961. *Seed identification manual*. University of California Press, Berkeley and Los Angeles.
- Martín, R., Rodríguez, A., and Delibes, M. 1995. Local feeding specialization by badgers (*Meles meles*) in a Mediterranean environment. *Oecologia* 101:45-50.
- Messick, J.P. 1987. North American Badger. In: *Wild furbearer management and conservation in North America*. Novak, M., Baker, J.A., Obbard, M.E & Malloch, B.(Eds.). Ontario Ministry of Natural Resources, Toronto, Ont. pp.587-597.
- Neale, J.C.C., and Sacks, B.N. 2001 *a*. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. *Canadian Journal of Zoology* 79: 1794-1800.
- _____, and Sacks, B.N. 2001 *b*. Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* 94: 236-249.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zutela, G., Murray, D.L., and Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79:1209-1222.
- Oehlert, G. W. 2000. *A first course in design and analysis of experiments*. W. H. Freeman and Company.

- Pianka, E.R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50: 1012-1030.
- Rosatte, R.C. 1987. Striped, Spotted, Hooded, and Hog-Nosed Skunk. In: *Wild furbearer management and conservation in North America*. Novak, M., Baker, J.A., Obbard, M.E & Malloch, B. (Eds.). Ontario Ministry of Natural Resources, Toronto, Ont. pp.599-613.
- Rosenzweig, M.L. 1966. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47: 602-612.
- Sanderson, G.C. 1987. Raccoon. In: *Wild furbearer management and conservation in North America*. Novak, M., Baker, J.A., Obbard, M.E & Malloch, B. (Eds.). Ontario Ministry of Natural Resources, Toronto, Ont. pp. 487-499.
- Sargeant, A.B. and Arnold, P.M. 1984. Predator management for ducks on waterfowl production areas in the northern plains. *Proceedings of the Vertebrate Pest Conference* 11:161-167.
- Schoener, T.W. 1974. Some methods for calculating competition coefficients from resource-utilization spectra. *American Naturalist* 108:332-340.
- _____. 1986. Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? In: *Community Ecology*. pp. 556-586. Diamond, J. & Case, T.J. (Eds). Harper & Row, New York.
- Scott-Brown, J.M., Herrero, S., and Reynolds, J. 1987. Swift fox. In: *Wild furbearer management and conservation in North America*. pp. 432-441. M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch. (Eds). Ontario Ministry of Natural Resources, Toronto, Ont.

- Sidorovich, V.E., Polozov, A.G., Lauzhel, G.O., and Krasko, D.A. 2000. Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus. *Z. Säugetierkunde* 65: 271-285.
- Smith, E. P. 1982. Niche breadth, resource availability, and inference. *Ecology* 63: 1675-1681.
- Sovada, M.A., Roaldson, J.M., and Sargeant, A.B. 1999. Foods of American badgers in west-central Minnesota and southeastern North Dakota during the duck nesting season. *American Midland Naturalist* 142:410-414.
- _____, A.M., Roy, C.C., and Telesco, D.J. 2001. Seasonal food habits of swift fox (*Vulpes velox*) in cropland and rangeland landscapes in western Kansas. *American Midland Naturalist* 145: 101-111.
- Systat. 2000. SPSS Inc. Systat 10. Statistics 1 and 2. Chicago, Illinois, USA.
- Tokeshi, M. 1999. *Species coexistence. Ecological and Evolutionary perspectives*. Blackwell Science, UK.
- Voigt, D.R., and Berg, W. 1987. Coyote. In: *Wild furbearer management and conservation in North America*. Novak, M., Baker, J.A., Obbard, M.E & Malloch, B. (Eds.). Ontario Ministry of Natural Resources, Toronto, Ont. pp. 345-357.
- _____. 1987. Red fox. In: *Wild furbearer management and conservation in North America*. Novak, M., Baker, J.A., Obbard, M.E & Malloch, B. (Eds.). Ontario Ministry of Natural Resources, Toronto, Ont. pp. 379-392.
- Wade-Smith, J., and Verts, B.J. 1982. *Mephitis mephitis*. *Mammalian Species*. 173:1-7.

White, P.J., Ralls, K., and Vanderbilt White, C.A. 1995. Overlap in habitat and food use between coyotes and San Joaquin kit foxes. *Southwest Naturalist*. 40:342-349.

Witmer, G. W., and DeCalesta, D. S. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. *Canadian Journal of Zoology*. 64:2333-2338.

Wu, H. 1999. Is there current competition between sympatric siberian weasels (*Mustella sibirica*) and Ferret Badgers (*Melogale moschata*) in a subtropical forest ecosystem of Taiwan? *Zoological Studies* 38:443-451.

Table IV-1. Frequency of occurrence of major food types (6) in stomachs of badgers (B), coyotes (C), foxes (F), raccoons (R) and skunks (S).

Food items	2000					2001					Overall 2000/2001				
	B (18)	C (9)	F (13)	R (47)	S (97)	B (33)	C (21)	F (27)	R (67)	S (79)	B(51)	C (30)	F (40)	R(114)	S (176)
Mammals	44.4	33.3	46.1	27.7	58.7	81.8	76.2	66.7	17.9	60.8	68.6	63.3	60.0	22.0	59.6
Amphibians	11.1	0	0	10.6	40.2	3.0	0	0	2.9	7.6	5.9	0	0	6.1	25.5
Insects	5.5	11.1	15.4	36.2	78.3	12.1	23.8	7.4	44.8	88.6	16.1	20.0	10.0	41.2	82.9
Wheat seeds (<i>Triticum</i> spp.)	11.1	11.1	7.7	55.3	3.1	0	4.8	0	37.3	3.8	3.9	6.7	2.5	44.7	3.4
Eggshells	27.7	11.1	15.4	38.3	20.6	39.4	23.8	14.8	53.7	51.9	35.3	20.0	15.0	47.4	34.9
Birds	11.1	33.3	53.9	21.3	22.7	6.1	28.6	44.4	38.8	36.7	7.8	30.0	47.5	31.6	29.0
Birds and Eggshells (combined)	38.8	44.4	69.2	59.6	43.4	45.4	52.4	59.3	92.5	88.6	43.1	50.0	62.5	78.9	64.7

Number of stomachs analyzed is in parenthesis

Table IV-2. Relative frequency of occurrence of all food types in stomachs of badgers (B), coyotes (C), foxes (F), raccoons (R) and skunks (S).

Food items	2000					2001				
	B (18)	C (9)	F (13)	R (47)	S (97)	B (33)	C (21)	F (27)	R (67)	S (79)
<i>Mammals</i>	51.8	27.3	42.8	15.7	22.6	55.5	51.4	52.6	7.0	23.8
Meadow vole <i>Microtus pennsylvanicus</i>	11.1	0	14.3	5.6	3.8	15.5	20.0	26.3	2.8	5.7
Deer mouse <i>Peromyscus maniculatus</i>	3.7	0	4.7	2.2	2.9	8.9	2.8	2.6	0	3.6
Red-backed vole <i>Clethrionomys gapperi</i>	7.4	0	4.7	4.5	4.2	11.1	2.8	2.6	1.4	9.3
Meadow jumping mouse <i>Zapus hudsonius</i>	7.4	0	4.7	1.1	10.0	2.2	0	0	0	0.5
Leming (<i>Synaptomys</i> spp.)	7.4	0	0	0	0	2.2	0	0	0	1.5
Red squirrel <i>Tamiasciurus hudsonicus</i>	7.4	0	4.7	2.2	0.4	6.7	0	2.6	0.7	0.5
Eastern chipmunk <i>Tamias striatus</i>	3.7	0	4.7	0	0.4	6.7	0	0	0	0
Ground squirrel (<i>Spermophilus</i> spp.)	0	0	0	0	0	0	5.7	0	0	0.5
Fox squirrel <i>Sciurus</i> spp	0	0	0	0	0	2.2	8.6	10.5	0.7	0
Snowshoe hare <i>Lepus americanus</i>	3.7	9.1	0	0	0	0	0	0	0	0
Deer (<i>Odocoileus</i> spp.)	0	18.2	0	0	0	0	5.7	0	0	0
Porcupine <i>Erethizon dorsatum</i>	0	0	4.7	0	0.4	0	2.8	0	0	0
Shrew (<i>Sorex</i> spp.)	0	0	0	0	0.4	0	0	0	0.7	2.1
Muskrat <i>Ondatra zibethicus</i>	0	0	0	0	0	0	2.8	5.2	0	0
<i>Amphibians</i>	7.4	0	0	4.5	13.0	2.2	0	0	0.7	2.1
Tiger salamander <i>Ambystoma tigrinum</i>	7.4	0	0	1.1	1.7	2.2	0	0	0	0
Unknown salamander	0	0	0	0	2.9	0	0	0	0	0
Chorus frog <i>Pseudacris triseriata</i>	0	0	0	0	4.2	0	0	0	0.7	2.1
Tree frog (<i>Hyla</i> spp.)	0	0	0	1.1	0.4	0	0	0	0	0
Wood frog <i>Rana sylvatica</i>	0	0	0	2.2	3.8	0	0	0	0	0
<i>Insects</i>	7.4	9.1	9.5	19.1	45.6	8.9	14.3	10.5	21.1	36.3
Coleoptera	3.7	0	0	14.6	19.2	4.4	11.4	5.2	16.2	19.7
Orthoptera	3.7	0	9.5	3.4	25.5	4.4	0	0	4.2	16.1
Other insects (Lepidoptera, Hymenoptera)	0	9.1	0	1.1	0.8	0	2.8	0	0.7	0.5
Wheat seeds	7.4	9.1	4.7	29.2	1.2	0	2.8	0	17.6	1.5
Eggshells	18.5	9.1	9.5	20.2	8.4	28.9	14.3	10.5	25.3	21.2
Birds	7.4	27.3	33.3	11.2	9.2	4.4	17.1	31.6	18.3	15.0

Number of gastrointestinal tracts examined is in parentheses.

Table IV-3. Niche breadth (possible range 0-1, calculated using Smith's [1982] index) and percentage of dietary overlap ([calculated using Renkonnen index; Krebs 1999]) among badgers (B), coyotes (C), foxes (F), skunks (S) and raccoons (R) in southern Saskatchewan.

	Dietary breadth					Percentage of overlap									
	Badger	Coyote	Fox	Raccoon	Skunk	B-C	B-F	B-R	B-S	C-F	C-R	C-S	F-R	F-S	R-S
2000	0.75	0.51	0.65	0.66	0.72	29.6	58.2	57.3	45.2	47.6	34.6	19.7	45.3	40.9	53.2
95 % C.I.	0.57 – 0.88	0.21 – 0.76	0.42 – 0.83	0.55 – 0.76	0.67 – 0.80										
2001	0.68	0.69	0.59	0.59	0.67	46.7	47.3	47.9	55.8	69.2	52.0	54.7	42.6	43.8	67.9
95 % C.I.	0.55 – 0.80	0.53 – 0.83	0.43 – 0.73	0.49 – 0.68	0.58 – 0.75										
Combined	0.74	0.72	0.69	0.65	0.75	47.3	54.7	52.4	50.2	66.9	52.8	46.2	45.6	44.7	59.9
95 % C.I.	0.64 – 0.83	0.58 – 0.83	0.57 – 0.80	0.58 – 0.72	0.69 – 0.80										

Confidence Intervals (95%) were calculated according to Smith (1982).

Table IV-4. Linear regression of the relative importance of frequency of occurrence of the 6 major food items among badgers, coyotes, foxes, skunks and raccoons in southern Saskatchewan.

Interaction	2000			2001		
	r	RMSE	<i>P</i>	r	RMSE	<i>P</i>
Badger-Coyote	0.49	14.36	0.32	0.91	14.98	0.01
Badger-Fox	0.42	14.93	0.40	0.74	23.72	0.09
Badger-Raccoon	0.04	16.48	0.94	0.09	35.41	0.86
Badger-Skunk	0.10	16.41	0.84	0.47	31.43	0.35
Coyote-Fox	0.98	2.92	0.00	0.92	12.10	0.01
Coyote-Raccoon	0.07	15.15	0.88	0.05	30.22	0.93
Coyote-Skunk	0.06	15.16	0.90	0.57	24.85	0.24
Fox-Raccoon	0.22	23.71	0.67	0.12	30.34	0.83
Fox-Skunk	0.11	24.19	0.84	0.35	28.58	0.49
Raccoon-Skunk	0.34	16.21	0.51	0.43	18.90	0.39

The pairwise coefficient of correlation is represented by r; RMSE is the root mean square error.