12-2008

Predator-Prey Relationships and Spatial Ecology of Jaguars in the Southern Pantanal, Brazil: Implications for Conservation and Management

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Recommended Citation

PREDATOR-PREY RELATIONSHIPS AND SPATIAL ECOLOGY OF JAGUARS IN

THE SOUTHERN PANTANAL, BRAZIL: IMPLICATIONS FOR

CONSERVATION AND MANAGEMENT

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Biology

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2008

ABSTRACT

Predator-prey Relationships and Spatial Ecology of Jaguars in the Southern Pantanal,

Brazil: Implications for Conservation and Management

by

Sandra M. C. Cavalcanti, Doctor of Philosophy

Utah State University, 2008

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The Pantanal wetland of Brazil is an important area for the conservation of jaguars (*Panthera onca*) and a stronghold for the species. Although our knowledge of jaguar ecology has increased since the first field studies in the mid 1980's, a detailed study of this cryptic species remains challenging. In the following chapters, we investigated the ecology of jaguars in the southern Pantanal of Brazil. In Chapter II, we examined the foraging ecology of jaguars, documenting predation rates, patterns, and species killed. We found individual jaguars differed in the selection of their prey. There were differences in the proportion of native prey versus cattle killed by individual cats. We found that cattle (31.7%), caiman (24.4%), and peccaries (21.0%) comprised the majority of their kills. The mean predation rate on all prey for all jaguars combined was 5.1 ± 5.0 (SD) days between kills. In Chapter III, we described jaguar habitat use and spatial patterns of predation in relation to vegetation and other landscape attributes.

Jaguars used some habitats disproportionately to their availability both in the wet and dry seasons. Forest and shrubland habitats were generally selected by jaguars. However, the type of vegetation did not have an influence on the locations of prey killed. Contrary to expectations, jaguars did not select forested habitats nor did they avoid open fields to make kills, but killed prey in these habitats proportionately to their availability. Our results do not support earlier findings about jaguar habitat use in the southern Pantanal but illustrate the highly opportunistic nature of jaguars. In Chapter IV, we examined space use, site stability and fidelity, movement rates, and interactions of jaguars. Our results suggested a pattern of spatial avoidance among females during the wet season. Among males, home range overlap was extensive, both in the wet and dry seasons, suggesting males did not retain exclusive ranges. Our study provided insights into the dynamic land tenure system of jaguars. Future research would benefit from radio-collaring a large number of individuals and monitoring them over a longer time span to provide a better understanding of their spatial ecology and social interactions.

(155 pages)

DEDICATION

This work is dedicated to the wild spirits of my father (in memoriam), my husband, Antonio, and my 1 year-old son, Nick. For you gatinho, and for you Nickinho, I hope you keep following your untamed spirits, wherever they may take you, for many years to come.

ACKNOWLEDGMENTS

respectively. A special thank you goes to my colleague and friend Silvia Rosa, for the unconditional support she gave me during the later stages of my program at Utah State University, including during the birth of our son. Thank you Silvia. Finally, I would like to thank my husband, Antonio Porfírio, who provided not only assistance of all sorts, but was there for emotional support during all stages of the project.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure   Page

CHAPTER I

INTRODUCTION

Jaguars *(Panthera onca)* constitute an important component of the megafauna of the Neotropics. This large carnivore is considered an indicator of ecosystem health or integrity (Eisenberg 1980, Noss 1995) as well as an umbrella species (Lambeck 1997). In addition, the species has aesthetic value to many cultures throughout its range. In Mexico, Central America, and Indian communities of South America, jaguars are ritualistic symbols of power and beauty and have been incorporated into many religious beliefs and ideologies (Saunders 1991, 1995, 1998; Rabinowitz 1999). In addition, jaguars elicit immense emotions among the public, as the greatest felid of the Neotropics.

Primarily due to land-use changes and subsequent habitat degradation, jaguars are distributed in a fraction of their former range. According to Sanderson et al. (2002), only 46% of their historic range is currently occupied by jaguars. As with many large carnivores, these cats require vast areas of relatively wild habitat. Most jaguar populations are now restricted to isolated reserves or inhospitable, remote areas where human densities are low (Woodroffe 2001, Hoogesteijn et al. 2002).

The Pantanal, a large seasonally inundated plain in South America, harbors abundant wildlife and is important for the long-term persistence of jaguars (Sanderson et al. 2002). In the savannas and gallery forests of the Pantanal, cattle ranching is a traditional activity, with thousands of cattle being grazed in areas used by jaguars and their native prey. Although jaguars exist in considerable numbers in this area (Soisalo and Cavalcanti 2006), they must coexist with an increasing number of humans and domestic cattle. Inevitably jaguars depredate cattle, contributing to the negative image of

the species amongst ranchers, therefore making jaguar conservation in the Pantanal a complex and challenging issue. Despite being illegal, many ranchers kill jaguars on their property in an effort to reduce the economic damage imposed by the cats. Livestock depredation is an important issue for carnivore conservation and finding solutions may be a pre-requisite to successful conservation of many species (Nowell and Jackson 1996, Sagør et al. 1997, Linnell et al. 1999).

The high mortality of jaguars and the increasing number of complaints about livestock depredation, requires a search for alternatives to these conflicts. However, a search for solutions will not be possible without first understanding the dynamics and patterns of depredation in affected areas. If we can identify the factors influencing jaguar predation on cattle, as well as depredation patterns they utilize, we may be able to apply alternative mitigation measures.

Prior research on jaguars has focused on their ecology, home range, and activity patterns (e.g., Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991, Quigley and Crawshaw 1992) with some information on jaguar predation of livestock. However, data on predation was mostly anecdotal or opportunistic. Although our knowledge of jaguar ecology has increased since the first field studies in the mid 1980's, a detailed study of this cryptic species remains challenging. From October 2001 through April 2004, we initiated a study of jaguar ecology in the southern Pantanal using Global Positioning System (GPS) radio collars allowing us to simultaneously monitor several jaguars, without direct observer intervention. We gathered information on animal movements continuously, independent of weather, time of day, or season.

In Chapter II, we examine the foraging ecology of jaguars, documenting kill rates, characteristics of prey killed (species, age), patterns of predation (circadian and seasonal), and the time spent at a kill site and between kills in relation to prey size. In Chapter III, we describe jaguar habitat use and spatial patterns of predation (on both domestic and native species) in relation to the type and distribution of vegetation and other landscape attributes. In Chapter IV, we examine space use, site stability and fidelity, movement rates, and interactions of jaguars, providing insights into the spatial and social ecology of jaguars in the Pantanal wetlands of west-central Brazil. Finally, in Chapter V, we present our synthesis of the overall research findings.

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CHAPTER II

FORAGING ECOLOGY OF JAGUARS (*PANTHERA ONCA)* IN THE SOUTHERN

PANTANAL, BRAZIL – PREDATION RATES, PATTERNS,

AND SPECIES KILLED

Abstract. The jaguar (*Panthera onca*) is a large carnivore of Central and South America. To date, kill rates and predation patterns by jaguars remains undocumented. Previous data on foraging was mainly determined by anecdotal predation events or scat analysis. We studied the foraging ecology of jaguars in the southern Pantanal, Brazil, documenting kill rates, characteristics of prey killed (species and age), patterns of predation (circadian and seasonal), and the influence of prey size on the duration at kill sites and the time interval between kills. Between October 2001 and April 2004, we captured and monitored 10 jaguars equipped with global positioning system (GPS) collars. During 30 months, we collected 11,787 GPS locations and identified 1,105 clusters of locations as sites of concentrated use (e.g., potential kill sites, bed sites, dens). Of these, we found prey remains at 415 kill sites and documented 438 prey items. Of the 438 prey killed, we documented 139 head of cattle (43 adults, 96 calves), 107 caiman (*Caiman crocodilus yacare*), 92 peccaries (mostly *Tayassu pecari*), 18 feral hogs (*Sus scrofa*), 17 marsh deer (*Blastocerus dichotomus*), 14 giant anteaters (*Myrmecophaga tridactyla*), 9 capybaras (*Hydrochaeris hydrochaeris*), 7 brocket deer (*Mazama americana* and *M. gouazoubira*), and a number of other avian, mammalian, and reptilian species. We found individual jaguars differed in their selection of species they killed. There were differences in the proportion of native prey versus cattle killed by individual cats. While all cats killed cattle, some killed a high proportion of cattle, while others

killed few cattle. Between males and females, there was no difference in the proportion of cattle they killed. In contrast, male jaguars killed a higher proportion of peccaries and deer than females. The mean predation rate for all jaguars was 5.1 ± 5.0 (SD) days between kills. Predation rates varied among individuals with the oldest jaguar having the lowest predation rate (7.1 ± 5.6 days between kills) and the youngest cat having the highest predation rate (3.6 ± 3.4 days). However, predation rates were not significantly different among the 10 cats. Jaguars stayed longer at a carcass and killed less frequently when preying on larger prey. Temporally, jaguar predation rates on peccaries steadily increased from the wet season of 2001-2002 to the dry season of 2004. In contrast, predation rates on cattle decreased during the same period. When jaguars killed was distributed across all times of the day and night. Our study provided previously unknown data on jaguar kill rates, predation patterns, and prey species killed in an area with both native prey and cattle.

INTRODUCTION

In many terrestrial ecosystems, predators can influence the behavior, distribution, and abundance of prey species (Lima and Dill 1990, Schmitz et al. 1997), as well as shape community dynamics, structure, and function (Hairston et al. 1960, Terborgh et al. 1999, Berger et al. 2001, Smith et al. 2003). Even though predation is a fundamental aspect of nature, documentation of predation events by large carnivores is extremely difficult owing to their nocturnal and secretive behavior. Among large felids, predation rates have been determined for cougars (*Puma concolor*) in temperate regions using conventional radio-telemetry to locate kill sites (e.g., Murphy 1998, Ruth 2004) and

recently using Global Positioning System (GPS) collars (Anderson and Lindzey 2003).

Kill patterns among African lions (*Panthera leo*) have been documented in grassland

ecosystems where direct observation was possible (e.g., Schaller 1972, Stander and

Albon 1993, Scheel and Packer 1995). For large cats occupying tropical ecosystems,

predation patterns are largely unknown due to the thick vegetation, absence of roads, and

lack of snow cover for backtracking to kill sites.

Jaguars *(Panthera onca)* are an important component of the megafauna of the

Neotropics. Due primarily to land use changes and consequent habitat degradation,

jaguars are now restricted to a fraction of their former range (Sanderson et al. 2002). As

with many large carnivores, these cats require vast areas of relatively wild habitat. Most

populations are restricted to isolated reserves or inhospitable, remote areas where human

densities remain low (Woodroffe 2001, Hoogesteijn et al. 2002). Currently, little is

known regarding kill rates and predation patterns of this elusive species. Much of the

foraging ecology presently known about jaguars is based upon scat analyses or anecdotal

observations.

The Pantanal, a large seasonally inundated plain in South America, harbors

abundant wildlife and is considered important for the long-term persistence of jaguars

(Sanderson et al. 2002). In the savannas and gallery forests of the Pantanal, cattle

ranching is a traditional activity for >200 years, with thousands of cattle grazed in areas

used by jaguars and their native prey. Jaguars exist in considerable numbers in this area

(Soisalo and Cavalcanti 2006), but they kill cattle. This situation inevitably leads to

human-carnivore conflicts often leading to the death of jaguars (Hoogesteijn et al. 2002,

Sáenz and Carrillo 2002, Polisar et al. 2003).

Prior research on jaguars has focused on their ecology, home range, and activity patterns (e.g., Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Quigley and Crawshaw 1992) with some information on jaguar predation of livestock. However, data on jaguar predation was mostly anecdotal or opportunistic. Since predation on livestock threatens the persistence of many populations of large carnivores, documentation of jaguar predation on native and domestic prey is needed for conservation plans (Nowell and Jackson 1996, Sagør et al. 1997, Woodroffe 2001). With the advent of GPS collars, Anderson and Lindzey (2003) demonstrated that prey remains of cougar kills could be relocated several months later and predation rates estimated based upon the duration of time a cougar remained in a location. We believed documentation of kill rates and patterns of predation by jaguars on native and domestic prey would be similarly possible utilizing GPS technology. Therefore, we investigated the foraging ecology of jaguars on a cattle ranch, specifically addressing the following questions: (1) what prey species do jaguars kill and how often do they kill? (2) Do predation rates change seasonally? (3) Do jaguars switch prey over time? (4) Do some cats specialize on livestock? (5) Do jaguars kill only at night? (6) Does the size of prey killed influence when jaguars kill again? To our knowledge, this is the first study on the foraging behavior of jaguars.

METHODS

The study area was located in the southern Pantanal, a flood plain of 140,000 km^2 located in west-central Brazil. The study site was a privately owned ranch of 460 km^2 with 7,000 beef cattle. Elevation ranges from 89 m to 120 m above sea level. The

climate includes a seasonal rainy season between October and March with an average monthly precipitation of 144.8 mm. The concentration of rains influences the level of the rivers which flood large areas in the wet season. The dry season, between April and September, has a monthly average precipitation of 47.7 mm. The hot and cool seasons coincide with the rainy and dry seasons, respectively. Low temperatures reach 18.5°C in June and July while high temperatures reach 42.5 $^{\circ}$C in October.

The vegetation is as a mosaic complex with influences from different biomes such as cerrado in central Brazil, the Paraguayan Chaco, and the Amazon Forest (Prance and Schaller 1982). The main habitats include open fields interspersed with islands of secondary forest, and gallery forests bordering temporary and permanent rivers. Potential prey include white-lipped (*Tayassu pecari*) and collared (*Pecari tajacu*) peccary*,* caiman (*Caiman crocodilus yacare*), marsh deer (*Blastocerus dichotomus*), feral hog (*Sus scrofa*), brocket deer (*Mazama americana* and *M. gouazoubira*)*,* giant anteater (*Myrmecophaga tridactyla*), armadillo (*Euphractus sexcinctus* and *Dasypus novemcinctus*), capybara (*Hydrochaeris hydrochaeris*), and various other mammals, birds, and reptiles. During the dry season, cattle are widely dispersed throughout the study area. During the wet season, cattle are herded to drier areas, but remain widespread over large pastures. Cattle are unguarded and wander free day and night.

Capture and radio collaring of jaguars

We searched areas on the ranch for recent jaguar tracks from a vehicle or horseback in the morning. If recent sign was found, we released trained hounds in an attempt to tree the cat. We immobilized treed cats with tiletamine hydrochloride and

zolazepam hydrochloride (Telazol,® Fort Dodge, São Paulo, Brazil), or a combination of Telazol and ketamine hydrochloride, using a dart fired from a CO_2 pistol or a rifle. Upon darting the animal, we removed the hounds from the immediate area. We examined each jaguar for body condition, sex, age, weight, and fitted them with a GPS collar (Simplex, Televilt International, Sweden) and released them at the site of capture. We estimated age by the presence of milk teeth or permanent dentition, and tooth color and wear (Ashman et al. 1983).

Radio tracking and analyses

We obtained locations from the GPS collars with a high degree of accuracy and precision (ground tests showed error was <10 m). The collar had a downloadable data retrieval system and conventional store on-board system. In 2002, we programmed the collars to record fixes every 2-hours between 1800 and 0600 hr (7 fixes/night). At the end of 2002, we changed the programming of the collars to record fixes every 2-hours throughout the 24-hour period, (12 locations/24-hr period). Due to the flat topography of the Pantanal, we included both 2-D and 3-D locations in our analyses.

We used a receiver to remotely download the data from the collars (RX-900, Televilt International, Sweden). We used the regular VHF transmitter in the collars both as a beacon and as a radio link for transfer of the coded GPS data to the remote receiver. We downloaded data every 21-24 days, with the same set of data being able to be downloaded on four consecutive days. The large number of individual locations provided continuous information on animal movements, independent of weather, time of day, or season. We recovered the collars for battery replacement every 10-11 months by

recapturing the jaguars using hounds. After each jaguar was recaptured, another collar
was attached to the animal while the data from the retrieved collar was downloaded
directly into a computer and the battery replaced before deployment on another
individual.

We identified potential predation sites by locations provided by the GPS collars
(Anderson and Lindzey 2003). After each remote data download, we plotted locations
from individual jaguars on a map of the study area (1:100,000) using ArcView
(Environmental Systems Research Institute, Redlands, California). Identification and
analysis of clusters of locations were used to determine potential kill sites. When two or
more consecutive locations were found <100 m from each other, we classed these sites as
potential kill sites (Anderson and Lindzey 2003). We entered the coordinates of location
clusters into a hand-held GPS receiver, then visited and searched each site for possible
prey remains. We searched the area on foot to a diameter of 50 m; if no prey remains
were found within that circle, the cluster was not considered a kill site. We recognize
that smaller prey items may have gone undetected with this method (i.e., either the prey
was completely consumed or the remains were carried from the kill site), but we did
locate and identify some prey items <5 kg in size (e.g., armadillo; raccoon, *Procyon
cancrivorus*).

The time elapsed between the GPS positioning of the jaguar and the field searches
for carcasses on those same positions ranged from one to 21 days. If a radioed jaguar
was in the vicinity of a particular cluster of locations at the time of searching, we
investigated the site after the cat moved away. For each prey item located, we recorded
the coordinates, species, and age class. When possible, we recorded the sex of the prey

species, but were often unsuccessful due to consumption or deterioration of the carcass. We considered the first location within the cluster to be the date and approximate time the predation event took place. Therefore, we were able to calculate predation rates throughout the year for each individual jaguar. We did not estimate biomass consumed or state of carcass decomposition due to the relatively fast rate of carcass deterioration in the tropics. Kill rates were estimated based on time intervals between known consecutive kills found for each cat. For seasonal comparisons, we calculated the number of caiman, peccaries, and calves killed by jaguars annually based on mean kill rates in the dry and wet seasons of each year; other prey species were killed too infrequently for seasonal comparisons. Results were analyzed in terms of composition (proportion of kills), frequency (# killed/month), and rate of killing (# days between kills) as these values represent different measures of predation and prey selection. For example, if one jaguar kills 5 caiman and 5 cattle in 30 days, then the composition is 50% caiman and 50% cattle, the frequency is 10 kills/month, and the rate is 3 days between kills. In contrast, if another cat kills 5 caiman and 5 cattle in 60 days, then the composition is the same, but the frequency is 5 kills/month and the predation rate is 6 days between kills.

RESULTS

Between October 2001 and April 2004, we equipped and monitored 10 jaguars (five adult males, one subadult male, four adult females) with GPS collars. Radioed jaguars were monitored for a total of 76 radio-months. Continuous monitoring of individual cats varied from 1.5 to 24 months (Table 1). We were able to simultaneously monitor three to five jaguars at any one time (Figure 1). Data collection occurred during

the wet seasons of 2001-2002, 2002-2003, 2003-2004, and the dry seasons of 2002, 2003, and 2004; although data from the latter was limited.

From 11,787 GPS locations, we identified 1,105 clusters of locations (i.e., potential kill sites, bed sites, dens). Of these, we were not able to check 155 clusters (14.0%) due to inaccessible terrain; 78 and 77 during the wet and dry seasons, respectively. Eleven clusters (1.2%) were related to social interactions between a pair of radioed cats (Cavalcanti and Gese, unpublished data).

Of the 939 remaining clusters we checked, we found no evidence of any prey item at 524 despite intensive search efforts. At these sites, we encountered either day beds, scratches on trees or the soil, scats, or simply no sign of the cats presence. We found prey remains at 415 location clusters which we considered kill sites. At these 415 kill sites, we documented 438 prey items (Table 2). At 23 kill sites, we found two carcasses of prey species killed by jaguars. Although both carcasses were fed upon, it was difficult to affirm if both prey had been actively hunted or which species had been killed first. At 15 sites, we found remains where one of the species killed (e.g., feral hog, peccary, armadillo, raccoon, or caiman) may have been scavenging a jaguar-killed carcass and was killed when the jaguar returned to the site. At the other sites, we found remains of species not known to eat carrion (e.g., calf, brocket deer, giant anteater, lesser anteater), suggesting the jaguar killed them, although not at the same time.

Composition of prey species killed

Of the 438 carcasses of prey found, 299 (68.3%) were native prey species and 139 (31.7%) were cattle. There was a significant difference in the proportion of native prey

versus cattle killed by individual jaguars (χ^2 = 57.07, df = 9, P < 0.0001); some jaguars had >50% of their kills consisting of cattle, while others did not exceed 5% (Table 2). Some cats appeared to specialize on a few species and others were more generalists (Table 2), but the number of prey species killed by individual cats was not different (χ^2 = 10.44, df = 8, P = 0.23). However, the proportion of prey species killed varied among the individual cats (χ^2 = 318.23, df = 9, P < 0.0001), indicating they selected different species, possibly due to varying prey availability or vulnerability, or individual preference among the jaguars. When we examined the proportion of large ($\geq$30 kg) prey only among the jaguar kills for which we had at least 15 kills (n = 9), we found the proportion of large prey killed varied significantly among individual jaguars for calves (χ^2 = 58.45, df = 8, P < 0.0001), caiman (χ^2 = 46.05. df = 8, P < 0.0001), and peccaries (χ^2 = 48.34, df = 8, P < 0.0001). In contrast, there was no difference in the proportion of kills of adult cows (χ^2 = 10.22, df = 8, P = 0.24), or deer (marsh deer and brocket deer combined; χ^2 = 11.04, df = 8, P = 0.19) killed by individual cats. Among radioed jaguars, female #2, female #3, and male #3 appeared to kill caiman more frequently than the other cats. Likewise, male #5 appeared to kill peccaries more frequently than the rest of the radioed jaguars (Table 2).

When comparing between the sexes, the distribution of prey species killed by male and female jaguars varied. There was no difference in the proportion of cattle killed by male (29.0%) and female (34.2%) jaguars (χ^2 = 1.36, df = 1, P = 0.24). Among cattle kills only, calves made up 65.8% and 73.3% of the kills by females and males, respectively (χ^2 = 0.09, df = 1, P = 0.34). Correspondingly, adult cows made up 34.2% and 26.7% of the cattle killed by female and male jaguars, respectively. In contrast, there

was a difference in the proportions of caiman, peccaries, and deer killed by male and female jaguars. Female jaguars killed caiman at almost twice the proportion than males (females: 31.2%, males: 16.9%; $\chi^2 = 12.02$, df = 1, $P = 0.0005$). However, for female #2 alone, caiman comprised 41.9% of her kills (Table 2). When we re-analyzed the data excluding her from the data set, we found no difference in the proportion of caiman killed by male versus female jaguars ($\chi^2 = 0.15$, df = 1, $P = 0.69$). In contrast, male jaguars killed peccaries at a higher proportion than females (females: 15.2%, males: 27.5%; $\chi^2 = 10.09$, df =1, $P = 0.0015$), even after we excluded male #5 (55.6% of his kills were peccaries) from our analysis. There was also a difference in the proportion of deer (marsh deer and brocket deer combined) killed by male (7.7%) versus female jaguars (3.4%; $\chi^2 = 3.84$, df =1, $P = 0.050$).

Although the jaguars differed in their distribution of prey species killed, caiman, peccaries, and cattle (calves and adult cows) comprised the majority (>75%) of all their kills. To examine the influence of climatic variation on prey selection, we examined the distribution of jaguar kills for the three major species (caiman, peccary, and cattle) during 2002 and 2003 (the driest and wettest of 8 years on the study site, respectively; Figure 2). The proportion of cattle (calves and adults combined) amongst jaguar kills decreased from 49.9% in 2002 to 19.2% in 2003 ($\chi^2 = 30.82$, df = 1, P < 0.0001). In contrast, the proportion of peccaries in jaguar kills increased from 9.6% in 2002 to 31.8% in 2003 ($\chi^2 = 28.59$, df = 1, P < 0.0001). Caiman comprised relatively similar proportions of jaguar kills in 2002 (19.1%) and 2003 (26.7%; $\chi^2 = 3.05$, df = 1, P = 0.08).

With respect to cattle being killed by jaguars, carcasses were classified as young (calves 1 day to 12 months of age) and adult (heifers and adult cows $\geq$12 months of age).

Calves accounted for 69% of the total livestock carcasses found (n = 96). The remaining

31% were heifers (n = 6), adult cows (n = 36), and an adult bull (n = 1). Of the adult cow

and bull carcasses found, 6 may not have been killed by jaguars since evidence suggested

they may only have been scavenged by jaguars.

Jaguar predation rates

We monitored individual cats for periods ranging from 1.5 to 24 months (0 = 8.25

months). The number of kills by individual jaguars during the interval they were

monitored ranged from 5 to 124 kills (Table 1). The mean predation rate on all prey

species for all jaguars was 5.1 ± 5.0 (SD) days between kills (95% confidence interval

[CI] = 0.1 to 10.1 days between kills). Predation rates varied among individuals jaguars

(Table 1) with the oldest cat (male #1) having the lowest predation rate. In contrast, a

subadult male (male #6) had the highest predation rate, but was accompanied by his

mother and sibling. Despite these apparent differences, predation rates were not

significantly different among the individual cats ($F = 1.624$; df = 8, 406; $P > 0.05$). The

mean predation rate for females and males was 5.0 ± 5.0 days between kills (95% CI = 0

to 10.0 days) and 5.3 ± 5.1 days between kills (95% CI = 0.2 to 10.4 days), respectively,

and was not different between the sexes ($t = 0.592$, df = 413, $P > 0.05$).

With regards to the various prey killed, jaguars killed on average 1 calf every 13.3

± 15.5 days. Adult cows were killed at a lower rate (25.5 ± 18.4 days between kills).

Caiman were killed on average every 13.7 ± 15.7 days and peccaries were killed every

14.8 ± 14.8 days. The amount of time elapsed from killing a prey item (n) to killing the

next prey (n + 1) significantly increased with increasing body mass of prey ($F = 2.996$; df

= 4, 347; $P = 0.019$). After killing and consuming a small prey item, a jaguar generally

killed again in a shorter time interval as compared to when they killed larger prey (Figure

3). Similarly, the length of time jaguars stayed at a carcass site significantly increased

with increasing body mass of prey ($F = 2.935$; df = 4, 430; $P = 0.021$) with smaller prey

species consumed more rapidly than larger prey species (Figure 4). The larger the prey,

the longer a jaguar generally stayed at the carcass, suggesting they utilized a significant

portion of the carcass. Although we could not document the amount of each carcass

consumed by jaguars, we assumed the continuous locations of a jaguar at a carcass site

was related to feeding, guarding, and perhaps prey caching.

Circadian timing of predation events

Jaguars are often considered a night time predator. Therefore, we examined the

time of day in which prey items were killed by assuming the first location at the carcass

represented the time of the kill. We only used data from jaguars on the 24-hr GPS

location schedule. Since the distribution of successful GPS location attempts throughout

the day was not similar among the radioed cats ($\chi^2 = 100.26$, df = 11, $P < 0.05$), we used

the proportions of acquired locations to test for differences in the times of the day of the

first known location of jaguars at kills of caiman, peccaries, cattle, and all species

combined. When we examined the frequencies of the times of kills in relation to the

proportion of locations obtained, it appeared the time of kills were distributed evenly

across all time periods (cattle: $\chi^2 = 13.27$, df = 11, $P = 0.2762$; peccaries: $\chi^2 = 13.10$, df =

11, $P = 0.2868$; caiman: $\chi^2 = 10.74$, df = 11, $P = 0.4652$; all species: $\chi^2 = 15.29$, df = 11,

$P = 0.1697$), suggesting jaguars did not select specific time periods to kill prey (Figure 5).

Seasonality of predation events

To determine whether jaguars were switching prey, we assessed the average number of the three major prey species killed by jaguars each season. Of the native prey remains found, 130 (43.5%) were found during the wet seasons. We found the remaining 169 (56.5%) in the dry seasons. For the cattle kills, 45 (32.4%) were found in the wet seasons and 94 (67.6%) in the dry seasons. When we examined the mean number of cattle, caiman, and peccaries killed by radioed cats throughout the study, a seasonal pattern of predation by jaguars emerged. The mean number of cattle killed by jaguars each month peaked in the dry seasons, although there appeared to be a difference between years (Figure 6). When we divided the cattle component into adults versus calves, the pattern suggested that calves were most heavily depredated during the dry season of 2002 compared to 2003, but with predation still occurring in the wet season but at a much lower frequency (Figure 7).

Although the frequency of predation on caiman appeared to be evenly distributed throughout 2002, we found that during 2003 and 2004 jaguar predation on caiman apparently peaked during the wet season (Figure 6). Coincident with this, jaguar predation on cattle decreased when predation on caiman increased. Although the frequency of jaguar predation on peccary appeared to be evenly distributed throughout 2002, it appeared to increase in 2003 and 2004. The mean number of peccaries killed

each month by jaguars was lowest during the wet seasons (February-March) and highest throughout the remainder of the year (Figure 6).

Since caiman, peccaries and cattle comprised 77.1% of all jaguar kills found, we analyzed the jaguars' kill rates for these three species throughout the study to examine the seasonal variation in predation rates of these major prey species from 2001 to 2004. Although the kill rates of cattle declined between 2002 and 2004 (Figure 8), this difference among the seasons was not significant ($F = 1.770$; df = 4, 101; $P = 0.141$). The same is true for jaguar predation rates on caiman which seemed to increase between the wet seasons of 2001-2002 and 2002-2003, but not significantly ($F = 1.767$; df = 4, 85; $P = 0.143$). Jaguar predation rates on peccaries were different between the seasons (Figure 8), increasing steadily between the wet season of 2001-2002 and the dry season of 2004 ($F = 4.675$; df = 4, 68; $P = 0.002$). Jaguar kill rates suggest an increasing reliability on peccaries as prey during the study.

DISCUSSION

Although jaguars are extremely powerful and able to subdue large prey species, our results indicated they are opportunistic and prey on a variety of species, including small prey. Jaguar feeding habits and the relative importance of different prey species varied considerably among geographically distinct populations (Oliveira 2002). We found jaguars killed 24 different species of prey on our site (Table 2). Since our data was based on the frequency of jaguar kills and predation rates, direct comparisons with studies based on scat analysis may be inappropriate. Nonetheless, if we examine the occurrence of prey species present in scats, independent of their quantity, and assume

jaguars kill the prey they consume, a comparison may still be possible. In contrast to our results, in Venezuela, jaguars preyed upon capybaras and collared peccaries, but killed caiman less than expected (Polisar et al. 2003). White-lipped peccaries were also important to jaguars in a study in southwestern Brazil, comprising 77% of their diet (Crawshaw et al. 2004). In Mexico, Nuñez et al. (2000) observed white-tailed deer (*Odocoileus virginianus*) comprised the majority of jaguar diet, but jaguar diets in Guatemala were dominated by smaller species like armadillo and coati (*Nasua nasua*; Novack et al. 2005). In the northern Pantanal, Dalponte (2002) found capybaras comprised the base diet of jaguars. In our study area, capybaras comprised only 2% of jaguar kills (Table 2). In addition to ungulates, we also documented jaguars killing other predators, including maned wolves (*Chrysocyon brachyurus*), crab-eating foxes (*Cerdocyon thous*), coati, and crab-eating raccoons (*Procyon cancrivorus*).

We found individual jaguars killed prey differentially, indicating either there was a learning or search image component involved in prey selection, there were individual preferences among the jaguars for certain prey, or that certain prey species varied in their availability or vulnerability in each jaguars territory. For example, female #2 killed five times as many caiman as female #1. Variations in prey consumption by jaguars likely reflect local patterns of prey occurrence and distribution (Dalponte 2002, Oliveira 2002). Unfortunately, given the nature of our study and the diversity of native prey species present, we were unable to examine the relationship between prey selection and prey availability.

We found a difference in the proportion of peccaries killed by male and female jaguars. A possible reason for this difference may be due to the movement patterns of

peccaries. Although peccaries exhibit regular and predictable movements within their home range (Fragoso 1998), their home ranges can be extensive, especially during flooding when their home ranges double in size (Fragoso 1998). This may facilitate predation by more mobile male jaguars that travel over larger home ranges. Alternatively, male jaguars with their larger body size may be more adept at selecting and killing peccaries from the herd without injury to themselves as compared to smaller female jaguars. Differential habitat use between male and female jaguars could also possibly explain this difference in predation rates on peccaries.

In our study, jaguar predation on caiman peaked during the wet season when caiman densities were generally lower (Coutinho and Campos 1996, Campos et al. 1994), but more widely dispersed across the landscape due to higher water levels and therefore available to more jaguars. In addition, the peak of egg laying for caiman also occurs during the wet season (Coutinho and Campos 1996), making female caiman less mobile and possibly more vulnerable to jaguar predation. One hypothesis was that jaguar predation on caiman should occur at higher proportions during the dry season, when only a few sites contain water of suitable depth and caiman are congregated (Coutinho and Campos 1996). However, the dry season is also the peak of the cattle calving season, thereby increasing the availability of vulnerable calves. Jaguars appeared to switch to this more vulnerable resource at that time.

Although jaguars killed a variety of native prey, cattle still comprised a major part of their kills. The importance of cattle to jaguars varies among jaguar populations. In some areas, jaguar predation on cattle is not a serious problem. In Mexico, Nunez et al. (2000) found jaguars did not kill livestock. Rabinowitz (1986) tracked two jaguars that

traveled regularly near cattle without causing problems. In the northern Pantanal, cattle were important in terms of available biomass (Schaller and Crawshaw 1980), but jaguar kill rates were not determined. Dalponte (2002) indicated that together with capybaras, cattle represented the base diet of jaguars in the northern Pantanal, representing 63% of items found in jaguars scats. Crawshaw and Quigley (2002) found cattle comprised 46% of jaguar kills in the southern Pantanal, although their data consisted of kills reported by ranch hands, who are generally more aware of cattle kills than kills of native prey. In addition, some native prey are smaller and may be killed and consumed in secluded sites making kills more difficult to find, and therefore may be underrepresented.

We note that the majority of studies of jaguar diets to date are based on the analysis of scats or carcasses found opportunistically. In contrast, we monitored jaguar movements every two hours and essentially followed them to document what they were killing. Although this sampling was not considered perfect as we may be have missed some small prey the cats killed and consumed in <2 hours, this methodology provided a less biased representation of kill rates. Therefore the predation rates presented could be considered a minimum estimate. However, we did locate remains of several small prey species (e.g., birds, caiman lizard, coati, small anaconda, armadillo). These constituted a small proportion of biomass killed and consumed when compared to the larger prey species.

When Crawshaw and Quigley (2002) examined 17 prey items obtained by homing in on radioed jaguars, they found 29% were cattle, while 41% were white-lipped peccaries. This is similar to our overall finding, which indicated cattle accounted 29.9% of jaguar kills. But because our study took place during two of the more extreme years in

terms of climatic conditions, we prefer to report the relative frequency of cattle among jaguar kills as ranging between 48.9% and 19.2%, reflecting the driest and wettest weather conditions during our study.

Our data on the age of cattle killed by jaguars is similar to other studies. In Venezuela, jaguars attacked young cattle (weaned calves and heifers 1-2 years of age) more often than adults (Hoogesteijn et al. 1993, Farrell 1999, Scognamillo et al. 2002). In northeast Argentina, cattle between 1-3 years comprised the majority of jaguar kills (Perovic 2002). In our study, calves accounted for 69% of all cattle killed by jaguars, higher than the 43% reported by Crawshaw and Quigley (2002) in the southern Pantanal. However, this could be an artifact of the methodology used. When jaguar kills are found opportunistically, there may be a bias in the size of prey one is able to find. Moreover, data from our study suggested the age class of cattle killed can vary among jaguars and environmental conditions.

Jaguars can kill mature bulls (Hoogesteijn et al. 1993), but we did not document a single jaguar attack on an adult bull, and only one instance of scavenging on a bull carcass. Contrary to the popular belief that jaguars kill the majority of their prey, we did find they scavenge as well. We are aware of only one such reference in the literature (Lopez-Gonzales and Piña 2002). We documented 6 occasions in which jaguars were located at carcasses of cattle that died from other causes. While the relative importance of cattle in the diet of jaguars can be determined by scat analysis, it does not confirm that the cattle were killed by jaguars.

While every jaguar we monitored killed cattle, there was a difference in the proportion of native prey and cattle killed by each cat. While some cats had >50% of

their kills as cattle, for other jaguars this proportion did not exceed 5%. These individual differences in prey killed raise the question of 'problem animals' (Linnell et al. 1999). The belief that destroying or removing a problem animal would end the predation problem (Rabinowitz 1986, Hoogesteijn and Mondolfi 1992) may not hold true in our area. The annual variation in kill rates likely reflected differences in availability or vulnerability of alternative prey; some jaguars that had >50% of their kills as cattle in 2002, decreased their predation rate on cattle in 2003. Some studies indicate livestock-depredating cats are more likely to be males than females (e.g., Rabinowitz 1986, Stander 1990, Chellam and Johnsingh 1993), for which we found no support. Some authors (Rabinowitz 1986, Stander 1990, Saberwal et al. 1994) suggest livestock-depredating cats are more likely to be subadults than adults. However, other studies report adults more likely to kill cattle than younger animals (Bowns 1985, Esterhuizen and Norton 1985). Because we only had one subadult jaguar accompanied by his mother and a sibling, we were unable to conclude whether the age of the jaguar made it more prone to kill cattle.

Some studies suggest the majority of livestock killers were animals that had been wounded, and therefore incapable of normal hunting behavior (Rabinowitz 1986, Fox and Chundawat 1988, Hoogesteijn et al. 1993). In two studies in Venezuela, the majority of the cats (75% and 53%) killed for depredation control had previously sustained severe wounds (Hoogesteijn et al. 1993). However, seemingly healthy animals also killed livestock. In our study, all radioed cats that killed cattle were in excellent physical condition at the time of capture, similar Schaller and Crawshaw (1980) and Hopkins (1989). Additionally, older and more debilitated individuals seemed to have no problem killing 'dangerous' native prey.

Rabinowitz (1986) suggested that once an individual jaguar preyed on cattle, it continued to treat cattle as a main source of food. Data from 2002 suggested that climatic conditions played a stronger role in jaguar prey selection than individual preference or propensity to kill livestock and that prey switching was common. Our study took place during extreme climatic conditions, and the majority of cattle losses occurred in 2002 when drought conditions were severe. Some native prey may have either migrated from the area (peccary), were concentrated only along the main river courses or lakes (caiman), or were reduced in number. Concurrently, due to low water levels, cattle were distributed throughout the ranch and available to all radioed jaguars. Like other large carnivores, jaguars may target livestock when livestock is readily available and native prey is less accessible. Given the nature of cattle operations in the Pantanal, it is likely that some degree of depredation on cattle will always occur. The high stocking rates of cattle (i.e., biomass) may indeed be supporting a high density of jaguars. We also recognize that the consequence of high stocking rates of cattle on the distribution and abundance of native prey populations is currently unknown.

The increase in kill rates by jaguars on peccaries during the study suggested there was an increasing reliability on peccaries as prey, either due to availability or selection. Although there is little known on the population dynamics of peccaries in the Pantanal, recent data suggested their population densities are high (9.63 individuals/km^2) but predation is rarely documented (Keuroghlian 2003). The increased importance of peccaries in the kills of jaguars could have important implications not only on the dynamics of the predator-prey system in the Pantanal, but also on jaguar-livestock conflicts as jaguar predation on cattle decreased as predation on peccaries increased.

Although jaguar predation on cattle continues to be a problem, maintaining alternate native prey populations may buffer these conflicts.

In summary, our study presented data on the feeding ecology of jaguars, documenting detailed information on jaguar kill rates and predation patterns. We found jaguars did not select specific time periods to kill their prey, suggesting kills were made opportunistically throughout the day and night. This result was not surprising given the mosaic vegetation providing ambush cover for jaguars. This kill distribution may also reflect the activity patterns of the prey killed by jaguars, as well as behavioral flexibility by jaguars to hunt during the day, not just at night. We found individual variation in jaguar prey selection under different climatic conditions. We found the length of time between kills, as well as how long a jaguar remained at a kill, were influenced by prey size. In addition, we illustrated the possible role native prey abundance could have on jaguar predation of cattle. Knowledge of predator-prey relationships will be important in guiding future management decisions and conservation plans for this large keystone predator in the face of an ever expanding human population.

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Table 1. Length of monitoring period, number of GPS locations acquired, number of kills found, and predation rates

for 10 jaguars, November 2001 to April 2004, southern Pantanal, Brazil.

Jaguar ID	Monitoring period (months)	# of GPS locations acquired	Number of kills found	Predation rate (days/kill±SD)
Adult male #1	10	1024	47	7.1 ± 5.6
Adult male #2	5	745	36	3.9 ± 3.2
Adult male #3	3	453	18	4.8 ± 4.8
Adult male #4	11	1543	40	6.0 ± 4.5
Adult male #5	6	721	36	5.1 ± 6.7
Subadult male #6	3	716	27	3.6 ± 3.4
Adult female #1	15	2025	80	5.3 ± 6.0
Adult female #2	24	3932	123	4.8 ± 4.5
Adult female #3	4	512	22	4.8 ± 4.5
Adult female #4	1.5	116	5	-

Table 2. Distribution of prey species (n, (% of kills)) detected at kill sites for 10 individual jaguars, November 2001 to April 2004, southern Pantanal, Brazil.

Prey	Adult female #1 (n=80)	Adult female #2 (n=123)	Adult female #3 (n=22)	Adult female #4 (n=5)	Adult male #1 (n=47)	Adult male #2 (n=36)	Adult male #3 (n=18)	Adult male #4 (n=40)	Adult male #5 (n=36)	Subadult male #6 (n=27)
tapir	0	0	0	0	0	0	0	1 (2.50)	1 (2.78)	0
birds[a]	0	1 (0.81)	0	0	1 (2.13)	1 (2.78)	0	0	0	0
calf	30 (37.5)	18 (14.6)	0	3 (60.0)	24 (51.1)	3 (8.33)	2 (11.1)	7 (17.5)	1 (2.78)	6 (22.2)
capybara	4 (5.0)	1 (0.81)	0	0	0	0	0	1 (2.50)	0	3 (11.1)
marsh deer	3 (3.75)	2 (1.63)	1 (4.54)	0	4 (8.51)	1 (2.78)	0	2 (5.0)	0	3 (11.1)
maned wolf	2 (2.50)	1 (0.81)	0	0	0	0	0	0	0	0
land turtle	1 (1.25)	0	0	0	0	0	0	0	0	0
caiman	10 (12.5)	52 (42.3)	9 (40.9)	1 (20.0)	4 (8.51)	8 (22.2)	7 (38.9)	3 (7.50)	8 (22.2)	5 (18.5)
crab eating fox	0	1 (0.81)	0	0	0	0	0	1 (2.50)	1 (2.78)	0
racoon	0	0	1 (4.54)	0	0	1 (2.78)	0	0	1 (2.78)	0
feral hog	3 (3.75)	4 (3.25)	1 (4.54)	0	6 (12.8)	1 (2.78)	1 (5.55)	2 (5.0)	1 (2.78)	0
coati	0	0	1 (4.54)	0	1 (2.13)	1 (2.78)	0	0	0	2 (7.40)
peccary[b]	7 (8.75)	23 (18.7)	5 (22.0)	0	4 (8.51)	11 (30.5)	6 (33.3)	14 (35.0)	20 (55.6)	2 (7.40)
anaconda	0	0	0	0	0	0	0	0	0	1 (3.70)
giant anteater	7 (8.75)	2 (1.63)	0	0	1 (2.13)	3 (8.33)	0	0	1 (2.78)	0
lesser anteater	1 (1.25)	1 (0.81)	0	0	0	3 (8.33)	0	2 (5.0)	0	0
armadillo[c]	2 (2.50)	0	3 (13.6)	0	0	0	0	1 (2.50)	0	0
adult cattle	9 (11.2)	16 (13.0)	1 (4.54)	1 (20.0)	2 (4.25)	2 (5.55)	2 (11.1)	5 (12.5)	0	4 (14.8)
brocket deer[d]	1 (1.25)	0	0	0	0	1 (2.78)	0	1 (2.50)	2 (5.55)	1 (3.70)
caiman lizard	0	1 (0.81)	0	0	0	0	0	0	0	0

[a] Includes an egret (*Egretta alba*), a jabiru stork (*Jabyru mycteria*), and a boat-billd heron (*Cochlearius cochlearius*).
[b] Although collared peccaries (*Tayassu tajacu*) were present, the vast majority killed by jaguars were white-lipped peccaries.
[c] Includes two species of armadillos present in the sudy area, *Euphractos sexcinctus* (n=4) and *Dasypus novencinctus* (n=1).
[d] Includes both species, *Mazama americana* and *Mazama gouazoubira*.

Figure 1. Monitoring periods for each individual collared jaguar. Solid lines show period in which cats were monitored with GPS collars.
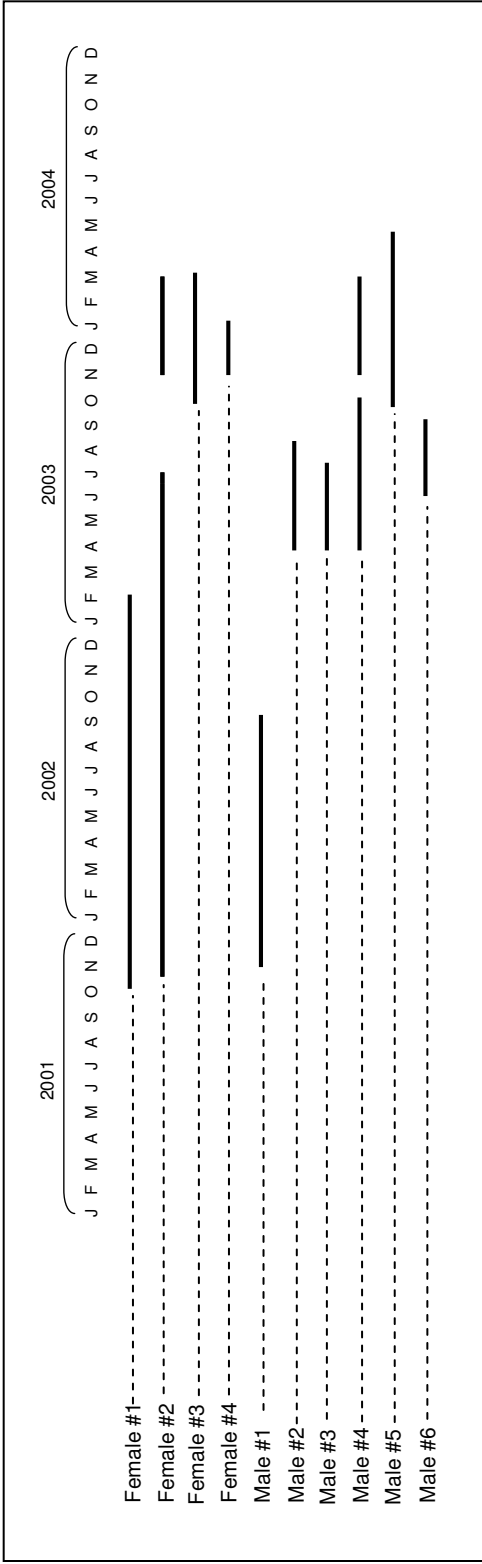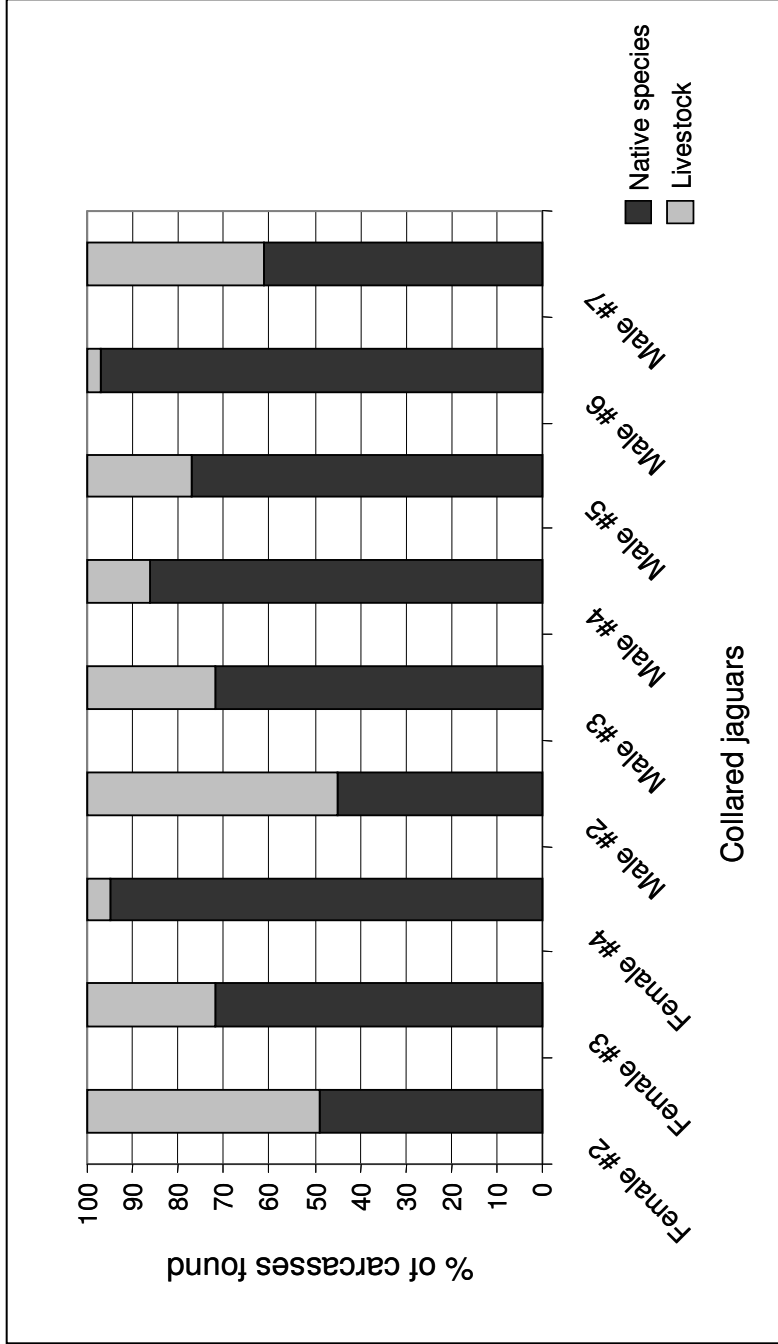
Figure 2. Distribution of native prey species and livestock killed by collared jaguars, November 2001 to April 2004, southern Pantanal, Brazil.
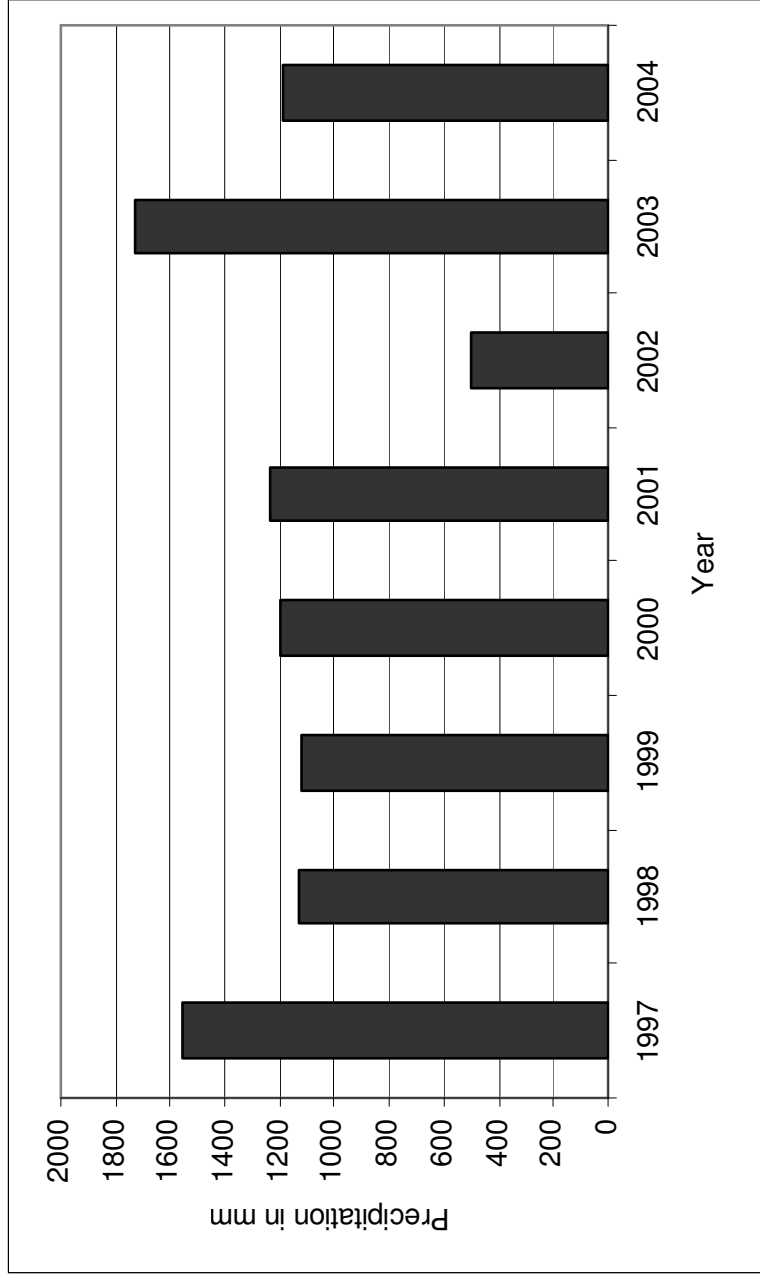
Figure 3. Total annual precipitation at the study site from 1997 to 2004, southern Pantanal, Brazil.
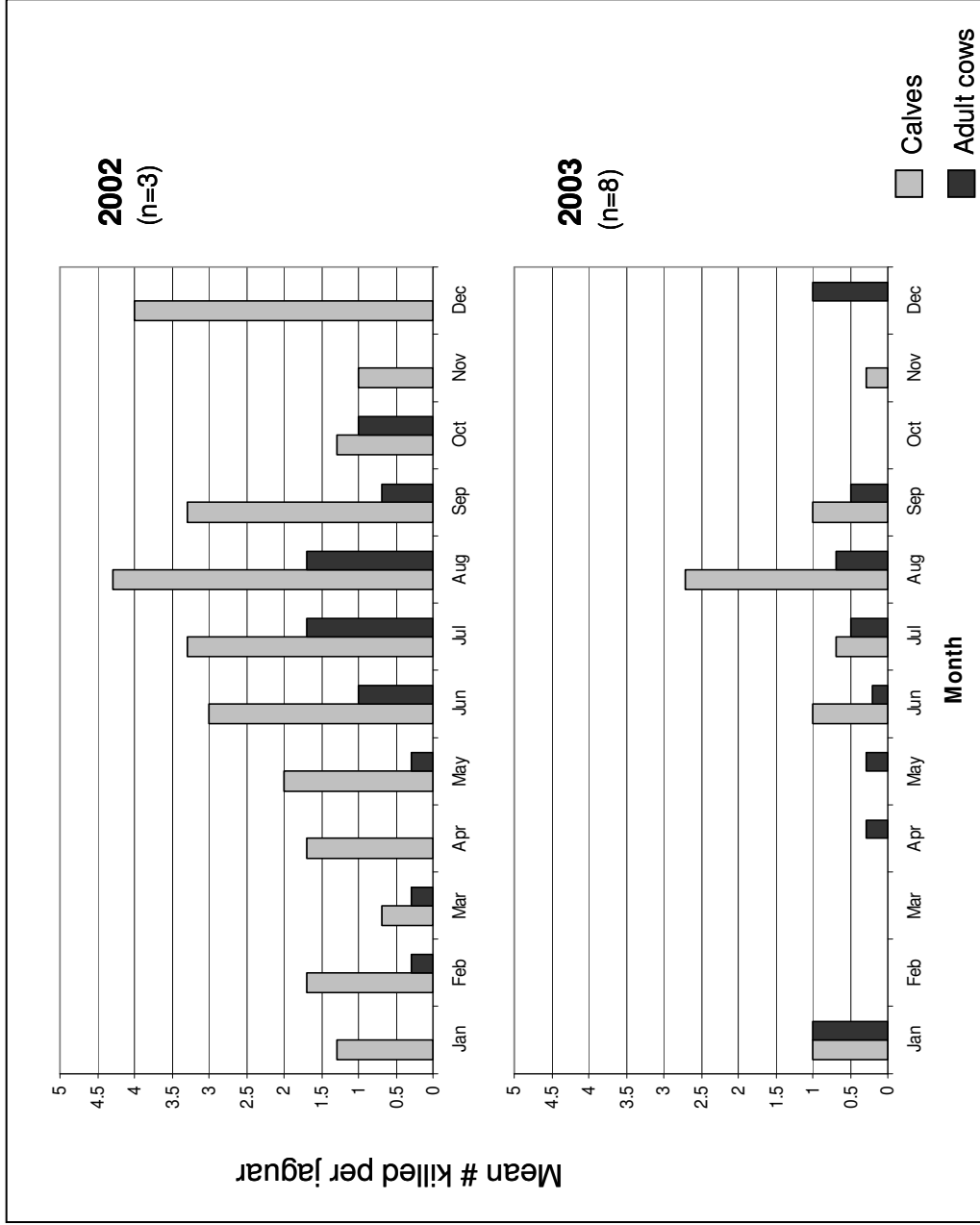
Figure 4. Mean number of adult cows and calves killed by radioed jaguars each month during 2002 and 2003 in the southern Pantanal, Brazil (n=number of collared cats monitored in that year).
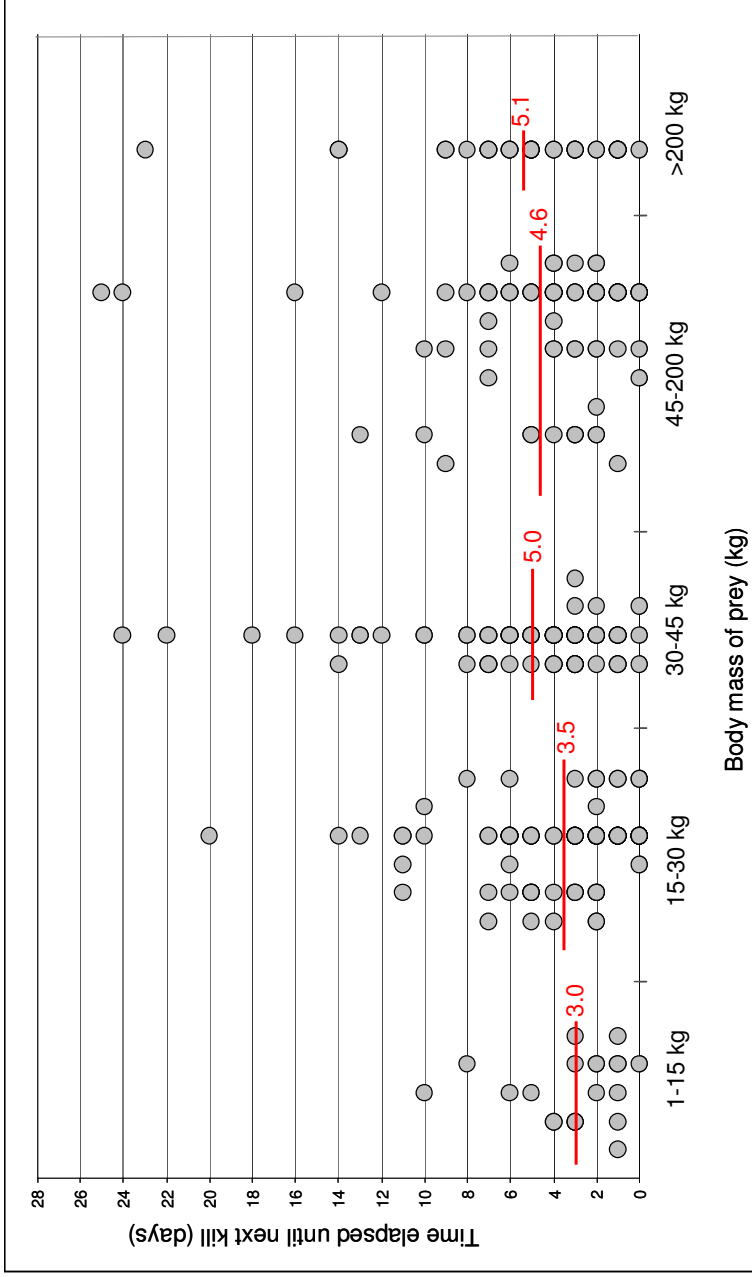
Figure 5. Time elapsed until the next kill by a jaguar in relation to the body mass of prey. Circles show time intervals (n=315) between consecutive kills by jaguars. Horizontal bars and numbers indicate mean values. Frequency distributions significantly differed among the five classes of prey body mass (F = 2.996; df = 4, 347; P = 0.019).
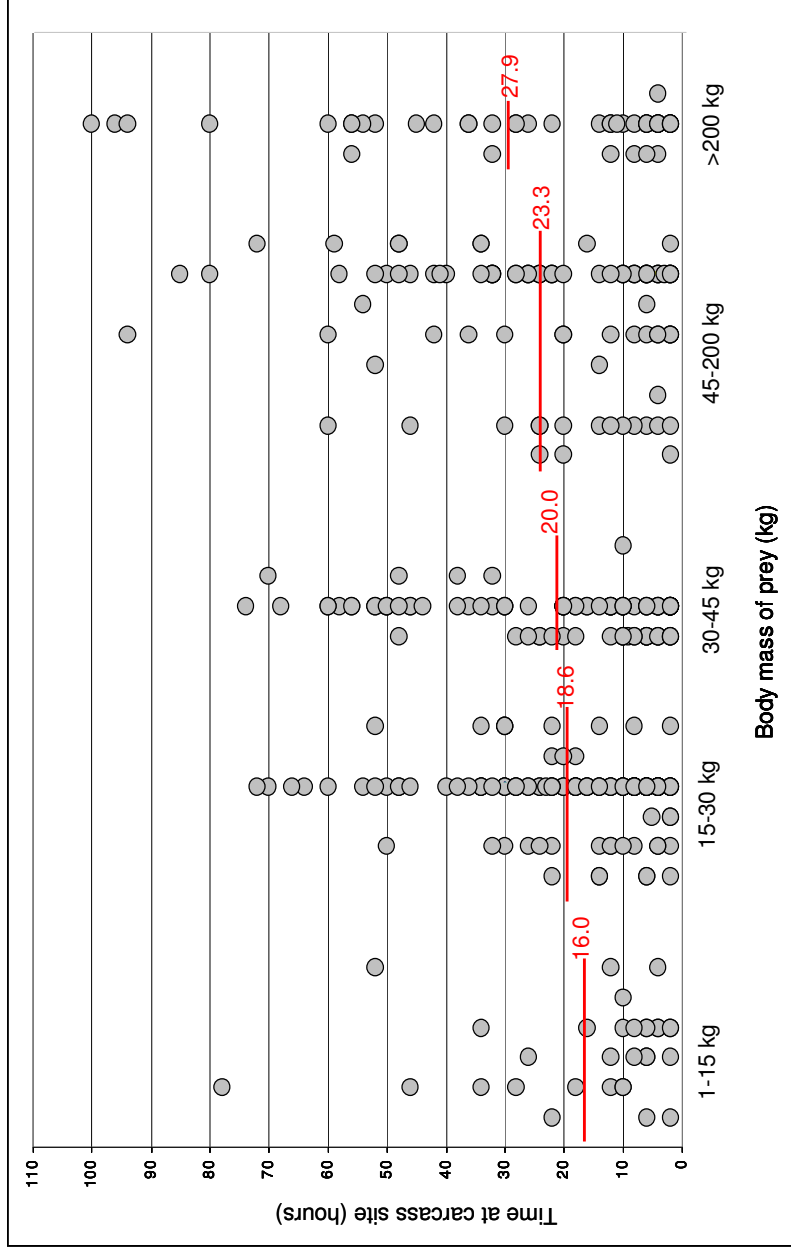
Figure 6. Length of time that a jaguar stayed at a carcass site in relation to the body mass of prey. Circles show

length of time (n= 436) jaguars stayed at location clusters that had prey. Horizontal bars and numbers indicate

mean values. Frequency distributions significantly differed among the five classes of prey body mass (F =

2.935; df = 4, 430; P = 0.021).
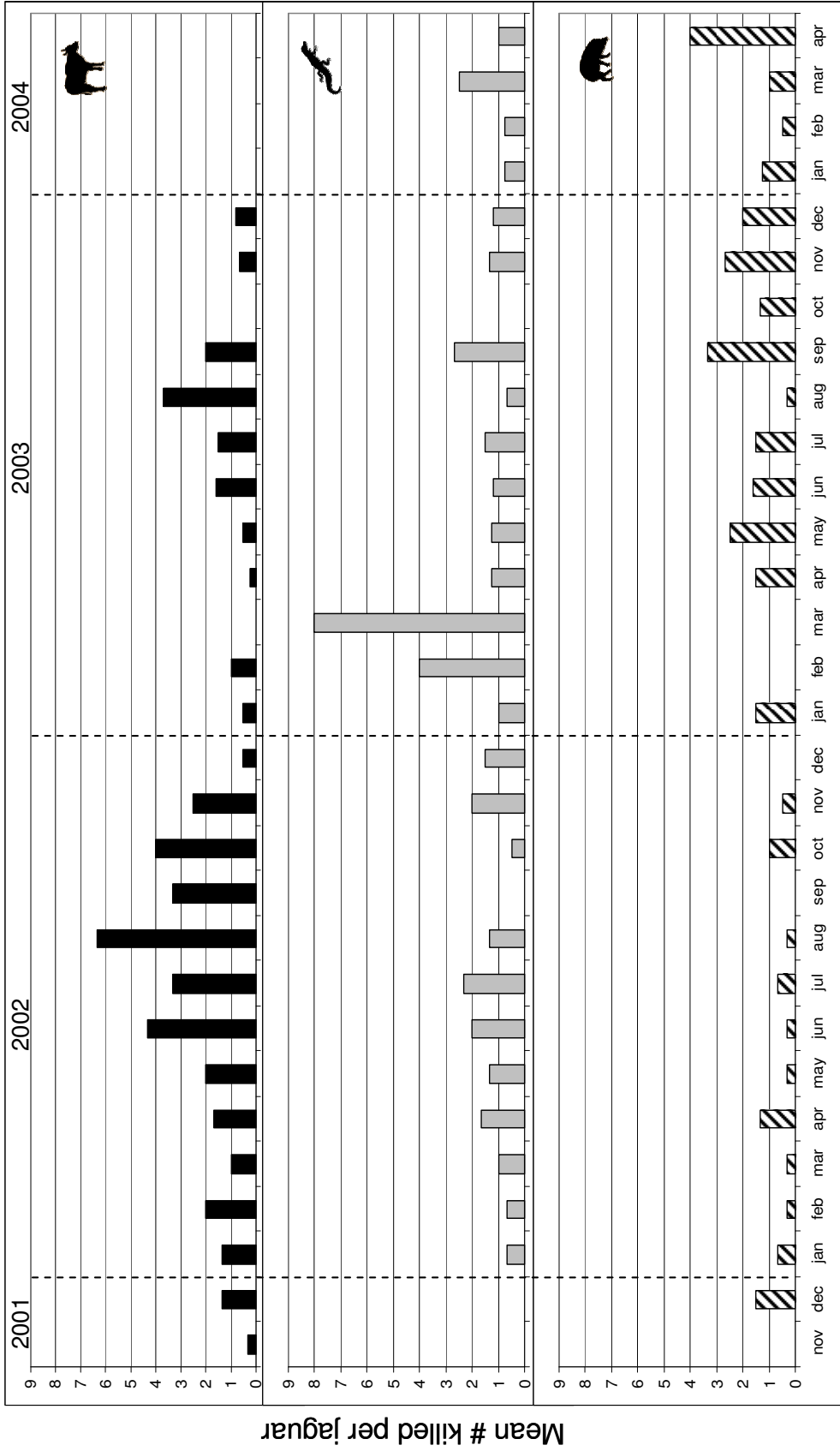
Figure 7. Distribution of the mean number of cattle, caiman, and peccary killed per month by collared jaguars, November 2001 to April 2004, southern Pantanal, Brazil.

43
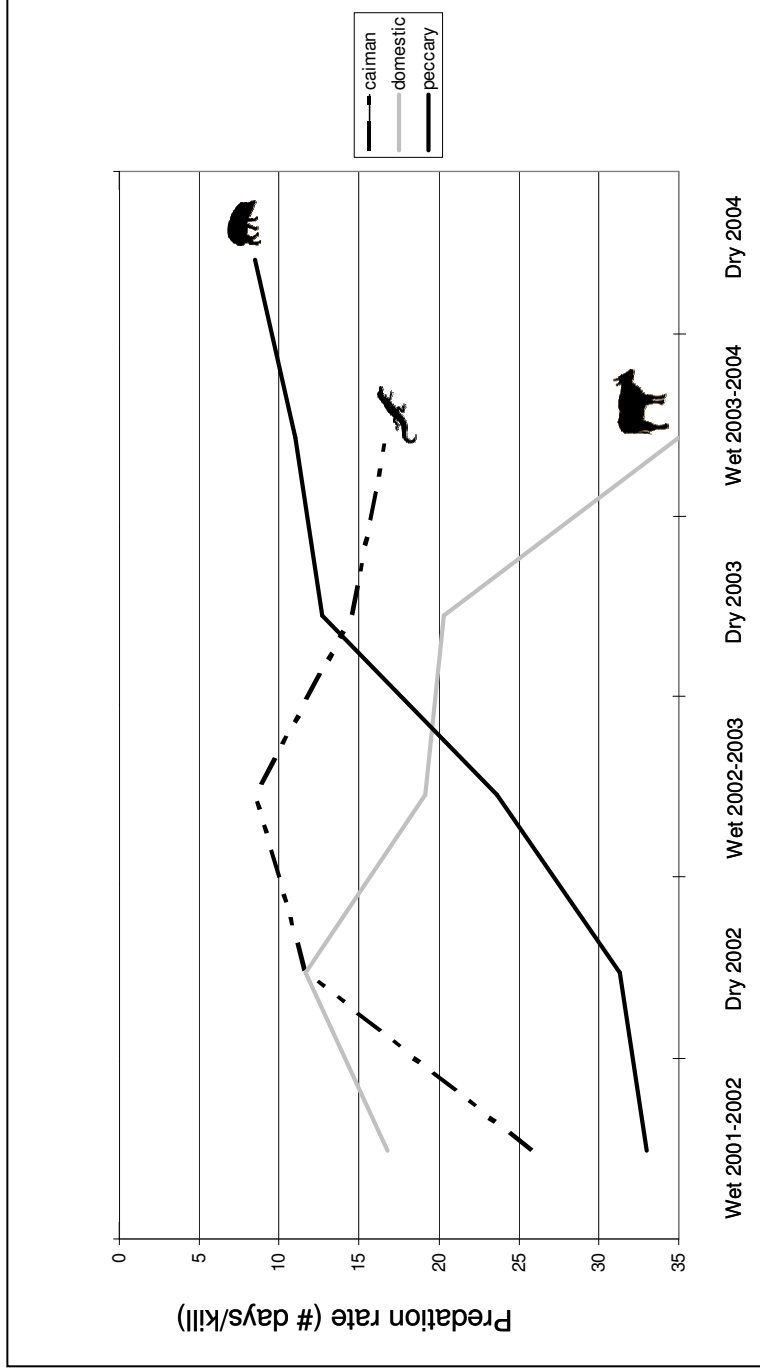
Figure 8. Seasonal variation in jaguar predation rates of caiman, peccary, and domestic cattle, November 2001 to April 2004, southern Pantanal, Brazil.
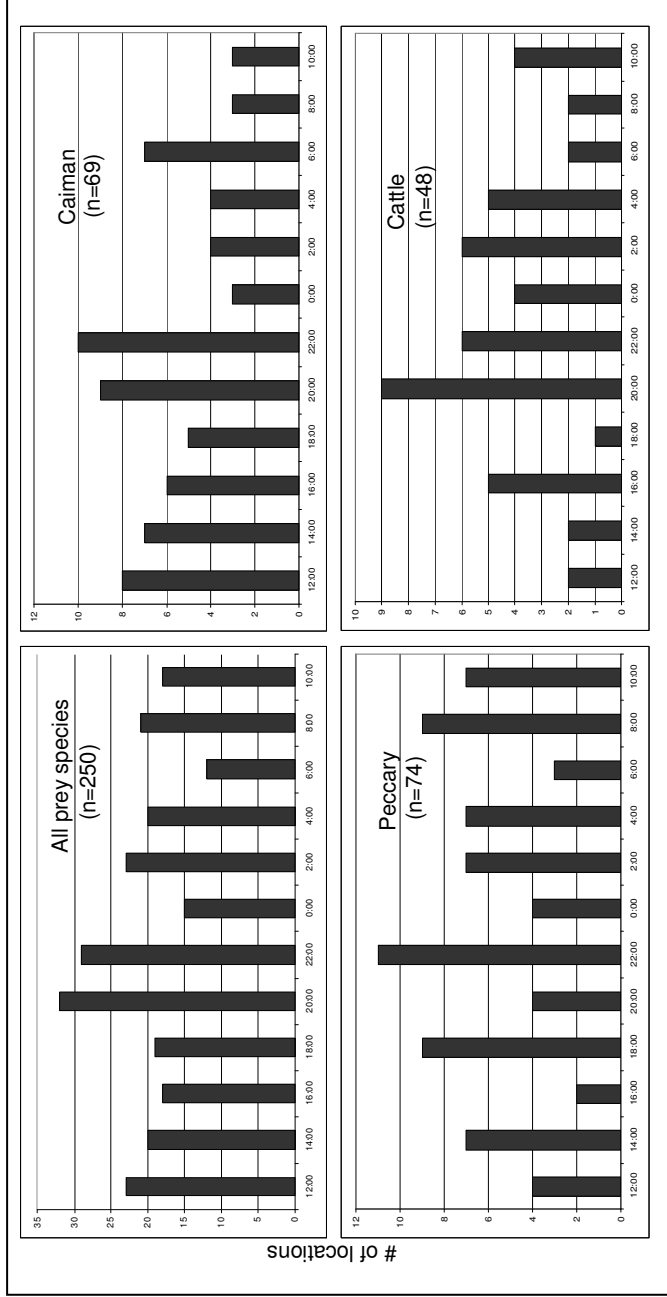
Figure 9. Distribution of first known locations at kills of all prey species, caiman, peccaries, and cattle throughout a 24-hour period, September 2002 to April 2004, southern Pantanal, Brazil.

CHAPTER III

JAGUAR HABITAT USE IN THE PANTANAL, BRAZIL – LANDSCAPE

ATTRIBUTES AND THEIR INFLUENCE ON PREDATION OF LIVESTOCK AND

NATIVE PREY

ABSTRACT The Pantanal in west-central Brazil is considered critical habitat for the long-term conservation of jaguars *(Panthera onca)*. The marked seasonal climate of the area and its influence on vegetation likely influences the relationship between jaguars and their prey. The current trend in the land-tenure system in the Pantanal is increasing human access to jaguar habitat that could influence habitat use by jaguars and interactions with prey. Jaguars in the Pantanal coexist with increasing numbers of humans and domestic cattle, a situation inevitably leading to cattle depredations by jaguars and a negative view of the cats among ranchers, making jaguar conservation a complex and challenging issue. To date, no study has located jaguar kills in a systematic way and documented an unbiased spatial distribution of jaguar kills. We used global positioning system (GPS) collars to describe jaguar habitat use and spatial patterns of predation in relation to habitat and landscape attributes. Jaguars used some habitats disproportionately to their availability in the wet and dry seasons. Forests and shrublands were generally selected by jaguars. However, the type of vegetation did not influence the locations of prey killed. Contrary to expectations, jaguars did not select forested habitats nor did they avoid open fields to make kills, but killed prey in these habitats proportionately to their availability. Cattle, caiman, and peccaries killed by jaguars (n = 327 carcasses) were distributed in the various habitats according to their availability with the exception of the dry season when caiman were killed mostly in shrublands and

peccaries were killed mostly in forests. Our results do not support earlier findings about jaguar habitat use and the spatial distribution of livestock depredations in the southern Pantanal. Our data suggest habitats other than forests may be equally important to the foraging habits of jaguars implying that habitat conservation in the Pantanal goes beyond conserving forested areas. Our results illustrate the highly opportunistic nature of jaguars where they appear to readily exploit an environment that is constantly changing and where food resources vary both temporally and spatially.

Prey abundance plays a significant role in determining the abundance of large carnivores (Karanth 1991, Carbone and Gittleman 2002). Yet the relationships between predator and prey involve more than their relative densities. Habitat characteristics play a major role in the movement patterns of predators and their use of habitats are influenced by the spatial structure of the landscape (Stander and Albon 1993). Hunting success for many ambush carnivores is highly dependent on the landscape, particularly cover (Stander 1992). Alternatively, spatial variation in vegetation structure can promote heterogeneity in refuge quality (Lewis and Eby 2002, Warfe and Barmuta 2004) and different vegetation structures may increase prey survival by reducing the predators' capacity to visually detect prey (Cooper and Crowder 1982, Babbitt and Tanner 1998). Therefore, habitat structure may play a significant role in the outcome of predator-prey interactions. Cats are specialized ambush hunters with the stalk being the most important and least variable part of the prey capture sequence (Kitchener 1991). Like other large cats, jaguars rely on a combination of cover, surprise, acceleration, and body weight to capture their prey (Schaller 1972, Hopcraft et al. 2005).

The Pantanal region in west-central Brazil harbors abundant wildlife and has been considered critical for the long-term conservation of jaguars (Sanderson et al. 2002). The habitat in the region is a mosaic of plant communities. Coupled with the marked seasonal climate of the area and its influence on vegetation cover, these spatially and temporally varied vegetation structures are likely to influence the relationships between jaguars and their prey.

Despite its rich array of wildlife species, the Pantanal is also considered a hot spot for conflicts between jaguars and cattle ranchers (Quigley and Crawshaw 1992, see Chapter II). Cattle ranching has been a traditional activity for ≥200 years in the flood plains of the Pantanal, with thousands of cattle grazing in habitats used by jaguars and their native prey. Although inaccessibility of the area has restricted agricultural deforestation in the Pantanal, over the past several decades ranches in the area have decreased in size as land has been subdivided among family members. This division has increased human access to areas that were formerly remote and had low densities of vehicles and people. This trend will likely continue, therefore increasing human access to jaguar habitat could influence habitat use by jaguars. In addition, this fragmentation of land has decreased cattle productivity (Santos et al. 2002). Therefore, to maintain economically viable operations many ranchers are opting to increase herd size. This intensification in grazing pressure increases the need for open pastures and introduced grasses (Prance and Schaller 1982), which further modifies native habitats and may influence jaguar habitat use and their relationships with prey species.

Although jaguars still exist in high density in the Pantanal (Soisalo and Cavalcanti 2006), they coexist with an increasing number of humans and domestic cattle. Inevitably

jaguars kill cattle, contributing to a negative view of the species among ranchers and making jaguar conservation in the Pantanal a complex and challenging issue. Over 95% of the Pantanal is comprised of privately owned ranches. Therefore, an effective conservation strategy for jaguars in the area must address the economic damage the large cats impose on livestock owners. To that end, management decisions and conservation measures should not only consider the foraging ecology of jaguars and relationships with domestic and native prey species (Chapter II), but should also be based on an understanding of jaguar habitat use.

To date, few studies have characterized jaguar habitat use and the spatial distribution of livestock damage as a function of vegetation cover and other landscape attributes (Quigley 1987, Hoogesteijn et al. 1993, Michalski et al. 2006). Some authors have reported jaguars kill livestock in areas with dense vegetative cover and have advised keeping herds away from forested areas (Rabinowitz 1986, Hoogesteijn et al. 1993). However, those studies were based on kills found opportunistically. To date, no study has located jaguar kills in a systematic way as to provide an unbiased assessment of the spatial distribution of jaguar kills. We investigated the patterns of jaguar predation on livestock and other prey species in the southern Pantanal, using global positioning system (GPS) collars (Chapter II). In this paper, we describe jaguar habitat use and spatial patterns of predation (on both domestic and native species) in relation to the type and distribution of vegetation and other landscape attributes.

METHODS

The study area was located in the southern Pantanal, a vast and diverse flood plain of 140,000 km^2 located in west-central Brazil, near the border with Paraguay and Bolivia.

The study site was a privately owned ranch of 460 km^2 with approximately 7000 beef cattle. With elevations ranging between 78 m and 120 m above sea level, the site was characterized by low areas subject to annual floods. Several temporary creeks and sloughs transected the study area. The Aquidauana River, up to 100 m in width, formed the northern boundary. Several baías (permanent lagoons) were distributed in the northern part of the study area. The climate was characterized by two distinct seasons. The wet season occurred between October and March, with an average monthly precipitation of 145 mm. The extremely low declivity of the area and the concentration of rains during this period influenced the level of the rivers, and led to the flooding of large areas. The dry season occurred between April and September, with a monthly precipitation of 48 mm. The hot and cool seasons coincided with the rainy and dry seasons, respectively. Low temperatures reached 12.5^{o}C in June and July while high temperatures reached 37.5 ^{o}C in October.

The vegetation is diverse, forming a mosaic with influence from different biomes such as cerrado in central Brazil, the Paraguayan Chaco, and the Amazon Forest (Prance and Schaller 1982). This pattern of different communities, frequently with abrupt changes, formed the main habitats within the study area. Open fields were interspersed with isolated islands of forest and gallery forests, which bordered temporary and permanent rivers. These habitats provided habitat for prey species, including white-lipped (*Tayassu pecari*) and collared (*Pecari tajacu*) peccary, caiman (*Caiman crocodilus yacare*), marsh deer (*Blastocerus dichotomus*), feral hog (*Sus scrofa*), brocket deer (*Mazama americana* and *M. gouazoubira*), giant anteater (*Myrmecophaga tridactyla*), armadillo (*Euphractus sexcinctus* and *Dasypus novemcinctus*), capybara (*Hydrochaeris*

hydrochaeris), tapir (*Tapirus terrestris*), and other mammals, birds, and reptiles. Cattle were widely dispersed throughout the study area, roaming open fields and brushlands, several kilometers from the ranch headquarters. During the wet season, herds were brought to drier areas, but still remained widespread over large pastures and fed in the flooded pastures. Cattle were unguarded and wandered free day and night.

Jaguar Locations

We captured, sedated, and radio-collared jaguars following techniques described in Chapters II and IV. Capture and handling methods for jaguars were approved by the Brazilian Institute of Renewable Natural Resources, and Institutional Animal Care and Use Committees at Utah State University and the U.S. Department of Agriculture's National Wildlife Research Center. We obtained locations from radio-collared jaguars from the GPS collars programmed to get fixes every 2-hours and downloaded them from the collars to a remote receiver every 3 weeks using methods described in Chapter II.

Habitat Use Analysis

We conducted a habitat use analysis using a land cover map of the study area using unsupervised classification techniques of two Landsat Thematic Mapper (TM) images (1:100,000 scale). We selected these images to enhance the hydrologic and phenological differences of the Pantanal ecosystem. The first image was a TM7 image acquired in August 2002, during the peak of one of the driest seasons on record. The second TM5 image was acquired in November 2004, after the beginning of the wet season and coinciding with ground truthing.

We first re-projected the images to UTM Zone 21 (South American Datum 1969) which was the coordinate system used for all jaguar locations. We compared the re-projected images to road and fence line vector layers obtained in-situ with portable GPS units to establish the spatial fidelity and accuracy of the re-projection. We cut both images to a smaller rectangular size covering the extent of the study site. We selected the smaller TM5 cut image as the base image as it presented the best geospatial accuracy when compared to the GPS data, and re-rectified the TM7 cut image to the TM5 image using approximately 60 control points visible in both images. We compared the re-rectified TM7 cut image to the base TM5 image using the swipe tool in ERDAS Imagine 8.7 (Leica Geosystems Geospatial Imaging, Norcross, GA), and noted areas of spatial mis-match for targeting with additional control points. We repeated the rectification process until the rectified TM7 image accurately matched the base TM5 image.

We merged the two spatially conforming TM 6-band rectangular images to obtain an 8-band image by sub-setting the TM2 (green), TM3 (red), TM4 (near-infrared) and TM5 (water absorption) bands from each image. We discarded the TM1 (blue) band due to smoke present in the 2002 image. We considered the TM6 (water absorption 2) band redundant for the purpose of the classification. We then classified the resulting 8 band image for the final vegetation map using unsupervised classification, with 120 classes, convergence threshold of 0.97 and unlimited iterations.

We conducted ground truthing in November 2004, by visiting 100 randomly generated coordinates within the study area and noting the vegetation type with field observations and digital photographs. We selected 28 of these points for use in the class interpretation procedure; 20 random and an additional 8 points selected to cover gaps of

information. We examined the 120 class image resulting from the unsupervised classification using the 28 data points to name the classes and group them into 9 habitat types described below. For the analysis, we used the final re-coded image, representing the habitat vegetation map obtained after grouping the 120 classes. We plotted all jaguar locations on this final image map and used them to identify the outer limit of the study area. We then cut the rectangular image to a polygon representing the outer boundary of the study area.

We characterized the study area into 9 habitats, according to the degree of canopy closure, vegetation density, and species composition: (1) Short open grassland was the most open habitat, comprised of various grass species, both native (*Andropogon bicornis, Leersia hexandra, Paspalum almum, Axonopus purpussii, Panicum laxum*) and introduced (*Brachiaria humidicula*) species 50 to 100 cm in height. (2) Open field with sparse trees was similar to short open grassland, but was interspersed with different species of deciduous, semi-deciduous, or palm trees (*Tabebuia spp., Ficus spp., Curatella americana, Copernicia alba, Sterculia spp.*). Some trees occurred in small islands of slightly elevated ground which remained dry during the wet season. (3) Herbaceous fields were comprised of a variety of species of wide leaves and soft stems that could be trampled by cattle (e.g., *Echinodorus macrophyllus*, *Heliconia spp., Cyperus giganteus, Ipomoea carnea fistulosa, Senna spp., Mimosa debilis*), varying in height from 50 to 200 cm, according to the season. They were usually submerged during the wet season. (4) Shrubland (tick savannah) was characterized by different shrubs (*Vernonia scabra, Annona dioica, Bauhinia spp., Psidium guineense, Cordia insignis, Combretum discolor, Calliandra parviflora*) and small trees (*Erythroxylum suberosum, Banara argutta,*

Alchornea discolor, Casearia decandra) varying in height from 2 to 4 m with dense cover. (5) Islands of secondary forest, open forest patches, and gallery forests were combined into one habitat, forests, and were characterized by trees with a high (6 to 20 m) and thick canopy. They were comprised of deciduous, semi-deciduous, and palm trees (*Ceiba samauma, Genipa americana, Guazuma ulmifolia, Sterculia apetala, Vitex cymosa, Bactris glaucescens, and Scheelea phalerata*), in addition to lianas (*Iresine macrophyla, Secondatia densiflora*) and epiphytes (*Cattleya nobilior, Cyrtopodium sp., Catasetum fimbriatum, Philodendron imbe*). The understory of forests varied from open to semi-closed to almost completely closed with acuri palms (*Atallea sp.*) or bromeliads (*Bromelia balansae* and *Ananas spp.*). (6) Wetland vegetation occurred in areas that were wet throughout the year and included *Eichhornia spp., Typha domingensis, Lymnocharis flava,* and *Oxycaryum cubense.* (7) Areas with drainage vegetation remained humid for longer periods into the dry seasons and were characterized by heterogeneous clumps of shrubs and herbaceous vegetation, usually thick and difficult to travel through. (8) Open water were areas of permanent lakes and rivers. (9) Bare soil/agricultural land were characterized by features such as the ranch headquarters and surrounding buildings.

To examine jaguar habitat use, we used all locations collected by the GPS collars, except locations within one day of capture. Individual home ranges were estimated using the 90% adaptive kernel estimator (Worton 1989), since this method has advantages over the minimum convex polygon method (Harris et al. 1990, Seaman and Powell 1996, Kenward et al. 2001, Barg et al. 2005). We used Home Range Extension (Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder

Bay, Ontario, Canada) for ArcView® 3.3 GIS (Environmentsl Systems Research institute, Inc., Redlands, California) to estimate kernel home ranges.

We examined jaguar habitat use at two levels (Johnson 1980): second order selection (i.e., use within the home range versus availability in the study area) and third order selection (i.e., use versus availability within the home range). To calculate habitat availability within the study area (i.e., 2nd order selection) we used our study area polygon, defined as the area encompassed by the juxtaposition of the home ranges of all radioed jaguars. We investigated habitat use by pooling all jaguar locations and examining their distribution in each habitat type in relation to habitat availability within the study area (2nd order selection) and in relation to distance to water. We calculated habitat availability for home ranges (3rd order selection) from home ranges for each jaguar. We used individual locations to assess whether jaguars demonstrated preference for specific habitat types within their home ranges (3rd order selection). For these analyses, we used chi-square goodness-of-fit tests. To determine which habitats were selected, avoided, or used according to their availability, we compared observed and expected proportions of locations using Bonferroni confidence intervals (Neu et al. 1974). To examine jaguar association with water, we compared the mean distance radioed jaguars were located from permanent sources of water to the mean distance from water of randomly generated locations. To assess whether there were seasonal differences in habitat preference, we divided locations into wet (October-March) and dry (April-September) seasons. We also examined whether there were any sex-specific preferences.

**Influence of Landscape Attributes
on Locations of Jaguar Kills**

We evaluated how habitat influenced jaguar kills by examining the distribution of

cattle and native species killed by jaguars in each habitat type using a chi-square

goodness-of-fit test. We predicted kills would be more frequent in areas characterized by

dense vegetation, or habitats that provided jaguars with cover and facilitated ambush of

prey. We also examined whether jaguars selected other features on the landscape, such as

distance from forest edge, distance from water, and distance from roads, to facilitate their

predatory ability on a seasonal basis. We classified the study area into categories of

distance to forest edge, distance to water, and distance to roads and examined the

distribution of jaguar kills in each of these categories using a chi-square goodness-of-fit

test. We compared jaguar kills during the wet and dry seasons with respect to their mean

distances from forest edge, distances from water, and distances from roads using a

Student's t-test. During the wet season, measurements of distance from water were based

on a digital map of rivers, lagoons, waterholes, and creeks distributed throughout the

study area. During the dry season, we excluded creeks from the analysis. To calculate

distance to forest edge, we created a base layer of forested areas larger than 30 x 30 m

(cell pixel size) within the study area. The distances from roads were from a digital map

of main roads and trails.

RESULTS

We used 11,684 locations from 10 radio-collared jaguars (five adult males, one

subadult male, and four adult females) captured and monitored from November 2001 to

April 2004; a cumulative total of 82.5 jaguar/months. Continuous monitoring periods for

individual cats varied from 1.5 to 24 months (Table 3). We were able to simultaneously

monitor three to five jaguars at any one time. Data collection occurred during the wet

seasons of 2001-2002, 2002-2003, 2003-2004, and the dry seasons of 2002, 2003, and

2004.

2nd Order Habitat Selection

The most frequent habitat types in the study area were shrubland (33%), open

field with sparse trees (29%), forest (19%), and open field (9%), followed by wetland

vegetation (3%), open water (3%), herbaceous field (2.1%), drainage vegetation (1.8%),

and bare soil/agricultural land (0.1%). The distribution of all jaguar locations in each

habitat type revealed that in general, jaguars used habitats disproportionately to their

availability both in the wet and dry seasons (Table 4). Forest and shrubland habitats were

used more than their availability (Table 5). Open field, open field with sparse trees,

wetland vegetation, open water, and bare soil/agricultural land habitats were generally

avoided by jaguars (Table 5). However, herbaceous field and drainage vegetation habitats

were only avoided during the wet season, but used according to their availability during

the dry season (Table 5). Although jaguars generally avoided wetland vegetation habitat,

the mean distance radioed jaguars were located from permanent sources of water ($\bar{x}$ =

1107.5 m, n = 6602, dry season locations only) was significantly smaller (t = -4.4390, df

= 6974, P < 0.00001) than the distance from water of randomly generated points within

the study area ($\bar{x}$ = 1262.3 m, n = 374).

The seasonal distribution of locations for males and females revealed that the

males did not select for forest habitat during the wet season, but used forested areas

according to their availability (Table 5). In addition, during the wet season, males did not

avoid open field with sparse trees habitat, but used these areas according to their

availability. In contrast to males, females did not avoid herbaceous fields during the wet

seasons but used them according to their availability (Table 5).

3rd Order Habitat Selection

Jaguars differed in the use of the different habitat types available within their

individual home ranges. Of the 6 radioed male jaguars, forest habitats were preferred by 5

male jaguars (Table 6). Male jaguar #6, the youngest of all radioed jaguars, was the

exception as he avoided forest habitats (Table 6). Three of the 4 radioed females used

forest habitats in proportion to availability (Table 6). Female # 2 used forest habitat in

excess to availability (Table 6). Shrubland habitats were selected by 7 out of 10 jaguars

(Table 6). Males #1 and 3, and female #4, did not select shrublands but used them in

proportion to availability (Table 6). Open fields were avoided by 9 of the 10 jaguars, with

the exception of female #3 which used it in proportion to availability. The same was true

for wetland vegetation habitats, which were avoided by 8 cats, but male #3 and female

#1, who used it in proportion to availability and more than expected, respectively (Table

6). With a few exceptions, herbaceous field and drainage vegetation habitats were

usually used according to their availability (Table 6). Open fields with sparse trees were

generally avoided, except by males #1 and #6, and female #4, who did not actively avoid

these habitats. Areas with open water were selected by some cats (n = 2), avoided by

others (n = 4), and used according to availability by the rest (n = 4) (Table 6).

Influence of Vegetation on Jaguar Kills

To evaluate the influence of the vegetation on jaguar kills, we analyzed the locations of 392 prey killed by radio-collared jaguars, including cattle (n = 130), caiman (n = 107), peccary (n = 90), feral hogs (n = 17), tapirs (n = 2), giant anteaters (n = 14), capybara (n = 9), marsh deer (n = 17), and brocket deer (n = 6). While the location of kills in some habitats occurred proportionate to their availability, in other habitats jaguar kills were encountered more often than expected (Table 7). Shrublands were used disproportionately to their availability, with almost half (49%) of all kills located in them. As opposed to our prediction, jaguars did not select forest habitats to make their kills, but made kills in forests in proportion to availability (Table 7). Similarly, jaguars did not avoid open fields for making kills, but kills in these areas occurred in proportion to availability (Table 7). Other habitats used proportionately to their availability included herbaceous fields and drainage vegetation. In addition to open water and bare soil, open fields with sparse trees and wetland vegetation habitats were generally avoided for killing prey (Table 7).

The influence of the vegetation structure on seasonal jaguar kills was examined by analyzing the locations of only cattle (n = 130), caiman (n = 107), and peccary (n = 90) killed by jaguars, due to the limited sample size of other native species. The seasonal distribution of jaguar kills suggests that the type of vegetation did not have a large influence on the locations of cattle, caiman, and peccary killed by jaguars (Table 7). Kills of these three species (n = 327) were generally distributed in the various habitat classes according to habitat availability both in the wet and dry season with the exception of wetland vegetation, open water, and bare soil habitats, which were usually avoided when

making kills of all three species both in the wet and dry season (Table 7). There were a

few other exceptions as well. During the dry season, jaguars avoided herbaceous fields

for killing caiman but used shrublands more than expected (Table 7). Fifty-five percent of

all caiman killed by jaguars during the dry season was located in shrubland habitats. In

contrast, when killing peccaries, jaguars avoided open fields with sparse trees but

selected forest habitats (Table 7). During the wet season, kills of cattle and caiman were

distributed in the various habitats according to their availability with the exception of

drainage vegetation, which was avoided when killing cattle (Table 7). Peccaries were

mostly killed in shrubland habitats (53% of all peccary killed during the wet season), but

open fields, herbaceous fields, and drainage vegetation were avoided when killing this

species (Table 7).

Jaguar's Selection of Features on the Landscape

Contrary to our expectation, the observed distribution of kills of cattle and caiman

occurred as expected in each category of distance to forest edge, both during the wet and

dry seasons. On the other hand, during the dry seasons, peccaries were killed within 50 m

of forest edges more often than expected (χ^2 = 20.70, df = 5, P = 0.0009) with 55% of the

peccary killed by jaguars being located within this distance category. When we compared

the mean distances of kills to forest edge during the wet and the dry seasons, we found

that during the wet season, cattle were killed significantly closer to the forest than in the

dry season (t = 1.9567, df = 128, P = 0.0263). The same was not true for jaguar kills of

caiman (t = 0.6355, df = 105, P = 0.2632) or peccary (t = 0.6781, df = 87, P = 0.2497).

With respect to the distance to water, during the wet season, the distribution of cattle (χ^2

= 10.75, df = 6, P = 0.0965), caiman (χ^2 = 7.78, df = 6, P = 0.2549), and peccary (χ^2 =

6.27, df = 6, P = 0.3941) killed by jaguars occurred according to the expected

distribution. During the dry season, the observed distribution of caiman and peccary

killed by jaguars within the different categories of distances to water occurred according

to expected (χ^2 = 7.70, df = 6, P = 0.2607, and χ^2 = 12.79, df = 6, P = 0.0600,

respectively). However, the same was not true for the distribution of cattle killed by

jaguars (χ^2 = 34.87, df = 6, P < 0.0001). Cattle were killed within 500 m from water less

often than expected and were killed between 1000-1500 m from water more often than

expected, with 35% of all cattle killed being located within this category. When we

compared the mean distances of kills to water during the wet and dry seasons, we found

that for all three species of prey, distances were significantly closer to water during the

wet season than in the dry season (cattle: t = 5.1034, df = 128, P < 0.0001; caiman: t =

2.3318, df = 105, P = 0.0216; peccary: t = 4.3996, df = 88, P < 0.0001).

The distribution of jaguar kills did not seem to be affected by the distribution of

roads and trails within the study area. The observed distribution of cattle, caiman and

peccary killed by jaguars within the different categories of distances to roads occurred as

expected (cattle: χ^2 = 13.67, df = 9, P = 0.1345; caiman: χ^2 = 13.47, df = 9, P = 0.1425;

peccary: χ^2 = 3.54, df = 9, P = 0.9386). When we compared the mean distances of kills to

roads during the wet and dry seasons, we found that the distances of cattle and caiman

killed by jaguars in the wet and dry seasons were not significantly different (wet: t =

0.3449, df = 128, P = 0.7307; dry: t = -0.6577, df = 105, P = 1.9828). During the wet

season, peccaries killed by jaguars were significantly closer to the roads than in the dry

season (t = 2.2368, df = 88, P = 0.0278).

DISCUSSION

Jaguars differed in the use of habitats available within their home ranges. They usually used shrublands and forested habitats more often than expected, and avoided open fields, open fields with sparse trees, wetland vegetation, and bare soil/agricultural land. Habitat composition within individual home ranges was similar among jaguars, even for habitats they used less than expected. Male jaguars usually used forested habitats more than their availability (3rd order selection); subadult male #6 was an exception. However, his behavior might have been influenced by movements of other cats, as during the period he was monitored he accompanied by his mother and female sibling. Among females, we had different results regarding their use of forest habitats at the 2nd and 3rd order selection levels. At the study area scale (2nd order selection) our results suggested females used forests more than their availability both in the wet and dry seasons. However, within their home ranges (3rd order selection), female jaguars did not select for forested habitats but used them as expected. This difference may have been influenced by the behavior of female #2 (Table 4). Her locations represented 60% of all female locations collected (Table 3). Nevertheless, the difference in the degree of forested habitat use between males and females within their home ranges (3rd order selection) is interesting. The limited mobility of females, their smaller home ranges, and the fact that prey are less vulnerable in areas recently hunted by predators (Brown et al. 1999), may force females to switch between forests and shrublands within their home ranges more often than the more mobile male jaguars. Given males have extensive home range overlap and are therefore less restricted in their movements than females (Chapter

IV), they may be able to spend more time in preferred habitats before they need to switch to another area to search for prey.

Shrublands were consistently selected as one of the preferred habitats for jaguars in our study. Shrublands were used more than expected by 70% of our radioed jaguars at the 3rd order selection. In addition, shrublands were also used more than expected at the 2nd order selection scale, in the wet and dry seasons for both male and female jaguars. Our results contrast with a prior study in the area (Crawshaw and Quigley 1991) which found jaguars used "open forests" less than expected. Although we did not differentiate degrees of forested habitat in our study, pooling islands of secondary forest, open forest patches, and gallery forests into one habitat, we suspect that our shrubland category may have been equivalent to what Crawshaw and Quigley termed "open forest." In their study, jaguars used gallery forests and forest patches more than expected, but avoided "open forest" (or cerrado) and grasslands. While forests may provide jaguars with key resources, other habitats may be equally important. Like other cats, jaguars rely on features of the landscape to approach their prey before attacking them. Shrublands may provide enough vegetative cover needed for jaguars to successfully ambush and kill their prey. In addition, hunting success is affected by factors other than cover. Vulnerability of prey species is equally important (Taylor 1976, Temple 1987). Jaguars in the Pantanal kill a variety of species with diverse ranging behaviors. Caiman for example, is one of the main species killed by jaguars in our study area (Chapter II). According to Campos et al. (2005), the behavior of adult male caiman is characterized by extensive seasonal movements between permanent and temporary lakes and rivers. These movements between different habitats may make them more vulnerable to predation by jaguars.

Indeed, the seasonal distribution of caiman killed by jaguars supports this hypothesis. During the dry season, caiman were killed by jaguars in shrubland habitats more than expected.

The pattern of habitat use by jaguars differed among the seasons. This is not surprising given the drastic changes in environmental conditions within the various habitats after each reoccurring flood. Although herbaceous fields and drainage vegetation were used as expected during the dry season, jaguars avoided them during the wet season. Optimal foraging theory predicts predators should choose the most profitable prey (MacArthur and Pianka 1966). However, profitability may be influenced by a combination of search time, encounter rates, and energetic costs of capture (Sunquist and Sunquist 1989). During the wet season, when herbaceous fields and drainage vegetation habitats become dense and difficult to move through, high search time and low encounter rates may make hunting in those habitats unprofitable.

The preference jaguars showed for forest habitat did not occur among males during the wet season. In addition, during these periods males did not avoid open field with sparse trees like they did the rest of the year, but used them according to their availability (Table 5). At the same time, peccaries killed by jaguars were encountered according to expected and more often than expected in open fields with sparse trees and shrublands, respectively (Table 6). During our study of jaguar foraging ecology, we found male jaguars killed peccaries at a significantly higher proportion than female jaguars (Chapter II). The switch in male habitat use from forests to open fields with sparse trees and shrublands during the wet season may reflect prey movement. Although during the wet season forests provide corridors of dry ground (Crawshaw and Quigley

1991) and are productive in terms of fruiting plant species (Ragusa-Netto and Fecchio 2006), other habitats may be equally important. Open fields with sparse trees were interspersed with many species of deciduous, semi-deciduous and palm trees, several of which are also fruiting in the wet season (Pott and Pott 1994, Ragusa-Netto and Fecchio 2006). The same may be true for shrubland habitats with multiple fruiting shrubs (e.g., *Erythroxylum suberosum, Banara argutta, Alchornea discolor, Casearia decandra*). Although open fields with sparse trees and shrublands were subject to a higher degree of flooding than forest habitats, peccaries may have used forests at night due to dry ground, but they foraged in these more open areas during the day (S. Cavalcanti, pers. obs.). Although peccaries used open fields with sparse trees, in habitats with plain open fields their carcasses were encountered proportionately less than expected, perhaps because these habitats did not provide the fruiting trees and the higher ground present in open fields with sparse trees.

Male jaguars selected forests (Table 5) during the dry season when kills of peccaries were found in forests more often than expected (Table 6). During the dry season, the forest floor is covered with fruits of the bacuri palm (*Attalea phalerata*), which drop during the winter and are important in the diet of peccaries and other prey species (Pott and Pott 1994). Additionally, during the dry season the distribution of peccary killed by jaguars occurred less than expected in open fields with sparse trees. During this period, these habitats become less lush, and devoid of the cover jaguars need for successfully stalking and killing prey. While cattle continued to be killed as expected in these areas, likely reflecting their grazing behavior, peccaries may become more wary in these environments and are subsequently killed less often in these habitats.

Other than these exceptions, the type of vegetation in general did not appear to have a large influence on the locations of cattle, caiman, and peccary killed by jaguars (Table 6). Contrary to expected, jaguars did not select forest habitats to make their kills nor did they avoid open fields for that purpose. They generally avoided wetland vegetation, open water, and bare soil, but kills of cattle, caiman, and peccaries were usually distributed among the vegetation types as expected.

It is important to note that our analyses of the locations of prey killed by jaguars were based on the assumption that prey were equally distributed in the various habitat types within the study area. Expected values used in the analyses were based on total area for each habitat type rather than specific prey distributions. This may have influenced some of our results. However, although we did not have detailed information on prey distribution throughout the study area, our results are based on >400 carcasses of prey killed by jaguars. Furthermore, published literature suggests that prey species use a variety of habitats in the Pantanal. Caiman for example, can build their nests in lake-surrounding forests, isolated islands of forests, open pasture fields, or floating vegetation (Campos 1993). Adult caiman undertake extensive movements through diverse habitats to move between temporary and permanent lakes and rivers (Campos 1993, Coutinho and Campos 1996). Although peccaries are frugivores and thus essentially forest animals, they are frequently observed in other habitats as well, from open fields with sparse trees to shrubland to wetland vegetation (Keuroghlian et al. 2004, Desbiez 2007, S. Cavalcanti, pers. obs.). Future studies on the spatial distribution of kills should consider the distributions of native species among the different habitat categories in their analyses.

In terms of selection for attributes of the landscape, jaguars did not seem to make their kills as anticipated (e.g., caiman would be killed closer to water during the dry season, when they gather together near water holes, lakes, and rivers). Distances to water, forest edge, and roads were not directly related to the distribution of caiman killed by jaguars. We found that during the wet season, jaguar kills of caiman were closer to water. However, we believe this result reflects the distribution and availability of water during the wet season, when caiman are widespread in the flooded savanna. We suggest in the wet season jaguars take advantage of the distribution and availability of caiman, while in the dry season, the seasonal movements of caiman between bodies of water increases their vulnerability to jaguar predation.

During the dry season, jaguar kills of peccaries were found within 50 m of forest edges more often than expected. This outcome is likely related to peccary use of forests during the dry season and the resulting higher frequency of jaguars encountering them in forested habitats. During the wet season, kills of peccaries were encountered closer to roads. The decreased movement of vehicles and people during the wet season could have influenced peccary movements. However, their mean distance to roads ($\bar{x}$ = 2,359 m) was considered large for the roads to have had a major influence on their kills. Similarly, distance to roads did not seem to affect the distribution of cattle killed by jaguars. During the dry season, cattle wander throughout the area as the lower and less dense vegetation facilitates their movements. During the wet season, fields become flooded and most roads are underwater. Therefore, roads are not necessarily easier to move along, except for the ones that are built on elevated dikes.

Distance to water did not play a role in the distribution of peccary killed by jaguars, although they were closer to water during the wet than during the dry season. As with caiman, this may reflect water availability and distribution. The same may have happened with kills of cattle as their distribution was not influenced by distance to water during the wet season. During the dry season however, cattle were killed close to water less often than expected. These results are opposite to our prediction, as we had anticipated jaguars would take opportunity of waterholes and river banks to kill cattle when they approached to drink. Nevertheless, cattle were killed between 1000-1500 m from water more often than expected. During the dry season, cattle may become more vulnerable to jaguars when they are far from water rather than when they are near it.

Some authors have discussed jaguar predation on cattle as a function of distribution, availability, or proximity of forest habitat (Rabinowitz 1986, Hoogesteijn et al. 1993, Michalski et al. 2006, Azevedo and Murray 2007). Hoogesteijn et al. (1993) compared 3 ranches in Venezuela with depredation problems and found cattle losses were associated with forested areas. Accordingly, the ranch with the lowest rates of jaguar predation on cattle was comprised of narrow strips of gallery forests along rivers and streams which were completely fenced, keeping cattle out of the forest. Rabinowitz (1986) reported jaguars readily killed livestock when they came into forested areas, but not when they were in open pastures. Quigley (1987) reported in the Pantanal all cattle kills found were located in gallery forests and forest patches, although a few were made at forest edges and dragged into cover. In contrast, our results in the southern Pantanal are opposite of these previous findings. It is important to note that during our study, we essentially followed the radioed jaguars. Given the high degree of accuracy and precision

of the GPS collars we used (Chapter II) and the high number of kills we located, our dataset was not constrained by the biases inherent in studies based upon reported kills. Our radioed jaguars did not select forested areas nor did they avoid open fields to kill cattle. With the exception of wetland vegetation, open water, and bare soil/agricultural land, the distribution of cattle killed by jaguars occurred as expected in each habitat class, as well as in relation to the distance from the forest edge. Nevertheless, during the wet season, cattle were killed closer to forest edges than in the dry season. During the wet season, although cattle are able to forage in chest-deep water, they needed dry ground on which to spend the night. Therefore, they might spend more time closer to islands and strips of forests, which are usually characterized by higher and drier ground during the peak of the wet season. In general, however, jaguar kills were located in habitats in proportion to the expected distribution.

Our results suggest habitats other than forests may be important for foraging by jaguars. Several authors have suggested keeping cattle herds away from forested areas as a strategy to minimize jaguar attacks (Rabinowitz 1986, Quigley 1987, Hoogesteijn et al. 1993, Michalski et al. 2006, Palmeira et al. 2008), but we recorded jaguar attacks on cattle in other habitats as well. In addition, given the heterogeneous patterns of vegetation distribution in the Pantanal, keeping cattle away from forests is impractical.

MANAGEMENT IMPLICATIONS

Some authors have suggested that the introduction of exotic grasses in the Pantanal should be implemented in areas originally covered by shrublands and native grasses as a way to minimize impact on arboreal vegetation (Comastri-Filho and Pott 1993, Comastri-Filho 1997). Although the conservation of large undisturbed blocks of

forests is vital for the conservation of jaguars throughout their range (Rabinowitz 1986, Crawshaw et al. 2004, Cullen et al. 2005, Michalski et al. 2006), we suggest that in the Pantanal, the intermingling of the different habitats and their dynamic cyclical nature through the wet and dry seasons plays a critical role in the relationships among jaguars and their prey. Thus, habitat conservation in the Pantanal goes beyond the conservation of forested areas. The conservation of other habitat types in their native form is equally important.

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Table 3. Length of monitoring period and number of global positioning system (GPS)
locations used in the analyses of habitat use for 10 jaguars between November 2001 -
April 2004 in the southern Pantanal, Brazil.

Jaguar ID	Monitoring period (months)	# of GPS locations used*
Adult male #1	10	995
Adult male #2	5	745
Adult male #3	3	453
Adult male #4	11	1500
Adult male #5	6	721
Subadult male #6	3	714
Adult female #1	15	2008
Adult female #2	24	3932
Adult female #3	4	500
Adult female #4	1.5	116

* Number of GPS locations included in the 90% adaptive kernel
estimates of home range (Worton 1989).

Table 4. Chi-square goodness of fit test results for the distribution of jaguar locations (n =

10 jaguars, n = 11,684 locations) among different habitat categories in the southern

Pantanal, Brazil, between November 2001 and April 2004.

		Year round	Wet season	Dry season
All jaguars combined	χ^2	1586.64	698.5	920.11
	df	8	8	8
	P	<0.0001	<0.0001	<0.0001
Males	χ^2	548.05	100.18	509.91
	df	8	8	8
	P	<0.0001	<0.0001	<0.0001
Females	χ^2	1065.29	667.98	428.24
	df	8	8	8
	P	<0.0001	<0.0001	<0.0001

Table 5. Habitat use (2nd order selection, Johnson 1980) by radio-collared jaguars (n = 6 males, n = 4 females) year round, and during the wet (October – March) and dry (April – September) seasons between November 2001 – April 2004 in the southern pantanal, Brazil. Negative signs (-) indicate avoidance of a particular habitat type. Positive signs (+) indicate selection and neutral signs (o) indicate neither avoidance nor selection, but use in accordance with availability of a particular habitat.

	Open field	Open field with sparse trees	Herbaceous field	Shrubland	Forest	Wetland vegetation	Drainage vegetation	Open water	Bare soil
All jaguars, year-round	-	-	o	+	+	-	-	-	-
All jaguars, wet season	-	-	-	+	+	-	-	-	-
All jaguars, dry season	-	-	o	+	+	-	o	-	-
Male jaguars year-round	-	-	o	+	+	-	o	-	-
Male jaguars, wet season	-	o	-	+	o	-	-	-	-
Male jaguars, dry season	-	-	o	+	+	-	o	-	-
Female jaguars year-round	-	-	o	+	+	-	-	-	-
Female jaguars, wet season	-	-	o	+	+	-	-	-	-
Female jaguars, dry season	-	-	o	+	+	-	o	-	o

Table 6. Habitat use within the home ranges (3rd order selection, Johnson 1980) of ten radio-collared jaguars (n = 6 males, n = 4 females) between November 2001 – April 2004 in the southern Pantanal, Brazil. Negative signs (-) indicate avoidance of a particular habitat type. Positive signs (+) indicate selection of a habitat and neutral signs (o) indicate neither avoidance nor selection, but use of a particular habitat in accordance to its availability.

Jaguar	Open field	Open field with sparse trees	Herbaceous field	Shrubland	Forest	Wetland vegetation	Drainage vegetation	Open water	Bare soil/ Agricultural land
Female #1	-	-	o	+	o	+	o	+	o
Female #2	-	-	o	+	+	-	o	-	-
Female #3	o	-	o	+	o	-	o	o	-
Female #4	-	o	o	o	o	-	-	o	-
Male #1	-	o	o	o	+	-	o	-	-
Male #2	-	-	o	+	+	-	o	-	-
Male #3	-	-	-	o	+	o	-	o	-
Male #4	-	-	o	+	+	-	o	o	-
Male #5	-	-	o	+	+	-	o	-	-
Male #6	-	o	+	+	-	-	o	+	-

Table 7. Occurrence of jaguar kills (n = 392) in the various habitat types between November 2001 and April 2004 in the southern Pantanal, Brazil. Negative signs (-) indicate occurrence in a particular habitat type with frequency below the expected. Positive signs (+) indicate occurrence of more kills than expected in a particular habitat and neutral signs (o) indicate occurrence of kills in a particular habitat in accordance to its proportion.

	Open field	Open field with sparse trees	Herbaceous field	Shrubland	Forest	Wetland vegetation	Drainage vegetation	Open water	Bare soil/ Agricultural land
All species Year-round	o	-	o	+	o	-	o	-	-
Cattle carcasses Dry season	o	o	o	o	o	-	o	-	-
Caiman carcasses Dry season	o	o	-	+	o	-	o	-	-
Peccary kills Dry season	o	-	o	o	+	-	o	-	-
Cattle kills Wet season	o	o	o	o	o	-	-	-	-
Caiman kills Wet season	o	o	o	o	o	-	o	-	-
Peccary kills Wet season	-	o	-	+	o	-	-	-	-

CHAPTER IV

SPATIAL ECOLOGY AND SOCIAL INTERACTIONS OF JAGUARS

(*PANTHERA ONCA*) IN THE SOUTHERN PANTANAL, BRAZIL

Summary

1. The Pantanal wetland of Brazil is an important area for the conservation of jaguars (*Panthera onca*) and a stronghold for the species. However, as the size of traditional large ranches in the Pantanal decrease, human access to prime jaguar habitat increases and human-altered landscapes may influence patterns of resource selection and space use by jaguars. Understanding the spatial and social dynamics, activity patterns, and movement rates of jaguars is important for management strategies that ensure their long-term survival.

2. We initiated a study of jaguar ecology in the southern Pantanal using global positioning system (GPS) radio collars to monitor jaguars simultaneously, independent of weather, time of day, or season. Between October 2001 and April 2004 we radioed 10 jaguars (6 males, 4 females), obtained 11,878 locations, and examined their space use, movement rates, and social interactions. We monitored between 3 and 5 jaguars at any one time.

3. Estimates of 90% kernel home ranges varied among study animals and seasons, ranging in size from 34.1 to 262.9 km^2. The size of core areas (50% isopleth) for both female and male jaguars did not differ between the seasons, but the size of their home ranges in the dry seasons were generally larger than in the wet seasons.

4. The stability of individual home ranges varied among the seasons and between individuals. While some females maintained ≥80% of their home ranges from one season to the next, other females used ≤50% of the home ranges they had used the previous season. Site fidelity within individual home ranges also varied as ≥70% of the core areas of some females were located in different sites within their home ranges.

5. Seasonal analysis of female locations suggested a pattern of spatial avoidance among females during the wet season. Among males, home range overlap was extensive, both in the wet and dry seasons, suggesting males did not retain exclusive ranges.

6. Overlap between males and females occurred both in the wet and dry seasons and female movements were not restricted within the ranges of individual males as previously suggested.

7. Jaguars were located <200m apart more often than expected, suggesting some degree of sociality among them.

8. The frequency with which female jaguars associated with males suggested either low conception rate, low survival rate of young, or that jaguars may be more social than previously thought. Interactions among males also suggested some degree of sociality.

9. Our study provided insights into the dynamic land tenure system of jaguars. While the yearly outline of jaguar locations suggested a spacing pattern based on extensive overlap, careful inspection of their locations suggested seasonal differences in jaguar spacing patterns. Future research would benefit from radio-collaring a large number of individuals and monitoring them over a longer time span to provide a better understanding of their spatial ecology and social interactions.

Introduction

Jaguars (*Panthera onca*) exist in distinct populations across a variety of habitats and regions characterized by tropical and subtropical forests, semi-deciduous forests, thorny forests, scrublands, savanna, and swamps (Oliveira 1994; Sanderson *et al.* 2002a). However, due primarily to land-use changes and consequent habitat degradation, jaguars have been restricted to a fraction of their former range (Sanderson *et al.* 2002a). Nonetheless, remaining habitats are being converted into areas of agriculture and resource extraction.

The Pantanal wetland of west-central Brazil is considered an important area for the conservation of jaguars and a stronghold for the species (Sanderson *et al.* 2002b; Soisalo & Cavalcanti 2006). In the Pantanal, traditionally large ranches have decreased in size while human access to prime jaguar habitat has increased as an infrastructure of roads has been built. This increasingly human-altered landscape will likely influence patterns of resource selection and space use by jaguars. Understanding the social dynamics, space use, activity patterns, and movement rates of large carnivores such as jaguars is important for developing management strategies that ensure their long-term survival and population persistence.

Previous studies provided insights into jaguar spacing, activity, and movements in the Pantanal (Schaller & Crawshaw 1980; Crawshaw & Quigley 1991). These authors noted that given the difficulties of their studies, their conclusions were speculative. Although our knowledge of jaguar ecology has increased since the first field studies in the mid 1980's, a detailed study of this cryptic species remains challenging. Most jaguar studies have either relied on small sample sizes or have been limited by logistical

difficulties (Schaller & Crawshaw 1980; Crawshaw & Quigley 1991; Scognamillo *et al.* 2002). Although locating animals from an aircraft improves coverage, high costs and weather conditions limit sampling strategies. Equally important and relevant to documenting spatial ecology of jaguars, is that aerial telemetry can only acquire daytime locations. Ground telemetry, although possible at night, is limited to areas accessible to researchers and may therefore yield biased information about carnivore space use and movement rates (Gese, Andersen & Rongstad 1990; Chavez & Gese 2006).

We initiated a study of jaguar ecology in the southern Pantanal using global positioning system (GPS) radio collars, which allowed us to simultaneously monitor several jaguars without direct observer intervention. We gathered information on animal movements continuously, independent of weather, time of day, or season. In this paper, we examined space use, site stability and fidelity, movement rates, and interactions of jaguars, providing insights into their spatial and social ecology in the Pantanal wetlands of west-central Brazil.

Materials and methods

We conducted the study on a 46,000 ha beef cattle ranch in the southern Pantanal of Brazil, a vast floodplain of 140,000 km^2 located in the geographic center of South America. The area was characterized by low areas subject to annual floods. The altitude ranged between 89 m and 120 m above sea level. The climate was seasonal with a rainy season between October and March and an average monthly precipitation of 144.8 mm. The dry season occurred between April and September with a monthly precipitation of 47.7 mm. The concentration of rains influenced the level of the rivers, flooding large areas in the wet season. The hot and cold seasons coincided with the rainy and dry

seasons, respectively. Low temperatures reached 18.5°C in June and July and high temperatures reached 42.5 $^{\circ}$C in October (Cavalcanti & Gese, unpublished data). The vegetation has been described as a mosaic complex, with influence from different vegetation types (biomes) such as the cerrado in central Brazil, the Paraguayan Chaco, and the Amazon Forest (Prance & Schaller 1982). Open fields were interspersed with isolated islands of secondary forest, which were important for both predator and prey species. Gallery forests bordered temporary and permanent rivers.

White-lipped peccary *(Tayassu pecari),* an important prey species for jaguars, were abundant in the area, as well as caiman *(Caiman crocodilus yacare)*, collared peccary *(Tayassu tajacu)*, marsh deer *(Blastocerus dichotomus)*, giant anteater *(Myrmecophaga tridactyla)*, and armadillo *(Euphractus sexcinctus).* During the dry season, cattle were widely dispersed throughout the study area. During the wet season, cattle herds were brought to drier areas, but still remained widespread. Cattle were always unguarded and roamed free during the day and night.

We captured animals with trained hounds at sites of frequent use as indicated by the presence of spoor. We immobilized treed cats with Telazol (Fort Dodge do Brasil, São Paulo, Brazil), or a combination of Telazol and ketamine hydrochloride, using a dart fired from a CO_2 pistol or a rifle. We examined immobilized animals for general body condition, sexed, aged, measured, weighed, fitted each cat with a Global Positioning System (GPS) collar (Simplex, Televilt International, Sweden), and released them at the site of capture. We estimated age based on the presence of milk or permanent dentition and tooth color and wear (Ashman *et al.* 1983).

Between October 2001 and September 2002, we programmed the GPS collars to acquire a location every 2 hours between 18 00 and 06 00 hr (7 locations/day). Between September 2002 and April 2004, we programmed them to acquire 12 locations/day (every 2 hours). We used a receiver (RX-900, Televilt International, Sweden) to remotely download data from the collars every 3 weeks. Due to the extent of the study area and limited access on the ground, we used an aircraft for aerial location and data download. Occasionally, we located radioed jaguars from the ground with a 4-element null-peak antenna system (White & Garrott 1990) mounted on a vehicle, or from horseback with a hand-held directional antenna, to download data from the GPS collar.

We recovered GPS collars for battery replacement using hounds as previously described. The GPS collars allowed for the simultaneous location of several individuals (within minutes of each other depending on satellite orbits) and provided an estimate of space use of each individual and documentation of social interactions, such as possible mating events.

We converted the locations for individual jaguars from latitude and longitude into the Universal Transverse Mercator grid system using GeoCAD (GeoCAD Information, Ltd., Campo Grande, Brazil). We then plotted individual locations on a map of the study area (1:100,000) using ArcView® 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA).

For comparisons with other studies, we estimated home range sizes using the 98% minimum convex polygon (MCP) method (Mohr 1947). However, these estimates were presented for the purpose of comparison only. For more accurate depictions of space use, we examined jaguar home ranges and their overlap using the 90% and 50% adaptive

kernel estimator (Worton 1989), given this method has advantages over the MCP method (Harris *et al.* 1990; Seaman & Powell 1996; Kenward *et al.* 2001; Barg, Jones & Robertson 2005). We considered a core area within the home range as the area enclosed by the 50% isopleth (Worton 1989; Seaman & Powell 1996). We used Home Range Extension (Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada) for ArcView® 3.3 to estimate both MCP and kernel home ranges.

We estimated home range size for each year to account for between-year differences in precipitation. Additionally, we calculated estimates of home range size for each individual jaguar for each season throughout the study (i.e., wet season 2001/2002, dry season 2002, wet season 2002/2003, dry season 2003, and wet season 2003/2004). We defined the wet season as October-March and the dry season as April-September.

We compared overlap between individual home ranges and their core areas among the different seasons to examine home range stability and fidelity to specific sites within their home range. We measured overlap among individual jaguars for each pair of individuals with overlapping home ranges and calculated separately for each season.

We used sequential locations collected every 2 hours to determine movement rates. We calculated movement rates only from sequential locations spaced 2 hours apart. The mean distance traveled per hour (km/hr) was used in comparisons among individuals during different times of the day (dawn: 0400 – 0800 hr; day: 1000 – 1400 hr; dusk: 1600 – 2000 hr; night: 2200 – 0200 hr) and during the different seasons using analysis of variance (ANOVA). To account for variation in activity caused by between-year differences in precipitation levels, we analyzed the data for each year.

Home range overlap is a rather large-scale approach of examining spatial avoidance, but does not account for temporal avoidance. We used individual locations collected simultaneously to determine if jaguars showed spatial-temporal avoidance of each other. We compared the average distance between simultaneous locations (or within a minute of each other) for each pair of jaguars with overlapping home ranges with the distance between them if the locations were randomly collected (Kitchen, Gese & Schauster 1999). For each pair of cats, we randomly paired all locations (their expected distance if they were moving independent of each other) and compared that value to the simultaneous locations. We used a Student's *t* test to compare the average simultaneous distance between individuals with that from the randomly paired locations (Kitchen *et al.* 1999). We assumed jaguars were avoiding each other if the simultaneous distances between them were significantly farther apart than the random locations. We performed this same analysis for the different seasons during our study. In addition, we divided simultaneous distances between pair of jaguars into distance classes and performed a chi-square contingency analysis to determine whether the frequency of counts of the different distance classes were different for distances between simultaneous (observed) and random (expected) locations between jaguars.

We also examined distances between simultaneous locations of jaguars to identify social interactions between individuals. We assumed jaguars interacted when they were located <200 m from each other (Kramer & Bonenfant 1997; Louis & Le Berre 2000). We used the dates of male/female pair locations and the duration of such encounters to determine social interactions and document when possible mating events may have occurred.

Results

We captured 10 jaguars (5 adult males, 1 subadult male, 4 adult females) between October 2001 and November 2003, and equipped them with GPS collars. We monitored radioed cats for a cumulative total of 76 months. Continuous monitoring periods for individual jaguars varied from 1.5 to 24 months (Table 8). We simultaneously monitored 3 to 5 jaguars at any one time. We obtained 11,787 locations on the 10 radioed individuals (Table 8). Data collection occurred during the wet seasons of 2001-2002, 2002-2003, 2003-2004, and the dry seasons of 2002, 2003, and 2004; data from the dry season of 2004 were limited.

HOME-RANGE SIZE

The mean 98% MCP home-range size for female jaguars (n = 4) during the wet seasons (2001-2002, 2002-2003, 2003-2004) was 57.1 ± 26.2 (SD) km^2 (95% CI: 30.9 - 83.3 km^2). Female home-range size was 69.1 ± 28.7 km^2 (95% CI: 40.4 - 97.8 km^2) in the dry seasons (2002, 2003). For male jaguars (n = 6), the mean 98% MCP home range size was 152.0 ± 79.1 km^2 (95% CI: 72.9 - 231.1 km^2) during the wet seasons (2001-2002, 2002-2003, 2003-2004), and 170.8 ± 97.3 km^2 (95% CI: 73.4 - 268.1 km^2) during the dry seasons (2002, 2003; Table 9).

Estimates of 90% kernel home range size varied among study animals and seasons, ranging from 34.1 to 262.9 km^2 (mean: 104.2 ± 71.3 km^2; Table 10). Among males, mean home-range size was 140.0 ± 57.0 km^2 (95% CI: 83.0 - 197.1) in the wet seasons and 165.8 ± 92.3 km^2 (95% CI: 73.5 - 258.1) in the dry seasons (t = 0.4883, df = 6, P = 0.3213). Female home-range size averaged 62.0 ± 27.7 km^2 (95% CI: 34.3 - 89.7)

in the wet seasons and 63.9 ± 23.3 km^2 (95% CI: 40.6 - 87.2) in the dry seasons (t = 0.114, df = 5, P = 0.4568).

Within the home ranges of females, areas of intensive use (core areas) averaged 14.5 ± 6.5 km^2 (95% CI: 8.0 - 21.0; Table 10). The sizes of core areas for female jaguars during the dry ($\bar{x} = 15.5$ km^2) and wet seasons ($\bar{x} = 14.1$ km^2) were not different (t = -0.2791, df = 3, P = 0.3991). Among males, core areas within their home ranges averaged 34.8 ± 13.6 km^2 (95% CI: 21.3 - 48.4). For male jaguars, the size of the core area during the wet seasons ($\bar{x} = 35.4$ km^2) was not different from the size of the core area during the dry seasons ($\bar{x} = 34.5$ km^2; t = 0.0965, df = 5, P = 0.4634).

Although the sizes of core areas did not significantly differ between seasons, the sizes of jaguar home ranges during the dry seasons were generally larger than in the wet seasons (Table 10). However, they varied from year to year, both individually and among cats. We examined individual home ranges among the different years of our study, since 2002 and 2003 were, respectively, the driest and the wettest of the last 8 years on the site. In the dry season of 2002, both females #1 and #2 increased their home ranges from the previous wet season by 51.5% and 28.7%, respectively. However, during the following wet season of 2002-2003, female #2 reduced her home range while female #1 increased hers by another 12%. Although she increased her home range, female #1 decreased her core area by 39%. Female #2 followed that same pattern during the subsequent wet season (2003-2004), when she increased her previous dry season home range by 13%. However, in contrast to female #1, she also increased her core area by 9%. Among all the females, female #3 had the largest home range within any season. She was also the female whose home range encompassed the driest portion of the study area.

Both males for which we had consecutive wet and dry season home range estimates (males #1 and #4), used smaller home ranges during the wet seasons (Table 10). In contrast to female #1, the sizes of their core areas were consistent with the sizes of their home ranges. Males #1, #3, and #4, which had the largest home ranges among males, were also the oldest males among the radioed jaguars. Male #3, although considerably older than male #4, had a smaller home range in the dry season. Male # 1 was also considerably older than male #4, however, the sizes of their home ranges were more comparable (Table 10). In contrast, subadult male #6, which had the smallest of the male home ranges within any season, was accompanied by its mother and sibling.

HOME RANGE STABILITY AND SITE FIDELITY

The stability of individual home ranges varied among the seasons and between individuals (Fig. 10). Female #1 maintained 87% and 80% of her seasonal home ranges from the wet season 2001-2002 to the dry season 2002 and from the dry season 2002 to the wet season 2002-2003, respectively. In contrast, while female #2 maintained 93% of her home range in the following wet season (2002-2003), she used only 45% of the area she had used the previous season. She then maintained 90% of this new home range through the following dry season in 2003. In the wet season 2003-2004, she again used only 56% of the area she had used the previous season.

Within the home ranges they maintained from one season to another, the overlap of core areas also varied. While female #1 maintained 80% of her HR from the dry season 2002 to the wet season 2002-2003, she maintained only 25% of the core area from the previous season; 75% of her core area was located in a different site. The same was true for female #2 who maintained most of her home range from the wet season 2001-

2002 to the dry season 2002, but used only 22% of the core area the following season, meaning that 78% of the core area was located in a different site within the home range. In the wet season of 2003-2004, her core area was located in a completely different area (Fig. 10).

Among males, our data also suggest individuals behaved differently. While male #1 maintained 99% of his home range between the wet season 2001-2002 and the subsequent dry season 2002, male #4 maintained only 37% of his home range between the dry season 2003 and the wet season 2003-2004. Although the overall area they used from one season to the next varied, males #1 and #4 maintained their core areas in similar proportions (43%; Fig. 10). Unfortunately, our data set was limited to comparisons among individuals for which we had data for at least two consecutive seasons.

HOME RANGE OVERLAP AMONG RADIOED JAGUARS

Although radioed females used common areas throughout the period they were simultaneously monitored, the seasonal analysis of their locations suggested spatial avoidance between them. During the wet seasons 2001-2002 and 2002-2003, females #1 and #2 had distinct, non-overlapping home ranges (Fig. 11a,b). Similarly, females #3 and #4, both monitored during the wet season of 2003-2004, did not overlap their home ranges with other radioed females. However, we documented overlap between female home ranges during the dry seasons. During the dry season of 2002, females #1 and #2 overlapped their home ranges (Fig. 11c). The area overlapping both home ranges encompassed 23.3 km^2, and represented 26.3% and 38.4% of the home ranges of females #1 and #2, respectively. In addition to the four females we radio-collared, we indirectly monitored a fifth female (female #5), based on the locations of her young (subadult male

#6). Therefore, assuming we can estimate her home range based on the locations of subadult male #6, his locations indicated that during the dry season of 2003, female #5 and her two offspring (subadult male #6 and a female sibling) overlapped with female #2 (Fig. 11d). The area of overlap encompassed 19.8 km^2 and represented 46.7% and 34.0% of the home ranges of females #1 and #5, respectively. Although we were unable to continuously monitor all radioed females throughout the study, or to radio every female in the study area, our data suggested that among females, there may be a pattern of spatial avoidance during the wet season.

Among male jaguars, extensive home range overlap occurred both in the wet and dry seasons. The area of overlap between the home ranges of any two males averaged 78.1 ± 20.2 km^2 (95% CI: 57.9 - 98.3). The most extensive overlap between the home ranges of males occurred in the dry season 2003, between males #2 and #3, the oldest of the males we monitored simultaneously. However, all males monitored in the dry season 2003 overlapped their home ranges with at least 3 other radioed individuals (Fig. 12), or at least 2 other radioed adult males, if we exclude subadult male #6, which was still accompanying its mother and sibling and may therefore not be considered an adult male with an established home range of his own. The area of overlap shared by males #2, #3, and #4 was 65.4 km^2, which represented 71.5%, 39.9%, and 24.8% of the home ranges of males #2, #3, and #4, respectively. In the wet season 2003-2004, males #4 and #5 overlapped their home ranges by 65.4 km^2, which represented 43.8% and 82.8% of their respective home ranges. Although we suspected there was additional overlap with the home ranges of other males during this season, we lost contact with the signals of males #2, #3, and #6.

Our data suggest younger individuals may have shared a larger proportion of their home ranges with same-sex conspecifics. In contrast with males #3 and #4, which overlapped 39.9% and 24.8%, respectively, males #2 and #5, the youngest of the adult males radioed, overlapped 71.5% and 82.8%, respectively, of their home ranges with other males.

Additional information from camera trapping during the same period suggested the presence of an additional 4 resident males whose home ranges could have overlapped with our radioed animals (Fig. 12), although we were unable to calculate their home ranges from camera trapping alone (Soisalo & Cavalcanti 2006).

Overlap between males and females occurred both in the wet and dry seasons. The area of overlap between the home ranges of a male and a female jaguar averaged $38.2 \pm 13.0 \text{ km}^2$ (95% CI: 25.3 - 51.0). We found that on average, a male jaguar overlapped 27.1% of his home range with a female. In contrast, females overlapped an average of 64.4% of their home range with a male (Table 11). A larger portion of their home range was shared with opposite sex conspecifics than same sex conspecifics. In the dry season 2003, female #2 overlapped her home range with at least 3 adult males (#2, #3, and #4) and her home range was entirely encompassed by the home range of male #3. During the wet season 2003-2004, she shared her home range with at least 2 adult males (#4 and #5) and her home range was almost entirely encompassed by the home range of male #4 (Fig. 13). Female #4 also overlapped her home range with at least these same two males. She shared 55.4% and 39.9% of her home range with males #4 and #5, respectively.

ACTIVITY PATTERNS AND MOVEMENTS

The average rate that a jaguar traveled per hour differed among time periods ($F = 28.263$, df $= 3, 4733$, $P < 0.001$), with the greatest rate of movement occurring at dusk (mean $= 0.27$ km/hr). The mean rate of movement at dawn was 0.25 km/hr and at night was 0.23 km/hr. Although jaguar movement rates did not significantly differ between dawn and night, they were different from movement rates during the daylight hours ($P < 0.001$) when jaguars traveled an average of 0.10 km/hr. Although the rate of movement by male and female jaguars did not differ during the day ($t = 0.466$, df $= 567$, $P = 0.642$), it was different during dawn ($t = -3.104$, df $= 1177$, $P = 0.002$), dusk ($t = -3.675$, df $= 1357$, $P < 0.001$) and night ($t = -7.607$, df $= 1628$, $P \leq 0.001$), with males moving at a higher rate than females (Fig. 14).

There was no difference in jaguar movement rates across the seasons during dawn ($F = 1.350$, df $= 4, 1174$, $P = 0.249$), day ($F = 2.494$, df $= 3, 565$, $P = 0.059$), or dusk ($F = 1.907$, df $= 4, 1354$, $P = 0.107$). However, their movement rates differed across seasons during the night ($F = 2.886$, df $= 4, 1625$, $P = 0.021$), with the greatest rate of movement occurring in the wet season of 2001-2002 (0.27 km/hr), followed by the wet season of 2003-2004 (0.25 km/hr).

SPATIAL-TEMPORAL ASSOCIATIONS

We investigated spatial-temporal avoidance between jaguars by comparing the mean distance between simultaneous locations of individual cats with the mean distance between them if they were randomly paired (Kitchen *et al.* 1999). We calculated distances for 2 pairs of jaguars in the wet season 2001-2002, 3 pairs in the dry season 2002, 1 pair in the wet season 2002-2003, 10 pairs in the dry season 2003, and 5 pairs in

the wet season 2003-2004. Distances between simultaneous locations of 2 jaguars did not differ from those if randomly arranged in any season (Table 12), suggesting they moved independent of each other, neither avoiding nor attracting each other.

The analysis of the frequency of counts in various distance classes suggested the observed counts were significantly different from expected (Table 13). We assumed cats came into contact when they were located <200m from each other, although the choice of distance classes was arbitrary. The distance between simultaneous locations for jaguars in the 0-200 m category averaged 41.1 ± 52.1 m (n = 54 locations), indicating they may have been close to each other and had a social encounter. Among the locations <200 m apart, there were 10 pairs of locations between males and 32 possible encounters between a male and female. Another 11 locations were close associations between 2 males. However, one of the males involved was subadult male #6, who was accompanied by his mother and female sibling. These interactions could have been between the entire family and another male.

INTERACTIONS BETWEEN MALE AND FEMALE JAGUARS

We used the dates of locations of male/female encounters and the duration of such interactions, as well as the reproductive status of females during captures to estimate when possible mating events may have occurred. In addition, we used clusters of female locations at a particular site as indicators of possible dens and the estimated age of young captured with their mothers to create a reproductive profile of radioed female jaguars.

When captured for the first time in November 2000, female #1 was accompanied by an adult male (male #7, also captured on the same day as female #1, but equipped with a traditional VHF radio collar and therefore not included in this paper) and exhibited

several scratch marks behind her neck and on her shoulders, characteristic of mating behavior (S. Cavalcanti, pers. obs.). Between September and October 2001, she was repeatedly located in a restricted area of approximately 160 m^2 for about 7 weeks, suggesting she had given birth to a litter. During her recapture at the end of October 2001, she was accompanied by a 2-month-old female cub. Given the approximate gestation period of 90-111 days (Ewer 1973; Hemmer 1979), this female had therefore mated around May/June 2001. Either she did not get pregnant from the November 2000 encounter with male #7, or she lost the litter. This female was subsequently located in the company of male #1 on 2 different occasions, for at least 4 hours in April 2002 and for 3 consecutive days during May 2002. The distances between their simultaneous locations (mean = 3.4 ± 4.0 m) and the length of their association suggested they could have been mating. If she had lost her 2001 litter, she could have gotten pregnant again and a third litter could have been born in August/September 2002. However, she associated with yet another male around February/March 2003, as she was pregnant during her recapture in April. We unfortunately lost contact with her radio collar in May 2003.

Female #2 was in the company of an adult male when she was captured in December 2000, as indicated by fresh pugmarks. During her recapture in October 2001, she was pregnant suggesting she had mated in September. Her litter would have been born around January 2002. In September 2002, we recaptured this female in the company of a male cub of about 7 months. However, 1 and 3 weeks prior to her recapture, this female was located in the company of male #1 for periods of 6 hours and 2 hours, respectively. She associated again with this same male for 3 days, 2 days after her recapture. The distances between their simultaneous locations averaged 29.7 ± 23.9 m. In

June 2003 she had encounters with 2 different adult males, # 3 and #4, for 16 hr and 4 hr, respectively. In the beginning of the following month (July 2003), this female was located in a restricted area for 12 consecutive days, suggesting she may have had another litter. Since gestation is 90-111 days (Ewer 1973; Hemmer 1979), her mating event could have been near the end of March or the beginning of April 2003. Therefore, she was probably already pregnant when she associated with males #3 and #4 in June. From November 30 to December 8, she was again located in the company of male #4 on 2 different occasions. When she was recaptured on November 20, she was in heat and had recently (<1 day) been mating. Four months later in March 2004, female #2 was once more located in the company of an adult male (#5) for 6 consecutive hours.

Female #4 was accompanied by male #5 the day she was first captured, in November 2003. She was again located with him a month after her capture, although for only a 2-hour period. Five months later (May 2004), she spent 5 days in the company of male #4. Although by this time both female #4 and male #5 were wearing traditional VHF collars, and we therefore could not get accurate distances between their simultaneous locations. Despite not being able to establish visual contact with them, their vocalizations (meowing characteristic of domestic cats in estrus) suggested they could have been mating during this period.

On another occasion, male #1 was located in a cluster of locations that we later determined to be an interaction with a non-collared female. We obtained a photograph of male # 1 accompanied by a non-collared female that was acquired at the same location, date and time coinciding with the male's locations.

Additional information from camera traps suggested females can come in contact with adult males before their young disperse. We obtained photographs of subadult male #6 accompanied by its mother and female sibling days after photographing her walking together with an adult collared male (male #4) (Soisalo & Cavalcanti 2006). In addition, locations of male #6 were associated with signs of a family group, such as large day beds.

INTERACTIONS BETWEEN MALE JAGUARS

On one occasion, we were able to detect 2 adult male jaguars (males #2 and #3) sharing the carcass of a feral hog. It was difficult to detect which one was responsible for the kill since their locations on that coordinate overlapped with regards to date and time. Given their difference in age ($\geq$4-5 years apart), we assumed these 2 males were not brothers from the same litter. On three other occasions, males # 2 and #4 where located 24, 150, and 198 m from each other. We were unable to find any carcasses of prey in the vicinity of their locations. In August 2003, these same 2 males were located 30 m from each other for a period of 40 hours. Again we did not find any carcasses of prey in the area.

We found male #3 dead after monitoring him for 3 months. From the constant vocalizations by at least 3 different individuals we heard the night prior to his death, in addition to hemorrhage and puncture marks on his skull and other parts of the body, we concluded he died as a result of an aggressive encounter with another male(s).

Discussion

Activity patterns and movements of jaguars have been previously documented (e.g., Schaller & Crawshaw 1980; Rabinowitz & Nottingham 1986; Crawshaw & Quigley

1991). Generally, jaguars are characterized as nocturnal (Almeida 1976; Nowak &

Paradiso 1983; Mondolfi, Michalangeli & Hoogesteijn 1986), although Crawshaw and

Quigley (1991) reported jaguars to be more diurnal. However, they included dawn and

dusk movements as part of daytime activity, whereas other researchers consider it

nightime activity. Nevertheless, these authors reported distinct activity peaks at dawn,

noon, and dusk. In contrast, we found jaguars were active at dawn and dusk, and travelled

significantly less during the day. In Crawshaw and Quigley's study (1991), although

there were no significant differences in activity between seasons, in the wet season

jaguars appeared to be more active during the daytime. In our study, there was no

difference in their movement rates at dawn, dusk, or day across the seasons. However, in

contrast to Crawshaw and Quigley's study, during the wet seasons, the jaguars moved at

a significantly higher rate during the night.

Despite a significant increase on our knowledge of jaguar ecology since the first

studies in the 1980's, information about their population dynamics remains scarce. In

addition to factors such as birth and death rates, and the immigration and emigration rates

of individuals, the density of a jaguar population in an area also depends on the type of

land tenure system, especially the sizes of their home ranges and the degree to which they

overlap. These factors, in turn, are influenced by different ecological conditions. Some

authors have suggested that the distribution and abundance of prey are the major

ecological factors influencing the social organization of carnivores (Sunquist 1981;

Sunquist & Sunquist 1989).

Previous studies have shown a wide variation in home range sizes of jaguars (e.g.,

Schaller & Crawshaw 1980; Crawshaw & Quigley 1984; Rabinowitz & Nottingham

1986; Crawshaw *et al.* 2004). According to Hoogesteijn and Mondolfi (1992) these large differences in jaguar home range sizes reflect the abundance or density of prey in a given habitat and the necessary movement by a jaguar to find prey. However, other factors play important roles in shaping the spatial structure of a population. Sandell (1989) suggested that while female territories are determined by food abundance and distribution, male territories are determined by the distribution of females. Dahle and Swenson (2003) reported that, within a population of brown bears (*Ursus arctos*), the size of home ranges was not linked to food availability.

Studies on the social ecology of solitary cats like tigers *(Panthera tigris)*, leopards *(Panthera pardus)*, and mountain lions *(Puma concolor)* suggest that the basic pattern of social organization in felids is one in which males occupy large, exclusive or little-overlapping ranges that encompass the home ranges of several females (Seidensticker *et al.* 1973; Sunquist 1981; Sunquist & Sunquist 1989; Bailey 1993). Our results suggest male jaguars do not retain exclusive ranges but overlap extensively year round. Previous studies on jaguars in the Pantanal (Schaller & Crawshaw 1980; Crawshaw & Quigley 1991) had either samples sizes too small to observe overlap among males, or based their conclusions on the locations of pugmarks and other indirect signs. Rabinowitz and Nottingham (1986) documented overlap among male home ranges in Belize. Their data suggested male jaguars had a dynamic land tenure system that constantly changed whenever established ranges became vacant. Nevertheless, all solitary felids encounter a variety of habitat types that vary significantly in resource distribution and availability. As a result, their land tenure systems likely exhibit some level of flexibility.

Sandell (1989) suggested that solitary males may have overlapping ranges if female density is low. Results from camera trap surveys in our study area conducted in 2003 and 2004 (Soisalo & Cavalcanti 2006) suggested that male:female ratio during those years was 1.5:1 and 1.2:1, respectively. In solitary carnivore species, the roaming of large areas by males may increase their reproductive success as they increase the number of females with which they can mate (Davies 1978; Lott 1984). Ostfeld (1985) argued that the spacing strategies of males depends solely on the spatial distribution of reproductive females and predicted males would have overlapping home ranges when female distribution was not clumped (i.e., when they were evenly distributed). Ims (1987) argued that in addition to the spatial component, female distribution has also a temporal component, suggesting that the number of reproductive females may vary both in time and space. Therefore, when female receptivity is asynchronous, males may have large, overlapping home ranges.

Our data suggested females have non-overlapping home ranges at least during part of the year (i.e., during the wet season). Additionally, their reproductive profile indicated a lack of an established mating season (i.e., asynchrony), suggesting they associated with males throughout the year. We found on average, a female overlapped 64.4% of her home range with a male home range. This suggested their home ranges, and therefore their movements, were not restricted within the ranges of individual adult males as had been previously suggested (Schaller & Crawshaw 1980; Rabinowitz & Nottingham 1986). Therefore, we suggest the mating system in jaguars may be one of a polygynous and promiscuous nature; a male likely mates with several females and a female mates with several males.

The reproductive profile of females, or the frequency with which they associated with male jaguars, suggested either low conception rate, low survival rate of young, or that jaguars may be more social than previously thought. As Leyhausen (1965) describes, "solitary" is not necessarily the opposite to "social." A species may be characterized as solitary, but an individual may eventually meet with conspecifics. Schaller and Crawshaw (1980) described four jaguars hunting for a week in the same small area. They also described sightings of a male with a female and two large cubs; and several sightings of two males, indicating the possibility of a social life beyond courtship and the raising of a litter. The associations between our collared animals, male #1 and female #2, during a period in which she was accompanied by her 6-7 month old cub corroborates this possibility. Male/male associations away from carcass sites may also suggest some degree of sociality, although these instances could be related to courtship behavior involving an uncollared female.

Our results showed variation in the land tenure system of jaguars throughout the study, with home ranges in the dry season generally larger than in the wet season, similar to previous studies (Crawshaw & Quigley 1991; Scognamillo *et al.* 2003). However, this pattern was not true for the duration of the study. Two of our collared females held larger home ranges in the wet seasons of 2002/2003 and 2003/2004 than in previous dry seasons. In their study in the Pantanal, Crawshaw and Quigley (1991) suggested the smaller home ranges of jaguars during the wet season reflected the concentration of their food resources to islands of dry land. However, the foraging ecology of jaguars in the area (Chapter II) suggested that the most important native prey species for jaguars (i.e., caiman and peccaries), were more widespread during the wet season (Coutinho &

Campos 1996; Fragoso 1998). Domestic cattle were also a significant prey item for jaguars and during the wet season they were confined to islands of dry ground. However, predation rates by jaguars were higher during the dry season (Chapter II), when cattle were more widespread. Therefore, the smaller home ranges during the wet season could be a reflection of factors other than prey distribution.

For females, dry ground on which to raise their young and the limited mobility of a litter may be factors contributing to smaller home ranges in the wet season. Alternatively, the shift to smaller ranges during the flooding season could also be a preference for drier ground, although jaguars were usually associated with water and their movements were not limited by water. Alternatively, the increase in home range size of the two females during the wet season could be related to an increase in roaming to meet prospective mates. Their reproductive profiles during these periods suggested they were not accompanied by young when they were associating with these different males. Although there is little evidence in the literature, mating with different males could be a strategy adopted by females to increase paternal uncertainty, thereby reducing the loss of their young to infanticidal males (Ebensperger 1998).

For both males and females, the size of the core areas during the wet season was not different from the dry season. Although they generally increased their overall home range in the dry season, the size of the core areas remained the same. However, site fidelity within the home range varied considerably. While a female jaguar may maintain her overall home range, she will change the areas she uses most intensively. There may be more than one preferred denning site within her home range and therefore site fidelity may not be strong.

Many jaguar studies to date, hindered by logistics and other difficulties inherent to studying large carnivores, may have offered an incomplete picture of their social organization. Analyses of total home ranges fail to identify intricacies of territorial behavior. Our data provided insight into the dynamic nature of the land tenure system of jaguars and their social interactions. Nevertheless, future research would benefit from the collaring of additional individuals and monitoring them over a longer time span to examine the key determinants of jaguar space use. Only then will we be able to fully understand their spatial ecology and social dynamics. Understanding the ultimate factors affecting the spatial organization of a species is fundamental to the successful design of effective conservation strategies. In addition, understanding how different ecological variables influence the land tenure system of jaguars will be important for the long-term conservation of this secretive carnivore.

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Table 8. Length of monitorig period and number os GPS locations acquired for each of
10 jaguars between November 2001 and April 2004 in the southern Pantanal, Brazil.

Jaguar ID	Monitoring period (months)	# of GPS locations acquired
Adult male #1	10	1024
Adult male #2	5	745
Adult male #3	3	453
Adult male #4	11	1543
Adult male #5	6	721
Subadult male #6	3	716
Adult female #1	15	2025
Adult female #2	24	3932
Adult female #3	4	512
Adult female #4	1.5	116

Table 9. Seasonal home range sizes (in km^2, 98% minimum convex polygon; Mohr, 1947) for 10 radio collared jaguars in the southern Pantanal, Brazil, from October 2001 to March 2004.

	Wet 01/02	Dry 2002	Wet 02/03	Dry 2003	Wet 03/04
Female #1	50.24	93.91	92.13	-	-
Female #2	37.10	75.80	40.43	37.64	37.18
Female #3	-	-	-	-	97.41
Female #4	-	-	-	-	45.24
Male #1	242.49	271.72	-	-	-
Male #2	-	-	-	114.08	-
Male #3	-	-	-	126.13	-
Male #4	-	-	-	277.13	117.28
Male #5	-	-	-	-	96.21
Male #6	-	-	-	64.93	-

Table 10. Seasonal home range sizes (in km^2, 90% adaptive kernel; Worton, 1989) for 10 radio collared jaguars in the southern Pantanal, Brazil, from October 2001 to March 2004 (n = number of locations, 50% = area in which the cat could be located 50% of the time, i.e., area of intensive use or core area, and 90% = estimate of the overall home range).

Jaguar ID	Wet 01/02			Dry 2002			Wet 02/03			Dry 2003			Wet 03/04		
	n	50%	90%	n	50%	90%	n	50%	90%	n	50%	90%	n	50%	90%
Female #1	576	9.10	43.02	963	24.41	88.66	486	14.85	99.38	-	-	-	-	-	-
Female #2	522	10.53	43.32	1070	10.77	60.75	1418	10.38	34.08	758	11.34	42.39	153	12.40	47.91
Female #3	-	-	-	-	-	-	-	-	-	-	-	-	512	28.15	100.80
Female #4	-	-	-	-	-	-	-	-	-	-	-	-	116	13.20	65.42
Male #1	265	46.24	191.96	752	53.05	252.80	-	-	-	-	-	-	-	-	-
Male #2	-	-	-	-	-	-	-	-	-	748	23.19	91.45	-	-	-
Male #3	-	-	-	-	-	-	-	-	-	453	36.16	163.82	-	-	-
Male #4	-	-	-	-	-	-	-	-	-	1124	44.56	262.87	419	39.35	149.20
Male #5	-	-	-	-	-	-	-	-	-	-	-	-	645	20.77	78.98
Male #6	-	-	-	-	-	-	-	-	-	716	15.36	58.23	-	-	-

Table 11. Areas of overlap (in km^2) between the estimated seasonal home ranges of collared jaguars in the southern Pantanal, Brazil. Data are presented for pairs of jaguars with overlapping territories during the wet seasons of 2001-2002, 2002-2003, and 2003-2004, and the dry seasons of 2002 and 2003. Columns 4 and 5 represent the percentage overlap represented by their original home ranges.

Jaguar pair (cat1/cat2)	Season and year	Area of overlap (km2)	% cat 1	% cat 2
M1/F1	wet 01/02	7.5	3.9	17.4
M1/F1	dry 02	41.2	46.5	16.3
M1/F2	wet 01/02	35.4	18.4	81.7
M1/F2	dry 02	60.6	24.0	99.7
M2/F2	dry 03	28.3	31.0	66.8
M3/F2	dry 03	42.4	25.9	100.0
M4/F2	dry 03	36.2	13.8	85.4
M4/F2	wet 03/04	47.1	31.5	98.2
M4/F4	wet 03/04	36.2	24.3	55.4
M5/F2	wet 03/04	31.1	39.3	64.9
M5/F4	wet 03/04	26.1	33.0	39.9
M6/F2	dry 03	19.8	34.0	46.8
M2/M3	dry 03	68.9	75.3	42.0
M2/M4	dry 03	70.1	76.6	26.7
M2/M4	dry 03	108.3	66.1	41.2
M2/M6	dry 03	43.5	47.6	74.8
M3/M6	dry 03	53.1	32.4	91.2
M4/M5	wet 03/04	65.4	43.8	82.8
M4/M6	dry 03	45.6	17.3	78.2
F1/F2	wet 01/02	23.3	26.3	38.4
F1/F2	wet 02/03	0.5	0.5	1.4

Table 12. Distances between pairs of jaguars in the southern Pantanal, Brazil,

October 2001 – April 2004 (n = numbers of pairs of locations).

Jaguar pair	Season	Simultaneous	Random	n	t	P
M1/F1	wet 01/02	10790	10876	141	-0.219	0.827
M1/F1	dry 02	11536	11862	538	-1.146	0.252
M1/F2	wet 01/02	7525	7271	122	0.562	0.574
M1/F2	dry 02	6826	7117	553	-1.197	0.231
M2/F2	dry 03	6725	6666	306	0.243	0.808
M3/F2	dry 03	5482	5232	190	0.781	0.435
M4/F2	dry 03	10920	10865	348	0.118	0.906
M4/F2	wet 03/04	9013	8865	38	0.133	0.895
M4/F4	wet 03/04	6566	7087	24	-0.828	0.412
M5/F2	wet 03/04	5050	4974	50	0.128	0.899
M5/F3	wet 03/04	4006	5050	15	-1.353	0.187
M6/F2	dry 03	6788	6665	174	0.432	0.666
M2/M3	dry 03	6681	6202	188	1.236	0.217
M2/M4	dry 03	8477	8666	429	-0.427	0.669
M2/M6	dry 03	4923	4465	278	1.621	0.106
M3/M4	dry 03	10790	11143	212	-0.575	0.566
M3/M6	dry 03	5760	6008	87	-0.868	0.387
M4/M5	wet 03/04	7134	7247	120	-0.254	0.800
M4/M6	dry 03	5534	5335	435	1.084	0.279
F1/F2	dry 02	7803	7875	723	-0.451	0.652
F1/F2	wet 02/03	8860	9078	374	-1.278	0.202

Table 13. Frequency of counts of distance classes for the distances between simultaneous

and random locations of pairs of jaguars in the southern Pantanal, Brazil, October 2001 –

April 2004.

Distance class (m)	Female/Female		Female/Male		Male/Male	
	Simultaneous	Random	Simultaneous	Random	Simultaneous	Random
0-200	1	0	32	1	21	1
200-500	0	2	9	5	8	12
500-1000	2	5	20	20	26	42
1000-2000	11	19	73	81	100	124
2000-4000	54	75	341	328	411	361
4000-8000	436	366	839	854	656	666
>8000	593	630	1185	1210	527	543
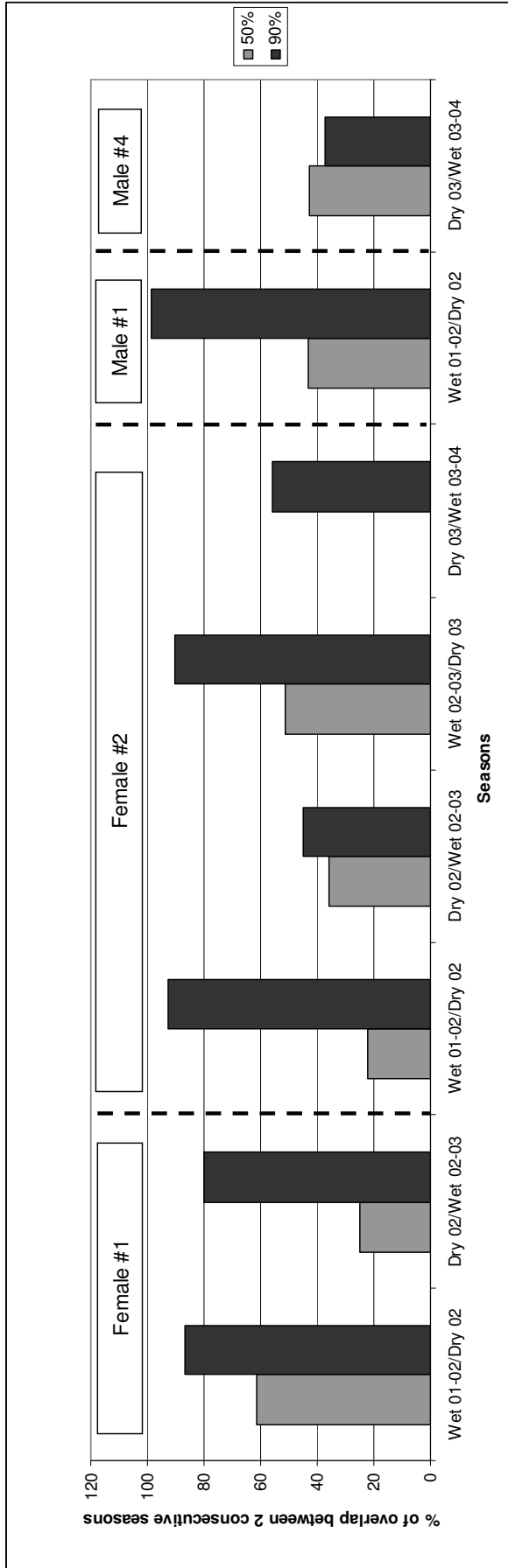
Figure 10. Percentage of overlap of the home ranges (dark grey bars) and core areas (light grey bars) of individual collared jaguars

between two consecutive seasons in the southern Pantanal, Brazil, October 2001 – April 2004.
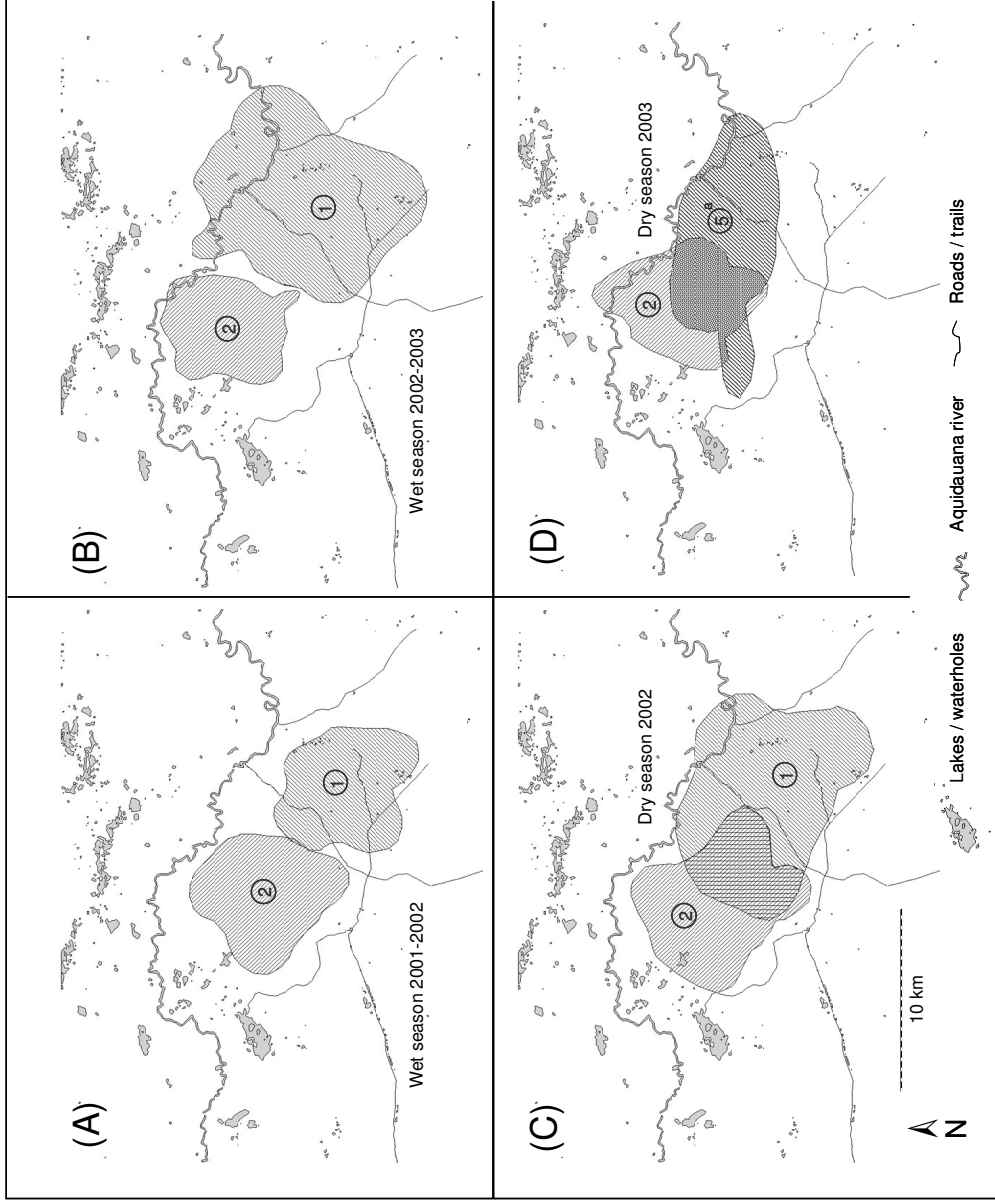
Figure 11. Seasonal home ranges (90% adaptive kernel) of female jaguars #1, #2, and #5 in the southern Pantanal, Brazil, October 2001-April 2004. [a] In addition to the 4 females we collared, we were able to indirectly monitor a fifth female (female #5, D) and estimate her home range based on the locations of her young, a subadult male which we radio collared (subadult male #6).
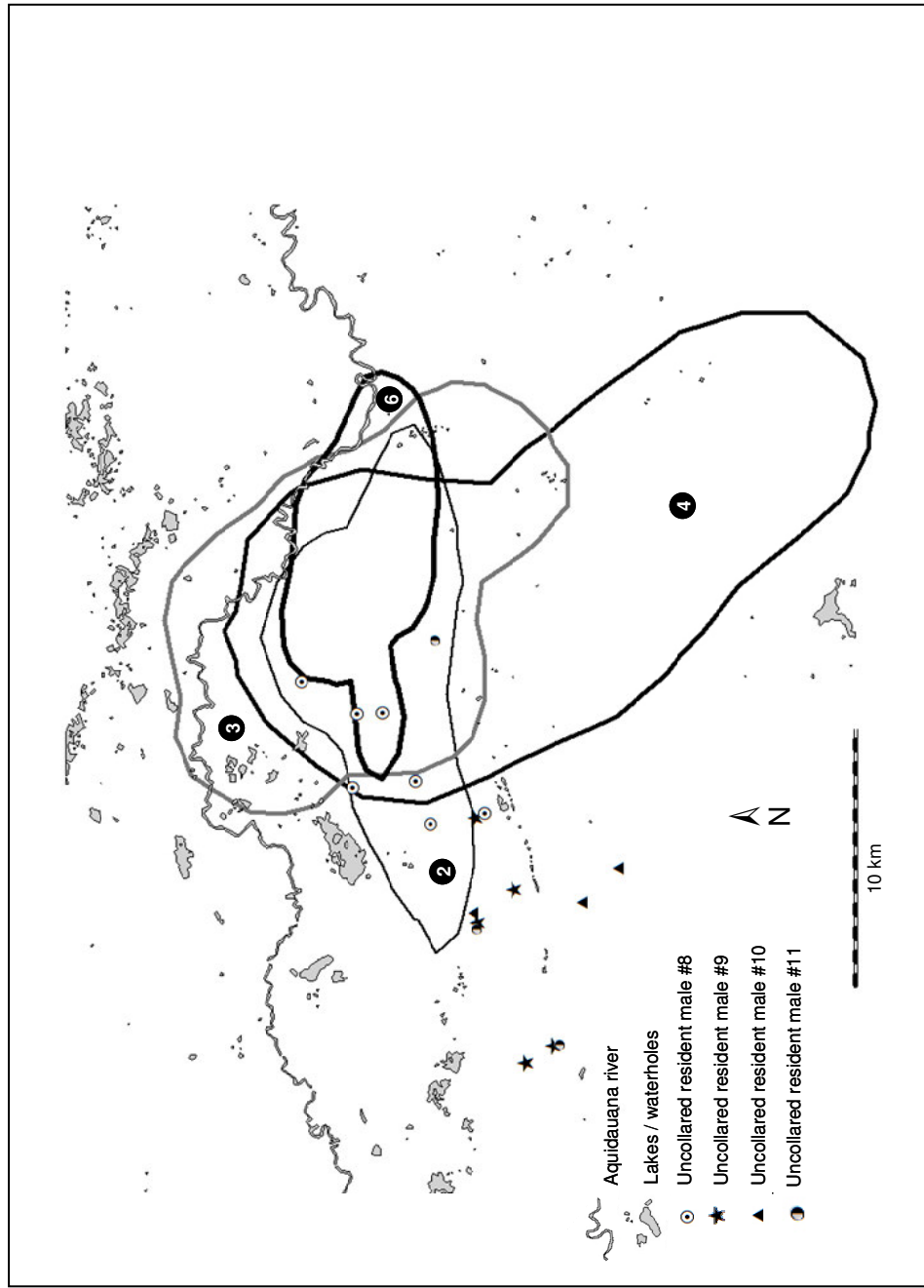
Figure 12. Overlaping home ranges of collared male jaguars during the dry season 2003 in the southern Pantanal, Brazil. Numbers in black circles identify individual home ranges. Additional symbols show the locations of uncollared resident males photographed by camera traps (Soisalo and Cavalcanti 2006).
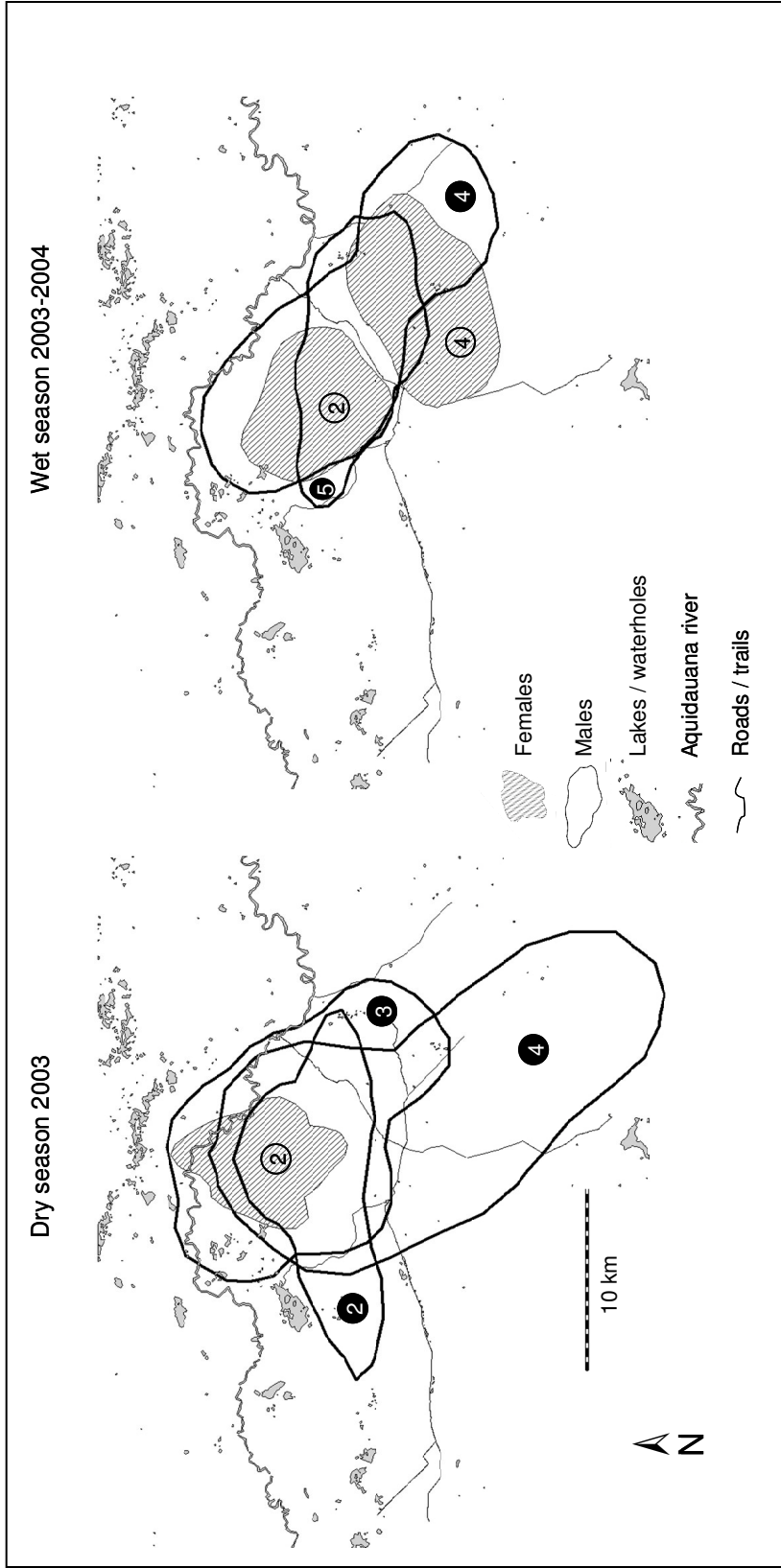
Figure 13. Home ranges (90% adaptive kernel) of male and female jaguars, southern Pantanal, Brazil, dry season 2003 and wet season 2003-2004.
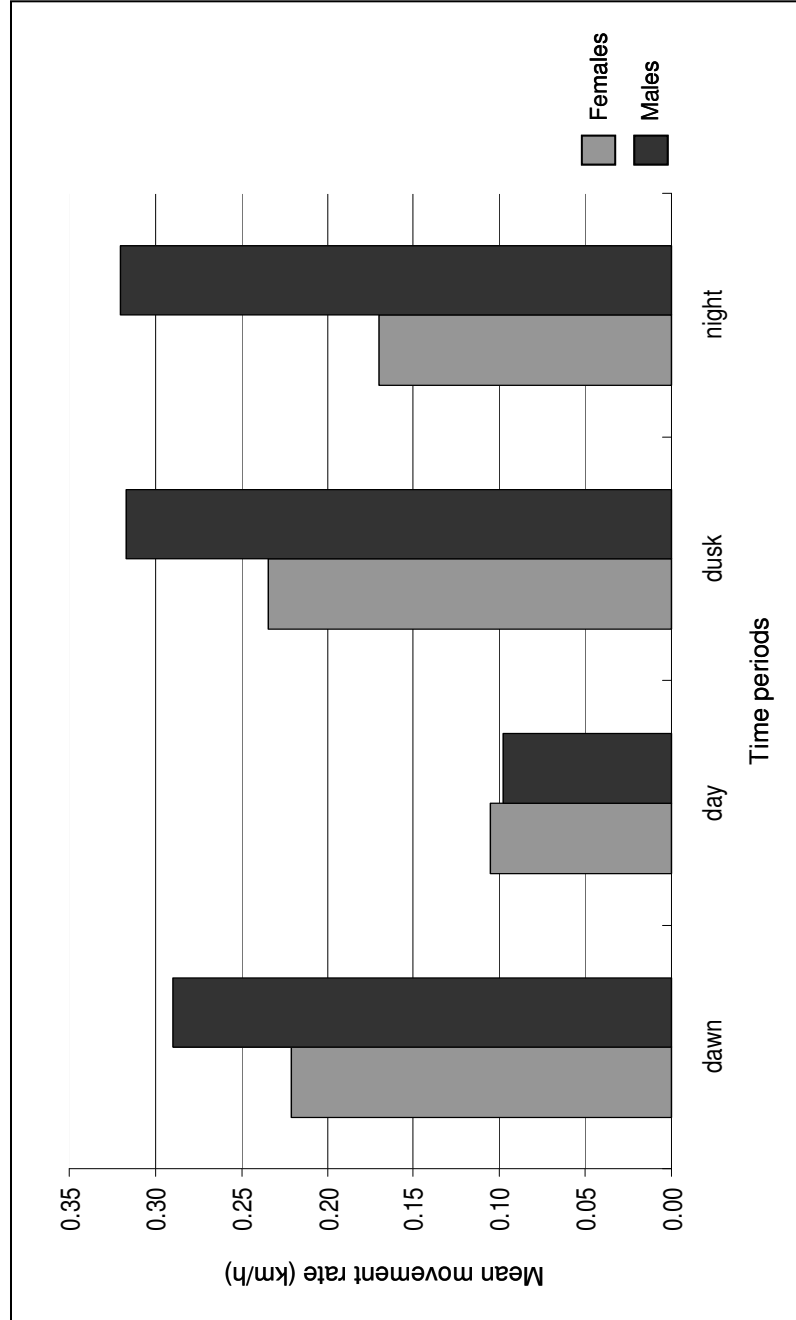
Figure 14. Mean movement rates of male and female jaguars over a 24-hour period from October 2001 to April 2004 in the southern Pantanal, Brazil.

CHAPTER V

CONCLUSION

Our study provided new insights on many ecologically important aspects of jaguar predation and behavior, illustrating the highly opportunistic nature of jaguars, in which they appear to take advantage of an environment that is constantly changing and where food resources vary both temporally and spatially. In addition, our results illustrate the dynamic nature of the land tenure system of jaguars, suggesting they have a more intricate social system than previously thought. Consequently, our data contradict some preconceived notions about jaguar ecology as it relates to depredation on livestock.

Back in 1914, Theodore Roosevelt put forth the idea that not all jaguars killed cattle (Roosevelt 2000). He noted that in Brazil, livestock depredation by jaguars was prevalent on ranches with a scarcity of wild prey but occurred infrequently in places with abundant wild prey. This early preconceived notion was contradicted by our results, which showed that even in an area with abundant wildlife, all jaguars killed cattle, although to varying degrees. But our results also question more recent preconceived notions. The 'problem-animal' paradigm (Linnell et al. 1999) is one of them. Although some studies indicate livestock-depredating cats are more likely to be males than females, we found no support for this contention as there was no difference in the proportion of cattle killed by male and female jaguars in our study. In addition, although it is possible females with young may teach their young to kill cattle as has been regularly suggested (A. Silva, V. Correia, A. T. Neto, B. Fiori, pers. comm.), our data does not support the conclusion that these are problem-animals. Availability of livestock and native prey, in

combination with climatic conditions appeared to have the most influence on jaguar predation patterns.

Our study elucidated other aspects of jaguar ecology and behavior that have direct implications for cattle management and consequently for jaguar-livestock conflict. For example, we found jaguars do not kill cattle only at night, but kill them opportunistically throughout the day and night. In addition, jaguars do not kill cattle only in forest or near forested areas, but kill them with similar frequencies in open pastures and other habitats as well. Another important finding with direct implications for understanding the nature of jaguar-livestock conflicts was that contrary to popular belief, jaguars do eat carrion and the possibility of misinterpreting the cause of death always exists. Additionally, although caiman, peccaries, and cattle formed the basis of the diet of jaguars, we found individual jaguars killed prey differentially, indicating either there was a learning or search image component involved in prey selection, there were individual preferences among the jaguars for certain prey, or that certain prey species varied in their availability or vulnerability in each jaguars territory.

Our study also showed jaguar predation on cattle can not only vary from one season to the next, but the annual variation in predation rates and prey selection can also be high, with direct consequences to both the incomes of ranchers and the conservation of jaguars, in the form of retaliatory persecution. This annual variation in jaguar kill rates, which likely reflect differences in availability or vulnerability of alternative prey, contradicts the belief that destroying or removing a problem animal would end the depredation problem (Rabinowitz 1986, Hoogesteijn and Mondolfi 1992). We found animals with >50% of their kills as cattle in 2002, decreased their predation rate on cattle

in 2003; some of them ceased to prey on cattle and increased their predation on other native species (e.g., peccaries).

Our study was conducted during years of extreme climatic conditions in the Pantanal when the majority of cattle losses occurred in 2002 under severe drought conditions. The main native prey species may have either migrated from the area (peccaries), were concentrated only along the main river courses or lakes (caiman), or were reduced in number. Cattle, on the other hand, were limited in their movements and were distributed throughout the ranch and available to all collared jaguars. Like other large carnivores, jaguars may target livestock in larger proportion at periods when native prey is less accessible. These are important aspects of jaguar ecology and behavior that need to be considered in any jaguar conservation plan proposed by local and federal authorities.

Although the Pantanal is considered important for jaguar conservation in the long-term (Sanderson et al. 2002), the area has some peculiarities that makes the conservation of jaguars and the alleviation of jaguar-livestock conflict a complex and challenging issue. In addition to the widespread problem of habitat destruction and the conversion of land into grazing pastures (Santos et al. 2002), there are other factors that directly and indirectly affect jaguar conservation. As previously mentioned, jaguars kill livestock and this creates a conflict with ranchers from an economic perspective. Aspects of jaguar ecology and behavior elucidated by our study have direct implications for this economic aspect of jaguar conservation. Instead of trying to curtail jaguar depredation on livestock through preventive measures, both ranchers and authorities should recognize the fact that cattle indeed comprise part of the regular diet of jaguars in the region and should invest in

alternative mitigation measures. The fact that jaguars regularly kill cattle in the Pantanal is not surprising given jaguars have coexisted with cattle for over two centuries in an area where the vegetation is a diverse mosaic, with open fields and marshes interspersing gallery forests and shrublands. Additionally, while depredation events may be related to a lack of natural prey (Saberwal et al. 1994, Vos 2000) forcing predators to seek alternative food sources, some authors have suggested the abundance of prey may influence depredation behavior as well. Schaller (1972) found that the more abundant a preferred species was, the more likely it was to fall prey to lions. This is likely to be the case in the Pantanal, where cattle represent not only a prey species with the largest available biomass in the area, but also the most vulnerable, when compared to native species. Authorities should therefore recognize the cost associated to grazing cattle in an area where jaguars exist in considerable numbers (Soisalo and Cavalcanti 2006) and the consequent need for a differentiated policy for the region, perhaps in the form of tax benefits, special lines of credit, or a regional increase in beef prices. Ranchers, on the other hand, should focus on increasing their production potential, curtailing losses due to rudimentary herd management and poor husbandry practices, which can be more significant than jaguar depredation (Hoogesteijn et al. 1993). Nevertheless, although predation on cattle in the Pantanal will likely always occur, the results from our study illustrate the importance of maintaining native prey populations as a possible means of minimizing these conflicts.

Recently, there has been an effort in the Pantanal to alleviate jaguar-livestock conflict in the form of a compensation program (Silveira et al. 2006). Although such programs have been implemented worldwide (Saberwal et al. 1994, Wagner et al. 1997, Vos 2000, Naughton-Treves et al. 2003, Swenson and Andrén 2005) their value and

weaknesses have been thoroughly discussed (Bulte and Rondeau 2005, Nyhus et al. 2003, 2005). Unverifiable losses, fraudulent claims, bureaucratic claim processes incurring long time lags, compensation values below full market value, lack of sustainable funding, high administrative costs, and moral hazard are some of the drawbacks associated with compensation programs (Bulte and Rondeau 2005, Nyhus et al. 2005, Zabel and Holm-Müller 2008). In addition, the success of such a program in the Pantanal can be notoriously difficult to monitor, because retaliatory, illegal killing of jaguars is often carried out clandestinely.

A more recent approach that has been proposed as an alternative to compensation programs is what is termed 'performance payments' (Nyhus et al. 2005, Zabel and Holm-Müller 2008). Rather than compensating ranchers for the negative aspect of jaguars (i.e., the economic losses they pose), local and national governments, and conservation organizations may want to consider making payments that are conditional on jaguar abundance in an area (Ferraro and Kiss 2002, Zabel and Holm-Müller 2008). For example, by focusing on the number of jaguar offspring or the annual density of jaguars in a particular area, these performance payments would give the paying agency the possibility to pay exactly and solely for the conservation goal it strives for and therefore could be an interesting solution to the jaguar-livestock conflict in the Pantanal.

However, it is very important to note that the problem goes beyond the economic aspect, as it has also a cultural quality that can be more difficult to address than the economic one. Cultural traditions in the Pantanal are deeply ingrained in the way of living of local inhabitants. Jaguars hunts, viewed as an act of bravery and dexterity among cowboys, increase their personal reputation within the community. These cultural

traditions coupled with the characteristics of the area and the lack of enforcement by wildlife authorities contribute to the regular illegal shooting of these cats, even in areas where absent owners have specifically banned the practice (S. Cavalcanti, pers. obs., B. Rondon, pers. comm., V. Correia, pers. comm., B. Fiori, pers. comm.).

Given that cowboys are ultimately the ones who will have a strong direct impact on jaguar conservation in the Pantanal, it would be reasonable to think about potential ways to involve them in a conservation program for the same jaguars they used to persecute. An assumption of a 'jaguar conservation performance payment' program like the one we portray is that the benefit received from protecting jaguars can create sufficient incentive for cowboys and their families to modify their attitudes toward the large cats. Giving cowboys a sense of sustained benefits from jaguars may influence the outcome of such a program in the Pantanal. Examples from the Amazon and Africa show that community-based resource management can be successful in wildlife conservation (Lewis et al. 1990, Castello 2004, Frost and Bond 2008). The challenge for this type of approach in the Pantanal however, is the land tenure system, characterized by very large tracts of land. About 95% of the Pantanal is privately owned (Seidl et al. 2001), suggesting that any jaguar conservation effort will be largely dependent upon the attitudes of ranchers. Nevertheless, if ranchers think in the long term and are willing to share the benefits of such a program with the people working on their land, the odds for success of this "jaguar conservation performance payment" program is likely to increase. Ranchers may channel payments to their workers in the form of community-based benefits like funds for local schools, small health clinics, churches and small workshops to encourage the selling of local crafts to visitors and tourists. This community-level

approach in the channeling of payments may even induce strong peer pressure on individuals: if a few cowboys kill a jaguar, this small group will decrease the benefits received by everyone in the local community. In addition, local people often have better information for monitoring their own members, but frequently have little incentive to do so.

The conservation of jaguars in the Pantanal entails the complex task of integrating ecological, economic, social, and cultural factors in the planning of effective interventions not only to decrease economic net losses cattle ranchers incur, but also to improve people's perceptions of jaguars as a species. To that end, it will be important to devise communication tools that bring ecological knowledge into the realm of the local community and make them active participants of a larger conservation scenario.

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population in the Brazilian Pantanal using camera-traps and capture-recapture
sampling in combination with GPS radio-telemetry. Biological Conservation
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depredation and compensation schemes in Sweden and Norway. Pages 323-339 *in*
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Kingdom.

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lupus signatus*) in the north of Portugal. Journal of Zoology 251:457-462.

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wildlife damage in North America. Wildlife Society Bulletin 25:312-319.

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carnivore conservation in Sweden. Conservation Biology 22:247-251.

CURRICULUM VITAE

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RELATED EXPERIENCE

Pantanal Conservation Center **–** Wildlife Conservation Society/Brazilian Foundation for Sustainable Development (Winter/2000 to Dec 2007): Coordinated a study on jaguar ecology and the problem of livestock depredation. Received and trained 14 students, several of which have since completed or are currently enrolled in graduate programs.

Predation Project - National Research Center for the Conservation of Natural Predators, Sorocaba, São Paulo, Brazil. (Summer/Fall 1998 and Fall/1999): Worked as the coordinator of the predation program developed at a national level in Brazil. Visited livestock property owners for assessments of damage caused by large carnivores to their properties.

Guard Llama Project - National Wildlife Research Center/Utah State University, Utah. (Fall 1994 to Fall/1997): Developed and conducted a study (MS Thesis) to evaluate physical and behavioral traits of llamas that are associated with aggressiveness these animals show toward coyotes and other sheep-threatening canids.

Predator Project **–** Utah State University, Department of Fisheries and Wildlife, Utah. (Winter/Spring 1994): Hired by the Department of Fisheries and Wildlife at Utah State University to elaborate a pamphlet on techniques in predator damage management.

Bear Research Project - Kodiak National Wildlife Refuge, Alaska. (Summer 1993): Assisted in the field recording data on brown bear *(Ursus arctos midendorfi)* social behavior and bear-human interactions in an area to have a Bear Viewing Program developed. Extensive hiking and camping required. Involved also by working with the public at the KNWR Visitor Center.

Coyote Research Project - Yellowstone National Park, Wyoming. (Fall/Winter 1992): Assisted in trapping, processing, and radio-telemetry activities. Included extensive hiking, animal tracking, and working for extended hours.

 Carnivore Research Project - Iguaçú National Park, Paraná, Brazil. (Fall 1990-Winter 1992): Assisted in field activities including trapping, sedation, biometrics and radio-telemetry monitoring of several species of Neotropical carnivores, including jaguars, ocelots, crab-eating foxes, tayras, and coaties as well as small mammal trapping and taxidermy. Also actively involved in an environmental education component of the project, giving lectures in schools and farms adjacent to the park, working with the local communities.

Wildlife Research & Environmental Education Society (SPVS) - Paraná, Brazil. (Fall/Winter 1991): Conducted an inventory of mammal species in an area to be flooded by the Jordão River Hydroelectric Dam. Involved intensive trapping and small mammal handling.

Biometrica Biological Evaluations and Environmental Management – Piracicaba, São Paulo, Brazil. (Fall 1990): Conducted a mammal survey as part of a Environmental Impact Study (EIS).

Pró-Fauna Inc. - São Paulo, Brazil. (Summer 1990): Assisted landowners with captive breeding programs of wildlife species. Prepared a proposal for a captive breeding program for pacas, (Agouti paca) submitted (and approved) to the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA).

GRANTS & RESEARCH SUPPORT

1999-2002	$ 41,247	National Scientific and Technological Development Council
2000-2007	$ 165,000	Wildlife Conservation Society
2001	$ 12,000	Conservation, Food, and Health Foundation
2007	$ 6,293	Fundaçào Boticário de Proteção à Natureza

INTERNSHIPS

Capybara Research Project - University of Paraná, Curitiba, PR., Brazil. (Winter 1990): Worked with a free-ranging capybara population on an island (Ilha do Mel, PR, Brazil), observing their social behavior. Involved two months of extensive hiking and camping.

Quinzinho de Barros Zoological Park - Sorocaba, S.P., Brazil. (Winter1989): Internship involving different aspects of zoo work, including animal restraint and handling, medication, and identification. Involved also in environmental education working with children.

Agroflorestal Monte Alegre Co. (CAFMA) - Agudos, S.P., Brazil. (Winter 1989): Monitored wildlife social interactions (deer, capybara, peccaries). Assisted in a pioneer project of elk hunting in a reforestation ranch.

Interdepartmental Center of Animal Husbandry and Wildlife Biology (CIZBAS) -
University of São Paulo, Brazil. (Summer 1988): Assisted in a research project on
capybaras and peccaries, recording observations of their social behavior in captivity. Oral
presentation given on animal social behavior to college-level students.

Agricultural & Animal Research Center of Pantanal (CPAP- EMBRAPA) - Corumbá,
MT, Brazil. (Winter 1988): Assisted in a field study on the nesting ecology of the
Paraguayan caiman (*Caiman crocodilus yacare*), including capture and marking of
animals, biometrics, nest locating and measuring, monitoring of incubation. Involved
extensive horseback riding and hiking in inundated areas.

LANGUAGES

Portuguese: Native language
English: Fluent
Spanish: Fluent

AWARDS

Received the Terry Millan Award from the Department of Fisheries and Wildlife at Utah
    State University (Summer 1996)
Appointed to the Honor Roll of the College of Natural Resources (Spring 1999)
Appointed to the Utah Chapter of Xi Sigma Pi National Forestry Honor Society for
    academic excellence (Fall 2004)

ADDITIONAL EXPERIENCE

-Graduate Student Representative for one year at Utah State University
-Coordinator of the Public Relations Committee for the Student Council for two years in
 college
-Immobilization of large mammals – Safe Capture International, Inc., Mt. Horeb, WI.
-Gun Safety and Bear Safety Programs - U.S. Fish & Wildlife Service/KNWR
-Avalanche Safety Program - Avalanche Forecast Center - SLC, UT
-Proficiency in computer programs plus GIS applications (ESRI ArcView), internet
 applications
-Experience with radio-telemetry equipment handling
-Experience in observation of animal behavior
-Experience with 4-wheel-drive vehicles and livestock trailers
-Experience with horseback riding

PRESENTATIONS

1988   Nesting Ecology of the Paraguayan Caiman – Agricultural & Animal Research
        Center of Pantanal (CPAP- EMBRAPA) - Corumbá, MT, Brazil.

1988   Animal Social Behavior – Interdepartmental Center of Animal Husbandry and Wildlife Biology (CIZBAS) - University of São Paulo, Brazil.

1991   Carnivore ecology in Iguaçu National Park, Foz do Iguaçu, Brazil.

1992   Studying the Carnivore community of Iguaçu National Park, Foz do Iguaçu, Brazil.

1996   Livestock Protection Dogs: a non-lethal alternative in predator damage management. Oral presentation given to graduate students as a guest speaker during a Wildlife Damage Management course Utah State University, Logan, UT.

1997   Livestock Protection Dogs: a non-lethal alternative in predator damage management. Oral presentation given to graduate students as a guest speaker during a Wildlife Damage Management course Utah State University, Logan, UT.

1998   Training in Wild Carnivore Damage Identification, Prevention, and Control. Organized a national course and conducted oral presentations on livestock predation management for 35 participants in Brazil

1999   Field Study Techniques. Organized a workshop and conducted oral presentations during a Brazilian conference on Neotropical Felid Conservation, Jundiaí, São Paulo.

1999   Wildlife Monitoring Through Radio-telemetry. Oral presentation to undergraduate students as a guest speaker at University of São Paulo, Piracicaba, São Paulo.

1999   Principles in Wildlife Damage Management. Oral presentation to undergraduate students as a guest speaker at University of São Paulo, Piracicaba, São Paulo.

2001   The ecology of jaguars in the Pantanal and the problem of livestock depredation. Oral presentation given to cattle ranchers during the I Workshop Jaguars, People, and Livestock: Living together with the world's third largest cat.

2001   Livestock depredations by jaguars and pumas in the Pantanal, Brazil – Seminar presented to graduate students in the Department of Fisheries and Wildlife at Utah State University.

2002   Livestock depredation – principles of predator identification. Oral presentation given as a guest speaker on a state course in wildlife management in Minas Gerais. Serra da Canastra National Park, Minas Gerais, Brazil.

2002   Wildlife Damage Prevention and Control. Oral presentation given as a guest speaker on a state course in wildlife management in Minas Gerais. Serra da Canastra National Park, Minas Gerais, Brazil.

2003   Aspects of livestock depredation by jaguars in the southern Pantanal, Brazil. Oral presentation given as a guest speaker during the Research and Conservation of Neotropical Carnivores Workshop, Atibaia, São Paulo, Brazil.

2003   Jaguar Project – 4 years studying jaguars in the southern Pantanal. Oral presentation as a guest speaker given to ecotourism guides at Refúgio Ecológico Caiman, Pantanal, Brazil.

2003   Livestock depredation by jaguars – what do we know. Oral presentation given as a guest speaker during the II Workshop Jaguars, People, and Livestock: Living together with the world's third largest cat. Instituto Parque do Pantanal, Campo Grande, Brazil.

2003   Factors influencing livestock depredation by jaguars in the southern Pantanal, Brazil. Pantanal Jaguar Research Meeting, Corumbá, Brazil.

2004   Jaguars in the Pantanal – a liability for livestock operations or a potential revenue for ranchers? Oral presentation given to graduate students of an economics course at USU. Utah State University, Logan, UT.

2004   Ecologia alimentar del jaguar en el sur de Pantanal, Brazil. Presentación en taller sobre jaguares, durante el VI Congresso de Manejo de Fauna en la Amazonia y Latino America, Iquitos, Peru.

2004   The foraging ecology of jaguars in the southern Pantanal – how do we follow jaguars and what do we know about their predation on cattle. Oral presentation given to traditional Pantanal ranchers as a guest speaker during the Annual Conference XII Dia do Homem Pantaneiro, Aquidauana, Mato Grosso do Sul.

2005   Foraging ecology of jaguars in the southern Pantanal – the problem of livestock depredation and the implications for their conservation. Society for Conservation Biology Annual Meeting, Brasilia, Brazil.

2005   Estimating the density of a jaguar population in the Brazilian Pantanal using camera traps in combination with GPS radio-telemetry. Society for Conservation Biology Annual Meeting, Brasilia, Brazil.

2005   Capturing and handling jaguars in the Pantanal, Brazil – what information can we get with GPS-based radio telemetry collars? – Oral presentation given as a guest speaker during a meeting of the Jaguar Conservation Team, Douglas, AZ.

2006   Jaguar ecology in the Pantanal – what have we accomplished and next steps – project update. Oral presentation given to Jaguar Conservation Program staff. Panama City, Panama.

2007   Jaguar ecology in the southern Pantanal. Oral presentation given as a guest speaker to Dr. Paul Erlich and Dr.Thomas Lovejoy and their guests during their visit to Fazenda Sete, Pantanal, Brazil.

2007   Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. Felid Biology and Conservation Conference, Oxford University, Oxford, UK.

2007   Jaguar Ecology in the Pantanal – data needed to develop a long term jaguar conservation plan. Dissertation presentation and defense, Utah State University, Logan, UT.

PUBLICATIONS

Cavalcanti, S. M. C. 1997. Evaluation of physical and behavioral traits of llamas *(Lama glama)* associated with aggressiveness toward sheep-threatening canids. M.S. Thesis, Utah State University, Logan. 58 pp.

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