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Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil

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Jaguars (*Panthera onca*) often prey on livestock, resulting in conflicts with humans. To date, kill rates and predation patterns by jaguars have not been well documented. We studied the foraging ecology of jaguars in an area with both livestock and native prey and documented kill rates, characteristics of prey killed, patterns of predation, 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 monitored 10 jaguars equipped with global positioning system (GPS) collars. We collected 11,787 GPS locations and identified 1,105 clusters of locations as sites of concentrated use (e.g., kill sites, bed sites, and dens). Of these, we found prey remains at 415 kill sites and documented 438 prey items. Kills were composed of 31.7% cattle (9.8% adults and 21.9% calves), 24.4% caiman (*Caiman crocodilus yacare*), 21.0% peccaries (mostly *Tayassu pecari*), 4.1% feral hogs (*Sus scrofa*), 3.9% marsh deer (*Blastocerus dichotomus*), 3.2% giant anteaters (*Myrmecophaga tridactyla*), 2.0% capybaras (*Hydrochoeris hydrochaeris*), 1.6% brocket deer (*Mazama americana* and *M. gouazoubira*), and other avian, mammalian, and reptilian species. Individual jaguars differed in the proportion of each species they killed and the proportion of native prey versus cattle. Although all 10 cats killed cattle, 5 killed a high proportion of cattle (>35% of kills), and 3 killed few cattle (<15%). Males (27%) and females (35%) killed cattle in similar proportions. In contrast, male jaguars killed a higher proportion of peccaries than did females, and female jaguars killed more caiman than did males. The mean kill rate for all jaguars was 4.3 days \pm 4.4 *SD* between known consecutive kills. The time interval to the next subsequent kill by jaguars increased with increasing prey size. Jaguars also increased the length of time at a carcass as prey size increased. Jaguar kill rates on peccaries steadily increased over the 4-year study. In contrast, kill rates on cattle decreased during the same period. Rainfall, and subsequent water levels on the Pantanal, was the main driver of seasonal kill rates by jaguars on cattle and caiman. As water levels increased, predation on caiman increased as caiman became more distributed throughout the landscape. Conversely, as water levels fell, caiman became less plentiful, and cattle were moved out into pastures thereby increasing their availability to more jaguars. DOI: 10.1644/09-MAMM-A-171.1.

Key words: Brazil, cattle, conflict, jaguar, kill rates, native prey, *Panthera onca*, predation

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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). The Pantanal, a large, seasonally inundated plain in South America, 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 has been 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 do kill cattle, which inevitably

leads to human–carnivore conflicts and the death of jaguars (Hoogesteijn et al. 2002; Polisar et al. 2003; Sáenz and Carrillo 2002). Ranchers believe they are unfairly burdened with high losses of cattle due to jaguar predation, although many members of the public believe ranchers exaggerate their losses.

Documentation of predation events by large carnivores is extremely difficult because of their nocturnal and secretive



behavior. The Western Hemisphere has 2 large felids, the cougar (*Puma concolor*) and the jaguar. Kill rates and predation patterns have been determined for cougars using conventional radiotelemetry to locate kill sites (Cooley et al. 2008; Murphy 1998; Ruth 2004a, 2004b) and more recently using global positioning system (GPS) collars (Anderson and Lindzey 2003). For jaguars, predation patterns are largely unknown due to the thick vegetation, absence of roads, and lack of snow cover for backtracking to kill sites when using conventional radiotelemetry techniques.

Much of what is known about jaguar foraging ecology is based on documentation of livestock killed (Azevedo and Murray 2007a; Palmeira et al. 2008), scat analyses (Garla et al. 2001; Novack et al. 2005), or a combination of scats and opportunistic observations of prey killed (Azevedo and Murray 2007b). To date, an intensive radiotracking study that systematically follows each cat and documents kill rates and predation patterns of individual jaguars has not been reported. Because predation on livestock threatens the persistence of many populations of large carnivores (Nowell and Jackson 1996; Sagør et al. 1997; Woodroffe 2001), documentation of jaguar predation on native prey and domestic livestock is needed for conservation plans.

With the advent of GPS collars prey remains of carnivore kills can be relocated a few weeks to several months later and predation rates estimated (Anderson and Lindzey 2003; Sand et al. 2005; Webb et al. 2008). We believed finding kill sites of jaguars would be similarly possible using GPS technology. Therefore, we investigated the predatory behavior of jaguars on a cattle ranch, specifically addressing the following questions: What prey species do jaguars kill, and how often do they kill? Do jaguars selectively prey on certain species? Do jaguar predation rates change seasonally? Do kill rates on livestock vary among individual jaguars? Does the size of prey killed influence the time jaguars spend at a carcass and when jaguars kill again? Do jaguars kill only at night? To our knowledge, this is the 1st study documenting kill rates and predation patterns of jaguars.

MATERIALS AND METHODS

Study site.—The study area was located in the southern Pantanal, a 140,000-km² floodplain located in west-central Brazil. Privately owned ranches comprise >95% of the Pantanal region. Because of the annual flooding cycle, cities and towns were located on the periphery of the Pantanal floodplain. The study site was a 460-km² privately owned ranch (Fazenda Sete) with ~6,000 beef cattle. Fazenda Sete has been a family-owned cattle ranch for several generations. Human density on the ranch was very low; approximately 25–30 people occupied the ranch headquarters complex. This low human density (0.05–0.07 people/km²) was typical of the region.

Elevation ranged from 89 to 120 m above sea level. The climate included a hot, wet season (October–March) with an average monthly precipitation of 145 mm and high temper-

atures reaching 42.5°C in October. The concentration of rains influenced the level of the rivers, which flooded large areas in the wet season. The dry season (April–September) had a monthly average precipitation of 48 mm with low temperatures reaching 18.5°C in June and July. Temperature and rainfall were measured using a weather station operated by the ranch.

The vegetation was a mosaic 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 included open fields interspersed with islands of secondary forest, and gallery forests bordering temporary and permanent rivers. Potential prey included cattle, white-lipped (*Tayassu pecari*) and collared (*Pecari tajacu*) peccaries, caiman (*Caiman crocodilus yacare*), marsh deer (*Blastocerus dichotomus*), feral hogs (*Sus scrofa*), brocket deer (*Mazama americana* and *M. gouazoubira*), giant anteaters (*Myrmecophaga tridactyla*), armadillos (*Euphractus sexcinctus* and *Dasybus novemcinctus*), capybaras (*Hydrochoeris hydrochaeris*), and various other mammals, birds, and reptiles. During the dry season cattle were dispersed widely throughout the study area. During the wet season cattle were herded to drier areas but remained widespread over large pastures. Cattle were unguarded and wandered free day and night.

Data collection.—We searched areas on the ranch for recent jaguar tracks from a vehicle or horseback in the morning hours. If recent sign was found we released trained hounds in an attempt to tree the cat (Hornocker 1970; Murphy 1998; Ruth 2004a, 2004b). We immobilized treed cats with a dosage of tiletamine hydrochloride and zolazepam hydrochloride (Telazol; Fort Dodge Animal Health, Fort Dodge, Iowa), or a combination of Telazol and ketamine hydrochloride (Fort Dodge Animal Health), administered via a dart fired from a CO₂ 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, and body mass and fitted them with a GPS collar (Televilt International, Lindesberg, 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). Age classes of jaguars were adult (>24 months old) and subadult (11–24 months); no kittens (<11 months) were radiocollared. Capture and handling protocols were approved by the Institutional Animal Care and Use Committees at the National Wildlife Research Center (QA-1194) and Utah State University (1202), and were consistent with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We obtained locations from the GPS collars with a high degree of accuracy and precision (ground tests with reference GPS collars showed error was <10 m—Anderson and Lindzey 2003; Bowman et al. 2000; Cavalcanti 2008). The collar had a downloadable data retrieval system and conventional store onboard system. In 2002 we programmed the collars to record fixes every 2 h between 1800 and 0600 h (7 fixes/night), targeting the nocturnal period when cats were most likely to be active or feeding on prey (Anderson and

Lindzey 2003; Beier et al. 1995). At the end of 2002, after documenting that the time for satellite acquisition was less than originally programmed and battery life was still 10–11 months, we programmed the collars to record fixes every 2 h throughout the 24-h period (12 locations/24-h period). This scheduling change for location acquisition did not influence the rate of finding kill sites; the frequency of identifying kill sites from clusters and finding kills was 37% for both relocation schedules.

We used a receiver (RX-900; Televilt International) to download the data remotely from the collars every 21–24 days. We used the very-high-frequency transmitter in the collars both as a beacon and as a radiolink for transfer of the coded GPS data to the remote receiver. 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 were downloaded directly into a computer and the battery replaced before redeployment.

We identified potential predation sites by locations provided by the GPS collars (Anderson and Lindzey 2003; Sand et al. 2005; Webb et al. 2008). 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 2 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 handheld GPS receiver, then visited and searched each site for possible prey remains. We systematically searched the area on foot to a diameter of 100 m (i.e., the size of the identified cluster), following the search procedures reported in Anderson and Lindzey (2003). If no prey remains were found within that circle, the cluster was not considered a kill site. This 100-m diameter was far in excess of the maximum error distance of the reference GPS collar locations (<10 m) and covered the area of the identified cluster. We recognize that smaller prey items might 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 several prey items <5 kg in size (e.g., armadillo and crab-eating raccoon [*Procyon cancrivorus*]). We classified kills into very small (<15 kg), small (15–30 kg), medium (>30–45 kg), large (>45–200 kg), and very large (>200 kg) prey.

The time elapsed between the GPS positioning of the jaguar and the field searches for carcasses on those same positions ranged from 1 to 21 days. We found that the frequencies of finding prey remains at kill sites were similar (34–38%) whether kill sites were investigated 1, 2, or 3 weeks after data download. If a radiocollared 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 (Murphy 1998; Ruth 2004a, 2004b). 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 because of consumption or deterioration of the carcass.

We estimated the relative abundance of mammalian prey across the study area using photographs from remote cameras positioned along remote roads and cattle and game trails (Kays and Slauson 2008; Kucera et al. 1995; Naves et al. 1996) during June–October 2003. The purpose of the remote camera survey was to estimate population size and density of jaguars on the site (Soisalo and Cavalcanti 2006), but the area covered by the cameras corresponded to the home ranges of the radiocollared jaguars during that time period. Each camera-trap station consisted of 2 cameras opposite each other 7–8 m apart with the infrared beam positioned at 45 cm in height. No lure or bait was used at any station, and cameras were checked every 1–2 days. A total of 16 camera stations was used to sample 3 similarly sized contiguous blocks of approximately 65 km² over a 20-day period (Soisalo and Cavalcanti 2006). Infrared-triggered cameras can acquire a representative sample of medium- and large-sized mammals because remote cameras are noninvasive and “capture” any animal walking past and triggering the infrared sensor beam between the cameras placed on the trail or road (Cutler and Swann 1999; Dajun et al. 2006; Jacobson et al. 1997; Kays and Slauson 2008). Cameras were positioned to cover the entire road or trail so that most mammalian prey species would have triggered the cameras. Thus cameras would have returned photographs of most predators and prey species with no inherent bias (Kays and Slauson 2008). Caiman do not travel roads and trails but follow water courses and were thereby unavailable for “capture.” We used an overall chi-square test (SPSS Inc., Chicago, Illinois) followed by partitioning of the chi-square value (Steel and Torrie 1980) to compare the frequency of prey in the photos to the frequency of prey in the jaguar kills (of the 7 prey species photographed) as a measure of jaguar prey selection among these 7 prey species over the same spatial area and temporal period. Because certain prey species might not travel the same trails as jaguars or other prey, or were too small to be photographed, we examined only the frequency of prey captured in the photographs versus the composition of the kills to reduce any inherent bias in the sample (i.e., we did not assume that the lack of a photograph of a particular prey species equated to low abundance).

Data analysis.—We analyzed the frequency of prey species found at kill sites using chi-square tests of independence (SPSS Inc.) to examine the influence of individual, sex, season, and year on the proportion of species killed. Kill rates and the time to the next kill were estimated based on the time interval elapsed (days) between known consecutive kills found for each cat (Murphy 1998; Ruth 2004a, 2004b). Only intervals in which all clusters were searched were used to estimate kill rates and the time to the next kill (i.e., if a cluster between 2 consecutive kill sites was not searched, that interval

was not used in the analyses). For seasonal comparisons we calculated the number of caiman, peccaries, and calves killed by jaguars based on the mean kill rate during the dry and wet seasons of each year; other prey species were killed too infrequently for seasonal comparisons. Time at a kill was the time interval (h) between the 1st and last location of the cat at the kill site.

We 1st used generalized linear models (Dobson 1990) using package “MASS” with procedure “glm” in program R (version 2.6.0—R Development Core Team 2007) to test for individual differences in kill rates, time to the next kill, and time at the kill site. We used generalized linear models for Poisson-distributed data because all of the response variables (kill rate, time to next kill, and time at the kill) used in our analyses were count variables skewed toward small values. Testing for a categorical individual effect (i.e., “ID”) was too demanding in terms of degrees of freedom (i.e., 9 individual jaguars), and we did not have sufficient sample size to test for such an effect on kill rates, time to the next kill, and time at the kill. To compensate for this shortfall we modeled individual jaguar identities (ID) as individual random effects. Individual random effects allowed us to account parsimoniously for repeated measures across individuals, in which some might be of higher quality than others, while economizing degrees of freedom. These degrees of freedom could then be allocated to other biological covariates of interest. We used generalized linear mixed models (Lindstrom and Bates 1990) using package “MASS” with procedure “nlme” in program R to account for individual random effect within a linear regression framework.

In addition to an individual random effect, we tested the effects of sex, seasons, and season-year (either treated as a factor or as a continuous covariate to save some degrees of freedom) on jaguar kill rates. The same covariate effects, plus the addition of prey size class, were tested on the time interval to the next kill and the time interval at the kill, with the exception of season. To estimate the potential for multicollinearity between covariates we calculated variance inflation factors (Fox and Monette 1992—package “car” with procedure “vif” in R) for each pair of covariates (e.g., season and season-year) prior to model selection (Neter et al. 1996). We found that season-year and season were collinear when we tested for their effects on time to the next kill and time at the kill. We retained season-year as a covariate of interest and excluded season, because only season-year had a significant effect on time to the next kill and time at the kill.

For model selection we used Akaike’s information criterion corrected for small sample size (AIC_c —Akaike 1973) defined as $AIC_c = -2 \times \log\text{-likelihood} + 2 \times d.f.$, where $d.f.$ is the number of degrees of freedom in the model. We also calculated Akaike model weights (w_i s) to compare models and determine which model(s) served as the best approximation(s) to the data: $w_i = \exp(-0.5 \times \Delta AIC_c) / \sum \exp(-0.5 \times \Delta AIC_c)$, where ΔAIC_c is the difference in AIC_c values between the best-performing model and the model of interest. If several models shared some weight in explaining the

variability within the data set (i.e., $w_i > 0$), or if ΔAIC_c was < 3 points, we discussed each model briefly and the effect of all of the covariates involved in these models. For each intercept and estimated slope parameter (β_i) that appeared in the best approximating model(s) we assessed the precision of each β_i based on the extent to which the 95% confidence interval (95% CI) for each β_i overlapped 0 (Graybill and Iyer 1994) to discuss the significance of each covariate effect on the response (either kill rate, time to the next kill, or time at a kill).

Jaguars are often considered nighttime predators. Therefore, we examined the time of day in which prey were killed by assuming the 1st location at the carcass represented the time of the kill. We then classified the time of the kill into 4 periods: morning (0400–0900 h), day (1000–1500 h), evening (1600–2100 h), and night (2200–0300 h). We used data from jaguars on the 24-h GPS location schedule only. Because the distribution of successful GPS location attempts throughout the day was not similar among the radiocollared cats ($\chi^2_3 = 56.44$, $P < 0.05$), we used the proportions of acquired locations to test for differences in the times of the day of the 1st known location of jaguars at kills of caiman, peccaries, cattle, and all species combined. We used chi-square goodness of fit (SPSS Inc.) to examine the influence of the 4 time periods on the frequency of kills made during those time periods; expected values were based on the frequency of locations acquired during the same time periods. Data collection occurred during the wet seasons (1 October–31 March) of 2001–2002, 2002–2003, and 2003–2004, and the dry seasons (1 April–30 September) of 2002, 2003, and 2004, although data from the dry season of 2004 were limited.

RESULTS

Between October 2001 and April 2004 we equipped and monitored 10 jaguars (5 adult males, 1 subadult male, and 4 adult females) with GPS collars. The subadult male was still with his mother and another subadult sibling; we therefore assigned those kills to his mother (adult female 5) and considered the kill rate to be that of a family group. Radiocollared jaguars were monitored for a total of 76 radiomonths. Continuous monitoring of individual cats varied from 1.5 to 24 months (Table 1); we were able to monitor 3–5 jaguars simultaneously during a single period.

From 11,787 GPS locations we identified 1,105 clusters of locations (i.e., potential kill sites, bed sites, and dens). Of these, we were not able to check 155 clusters (14.0%)—78 and 77 during the wet and dry seasons, respectively—because of inaccessible terrain. Eleven clusters (1.0%) were related to social interactions between radiocollared cats. Of the 939 remaining clusters, we found no evidence of any prey item at 524 clusters despite intensive search efforts. At these sites we encountered 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 considered kill sites and documented 438 prey items of > 19 prey species (Table 2). At 23 kill sites we

TABLE 1.—Length of monitoring period, number of global positioning system (GPS) locations acquired, number of kills found, kill rates, and number of kill intervals for 10 jaguars, November 2001–April 2004, in the southern Pantanal, Brazil.

Jaguar	Monitoring period (months)	No. GPS locations acquired	No. kills found	Kill rate (days/kill \pm SD)	No. kill intervals
Adult male 1	10	1,024	47	5.4 \pm 4.7	29
Adult male 2	5	745	36	3.1 \pm 2.6	28
Adult male 3	3	453	18	2.8 \pm 2.1	13
Adult male 4	11	1,543	42	5.8 \pm 5.0	34
Adult male 5	6	721	36	4.4 \pm 5.7	35
Adult female 1	15	2,025	80	4.5 \pm 4.8	73
Adult female 2	24	3,932	124	4.1 \pm 3.9	98
Adult female 3	4	512	22	4.1 \pm 4.2	16
Adult female 4	1.5	116	5	—	—
Adult female 5 ^a	3	716	28	3.6 \pm 3.6	24

^a Adult female 5 was accompanied by 2 subadult offspring.

found 2 carcasses of prey species killed by jaguars. Although both carcasses were fed upon, it was difficult to determine if both species had been actively hunted or which species had been killed 1st. At 15 sites we found remains where 1 of the species killed (e.g., feral hog, peccary, armadillo, raccoon, or caiman) could have been scavenging a jaguar-killed carcass and was killed when the jaguar returned. At the other sites we found remains of species not known to eat carrion. When we examined how long a jaguar stayed at a kill site and how soon

they would kill again, we used the body size of the 2 prey species combined for these sites.

Composition of prey species killed.—Of the 438 carcasses of prey found, 299 (68%) were native prey species and 139 (32%) were cattle. In addition to the expected ungulate species, we documented jaguars killing other predators, including maned wolves (*Chrysocyon brachyurus*), crab-eating foxes (*Cerdocyon thous*), coati (*Nasua nasua*), and crab-eating raccoons. We found a difference among individual jaguars in the proportion of native prey (all native species combined) versus cattle that were killed ($\chi^2_9 = 57.07$, $P < 0.001$). Some jaguars had >50% of their kills consisting of cattle, but others did not exceed 5% (Table 2). Although some cats appeared to kill only a few prey species (Table 2), species frequency in their kills did not differ among the cats ($\chi^2_8 = 10.44$, $P = 0.23$). However, the proportion of each prey species killed varied among the individual jaguars ($\chi^2_9 = 318.23$, $P < 0.001$), indicating they likely selected different prey species, possibly due to varying prey availability within their home ranges, prey vulnerability, or individual preference.

When we examined only the proportion of large prey (≥ 30 kg) killed by individual jaguars for which we had at least 15 kills ($n = 9$ cats), we found the proportion of large prey killed varied among individual cats when preying on livestock calves ($\chi^2_8 = 58.45$, $P < 0.001$), caiman ($\chi^2_8 = 46.05$, $P < 0.001$), and peccaries ($\chi^2_8 = 48.34$, $P < 0.001$). In contrast, we found no difference in the proportion of adult livestock

TABLE 2.—Distribution of 438 prey (number of kills [n] with percentage of kills in parentheses) found at 415 kill sites for 10 radiocollared jaguars, November 2001–April 2004, in the southern Pantanal, Brazil.

Prey	Adult female 1 ($n = 80$)	Adult female 2 ($n = 124$)	Adult female 3 ($n = 22$)	Adult female 4 ($n = 5$)	Adult female 5 ($n = 28$)	Adult male 1 ($n = 47$)	Adult male 2 ($n = 36$)	Adult male 3 ($n = 18$)	Adult male 4 ($n = 42$)	Adult male 5 ($n = 36$)	Total ($n = 438$)	% of kills
Cattle												
Calf	30 (37.5)	19 (15.3)	0	3 (60.0)	7 (25.0)	24 (51.1)	3 (8.3)	2 (11.1)	7 (16.7)	1 (2.8)	96	21.9
Adult	9 (11.3)	16 (12.9)	1 (4.5)	1 (20.0)	4 (14.3)	2 (4.3)	2 (5.6)	2 (11.1)	6 (14.3)	0	43	9.8
Native prey												
Caiman	10 (12.5)	52 (41.9)	9 (40.9)	1 (20.0)	5 (17.9)	4 (8.5)	8 (22.2)	7 (38.9)	3 (7.1)	8 (22.2)	107	24.4
Peccary ^a	7 (8.8)	23 (18.5)	5 (22.7)	0	2 (7.1)	4 (8.5)	11 (30.6)	6 (33.3)	14 (33.3)	20 (55.6)	92	21.0
Feral hog	2 (2.5)	4 (3.2)	1 (4.5)	0	0	6 (12.8)	1 (2.8)	1 (5.6)	2 (4.8)	1 (2.8)	18	4.1
Marsh deer	4 (5.0)	2 (1.6)	1 (4.5)	0	3 (10.7)	4 (8.5)	1 (2.8)	0	2 (4.8)	0	17	3.9
Giant anteater	7 (8.8)	2 (1.6)	0	0	0	1 (2.1)	3 (8.3)	0	0	1 (2.8)	14	3.2
Capybara	4 (5.0)	1 (0.8)	0	0	3 (10.7)	0	0	0	1 (2.4)	0	9	2.0
Lesser anteater	1 (1.3)	1 (0.8)	0	0	0	0	3 (8.3)	0	2 (4.8)	0	7	1.6
Brocket deer ^b	1 (1.3)	0	0	0	1 (3.6)	0	1 (2.8)	0	2 (4.8)	2 (5.6)	7	1.6
Armadillo ^c	2 (2.5)	0	3 (13.6)	0	0	0	0	0	1 (2.4)	0	6	1.4
Coati	0	0	1 (4.5)	0	2 (7.1)	1 (2.1)	1 (2.8)	0	0	0	5	1.1
Birds ^d	0	1 (0.8)	0	0	0	1 (2.1)	1 (2.8)	0	0	0	3	0.7
Crab-eating fox	0	1 (0.8)	0	0	0	0	0	0	1 (2.4)	1 (2.8)	3	0.7
Maned wolf	2 (2.5)	1 (0.8)	0	0	0	0	0	0	0	0	3	0.7
Raccoon	0	0	1 (4.5)	0	0	0	1 (2.8)	0	0	1 (2.8)	3	0.7
Tapir	0	0	0	0	0	0	0	0	1 (2.4)	1 (2.8)	2	0.5
Anaconda	0	0	0	0	1 (3.6)	0	0	0	0	0	1	0.2
Caiman lizard	0	1 (0.8)	0	0	0	0	0	0	0	0	1	0.2
Land turtle	1 (1.3)	0	0	0	0	0	0	0	0	0	1	0.2

^a Although collared peccaries (*Pecari tajacu*) were present, the majority of peccaries killed by jaguars were white-lipped peccaries (*Tayassu pecari*).

^b Includes both species: *Mazama americana* and *Mazama gouazoubira*.

^c Includes both species: *Euphractus sexcinctus* and *Dasyurus novemcinctus*.

^d Includes great egret (*Ardea alba*) and jabiru stork (*Jabiru mycteria*).

($\chi^2_8 = 10.22$, $P = 0.24$), or deer (marsh deer and brocket deer combined; $\chi^2_8 = 11.04$, $P = 0.19$) killed by individual cats. Among radiocollared 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 other jaguars (Table 2).

When comparing the sexes, the distribution of prey species killed by male and female jaguars varied. No difference was found in the proportion of kills composed of cattle between male (27%) and female (35%) jaguars ($\chi^2_1 = 2.66$, $P = 0.10$). Among just cattle, calves made up 75% and 66% of the kills made by males and females, respectively ($\chi^2_1 = 1.47$, $P = 0.22$). Correspondingly, adult cows made up 25% and 34% of the cattle killed by male and female jaguars, respectively. In contrast, we noted a difference in the proportions of caiman and peccaries killed by male and female jaguars. Proportionately, male jaguars killed about one-half as many caiman as did females (males: 17%, females: 30%; $\chi^2_1 = 9.64$, $P = 0.002$). However, caiman comprised 42% of kills made by female 2 alone (Table 2). In contrast, male jaguars killed peccaries at a higher proportion than did females (males: 31%, females: 14%; $\chi^2_1 = 17.24$, $P = 0.0001$). No difference ($\chi^2_1 = 0.87$, $P = 0.35$) was observed in the proportion of deer (marsh deer and brocket deer combined) killed by male (7%) versus female (5%) jaguars.

Although jaguars differed in the distribution of prey species killed, caiman, peccaries, and cattle (calves and adult cows) comprised the majority (>75%) of all kills. To examine the influence of climatic variation on prey killed we examined the distribution of jaguar kills for these 3 major prey species (caiman, peccaries, and cattle) during 2002 (<550 mm of rainfall) and 2003 (>1,700 mm of rainfall), which were the driest and wettest of 8 years (1997–2004) on the study site. The proportion of cattle (calves and adults combined) among jaguar kills decreased from 50% in 2002 to 19% in 2003 ($\chi^2_1 = 30.82$, $P < 0.001$). In contrast, the proportion of peccaries in jaguar kills increased from 10% in 2002 to 32% in 2003 ($\chi^2_1 = 28.59$, $P < 0.001$). Caiman comprised relatively similar proportions of jaguar kills in 2002 (19%) and 2003 (27%; $\chi^2_1 = 3.05$, $P = 0.08$).

Carcasses of cattle being killed by jaguars were classified as young (calves 1 day to 12 months of age) and adult (heifers and adult cows ≥ 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 cows and bull carcasses found, 6 might not have been killed by jaguars because evidence suggested that they may have been scavenged (i.e., the site did not indicate a predatory attack and the carcass lacked wounds and hemorrhaging—Bowns 1985). We included these 6 carcasses in the prey composition (i.e., the jaguar did feed on them), but excluded them from the estimates of kill rates (i.e., the jaguar might not have killed them).

Relative prey selection.—We obtained 1,765 photographs from June to October 2003 of 7 prey species—cattle, deer, peccaries, giant anteaters, tapirs (*Tapirus terrestris*), feral

TABLE 3.—Relative frequency of 7 mammalian prey species in 1,765 photographs from remote camera surveys compared to 67 jaguar kills, June–October 2003, in the southern Pantanal, Brazil. *df.* = 1 in each analysis.

Species	% frequency			
	Photographs	Kills	χ^2	<i>P</i>
Cattle	79.3	38.8	13.59	< 0.001
Deer	8.4	14.9	3.20	0.074
Peccary	6.6	35.8	71.41	< 0.001
Giant anteater	3.1	4.5	0.42	0.516
Tapir	2.0	1.5	0.09	0.759
Feral hog	0.3	4.5	22.42	< 0.001
Brazilian agouti	0.3	0	0.19	0.666

hogs, Brazilian agoutis (*Dasyprocta leporina*)—during the remote camera survey (M. K. Soisalo, pers. comm.). During the same interval we found 67 kill sites of the radiocollared jaguars. Overall there was a difference in the number of prey species found between the photos and kills ($\chi^2_6 = 111.32$, $P < 0.001$). When we partitioned the chi-square value among the 7 prey species, for all jaguars combined, 3 prey species (deer, peccaries, and feral hogs) were killed at a higher frequency than photographed and could be considered prey that were selected by jaguars (Table 3). Three prey species (giant anteaters, tapirs, and agoutis) were neutral in preference among jaguar kills, and cattle were killed less frequently by jaguars than the frequency of cattle in the photographs.

Kill rates.—The number of kills by individual jaguars during the interval they were monitored ranged from 5 to 124 kills (Table 1). Of the 415 kill sites found, we were able to determine the length of time between 2 known consecutive kills for 350 kill intervals; the remaining intervals between consecutive kills contained clusters that were not searched. Using these 350 known kill intervals, we estimated that the mean predation rate on all prey species for all jaguars was 4.3 days \pm 4.4 *SD* between kills. The family group (adult female 5) had a kill rate shorter than the overall average, but it was not the shortest kill rate.

The model selection analyses showed that the best-performing model retained a fixed effect of season and an individual random effect of ID on jaguar kill rates (Table 4). The model explained 42.6% of the overall AIC_c weight and outperformed the 2 next best models by only 0.85 AIC_c points (i.e., the model retaining an additive effect of sex and season, and an individual random effect) and 0.904 AIC_c points (i.e., the model retaining an interaction between sex and season, and an individual random effect). Although the 3 top models shared some weight in explaining the data, the effect of sex in the 2nd and 3rd best-performing models was not significant. The mean kill rate for male jaguars was 4.5 \pm 4.6 days between kills ($n = 139$ intervals), and female jaguars had a predation rate of 4.2 \pm 4.2 days between kills ($n = 211$ intervals). In a model testing for an additive effect of sex and season on kill rates, we found: $\beta_{\text{SEX}} = 3.476$ (95% *CI* = -0.188 – 0.983 ; $t = 0.678$, $P = 0.519$). In a model testing for

TABLE 4.—Selection results for models testing for the effects of sex (SEX), season (SEA), season-year (continuously SYc), and identity (ID) on jaguar kill rates. All models except the model testing for an effect of ID alone (generalized linear model without random effect) are generalized linear mixed models (see text for details) controlling for individual heterogeneity via an individual random effect (re(ID)).

Model covariates	AIC _c	df.	Δ_i	$\exp(-0.5 \times \Delta_i)$	w_i
SEA + re(ID)	2,016.516	2	0.000	1.000	0.426
SEX + SEA + re(ID)	2,017.371	3	0.855	0.652	0.278
SEX \times SEA + re(ID)	2,017.420	4	0.904	0.636	0.271
SYc + re(ID)	2,023.788	1	7.272	0.026	0.011
SEX + SYc + re(ID)	2,024.755	3	8.239	0.016	0.007
NO MODEL + re(ID)	2,026.777	1	10.261	0.006	0.003
SEX \times SYc + re(ID)	2,027.405	4	10.889	0.004	0.002
SEX + re(ID)	2,027.787	2	11.271	0.004	0.002
ID	2,033.000	9	16.484	0.000	0.000

an interaction between sex and season, we found: $\beta_{\text{SEX}} \times \beta_{\text{SEA}} = 0.381$ (95% CI = $-0.631-1.392$; $t = 0.376$, $P = 0.707$).

In the best-performing model we found that both the intercept (i.e., a baseline effect of the dry season on kill rates) and $\text{SEASON}_{\text{wet}}$ (an effect of the wet season on kill rates in comparison to the baseline effects of the dry season) had a significant effect on jaguar kill rates: $\beta_{\text{intercept}} = 3.678$ (95% CI = $3.351-4.005$; $t = 11.247$, $P < 0.001$) and $\beta_{\text{SEAwet}} = 1.676$ (95% CI = $1.194-2.1575$; $t = 3.479$, $P < 0.001$). These results suggest that both the dry and wet seasons have a significant effect on jaguar kill rates but that the effect of the dry season was >3 times higher than the effect of the wet season on kill rates. Mean jaguar kill rates were 3.7 ± 2.8 ($n = 108$ intervals), 3.7 ± 3.2 ($n = 101$ intervals), and 3.5 ± 2.3 days between kills ($n = 6$ intervals) for the dry seasons of 2002, 2003, and 2004, respectively. Mean jaguar kill rates were 8.8 ± 7.2 ($n = 32$ intervals), 3.2 ± 2.6 ($n = 38$ intervals), and 4.9 ± 5.7 days between kills ($n = 65$ intervals) for the wet seasons of 2001–2002, 2002–2003, and 2003–2004, respectively. We also detected “unobserved” individual variability in kill rates (i.e., variability that was not explained by observed covariates, such as seasons). The individual random effect centered at 0 reached a standard deviation of 0.373, with associated residuals = 4.285. This result suggests that there are important unobserved individual differences in the rate at which jaguars kill. Thus, additional effort should be placed into collecting other biological information to explain more of this variability (e.g., prey availability within each home range).

With regard to the frequency with which various prey were killed, jaguars killed on average 1 livestock 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 on average every 14.8 ± 14.8 days. When we examined the mean number of cattle, caiman, and peccaries killed throughout the study, a seasonal pattern of predation by jaguars emerged. The mean number of cattle (adult and calves) killed by jaguars each month peaked in the dry seasons, although a difference among

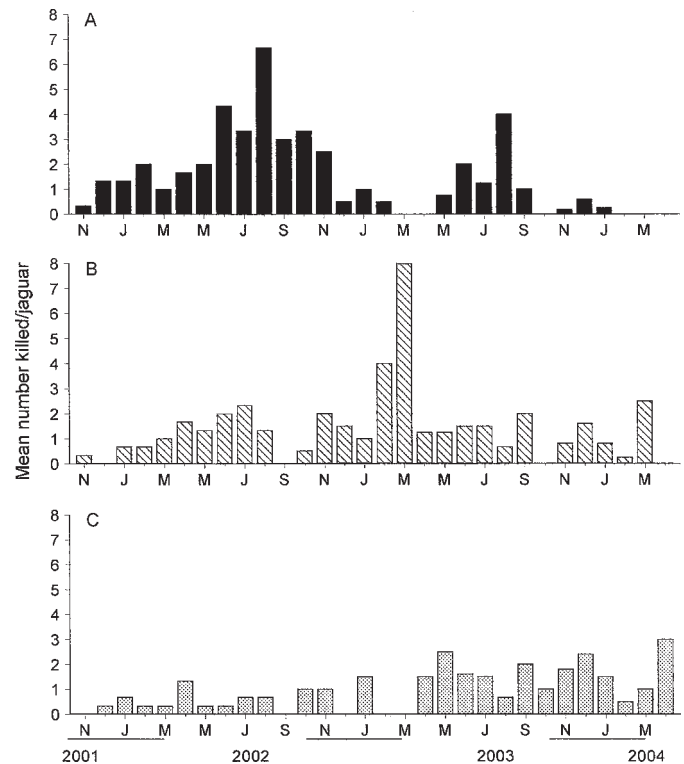


FIG. 1.—Distribution of the mean number of A) cattle, B) caiman, and C) peccaries killed monthly per radiocollared jaguar, November 2001–April 2004, in the southern Pantanal, Brazil. Lines under the months indicate the wet season.

years was apparent (Fig. 1). 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 (Fig. 2).

Although the frequency of predation on caiman appeared to be distributed evenly throughout 2002, we found during 2003 and 2004 that jaguar predation on caiman apparently peaked during the wet season (Fig. 1). Coincident with this, jaguar predation on cattle decreased when predation on caiman increased. Although the frequency of jaguar predation on peccary appeared to be distributed evenly 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 (Fig. 1).

Because caiman, peccaries, and cattle comprised 77% of all jaguar kills found, we analyzed the seasonal kill rates of jaguars for these 3 main prey species from 2001 to 2004; other prey species were killed too infrequently to allow for seasonal comparisons. Kill rates of cattle generally declined from highs of 16.8 and 11.6 days between kills in the wet season of 2001–2002 and dry season of 2002, respectively, to 19.2 and 20.3 days between kills in the wet season of 2002–2003 and dry season of 2003, respectively, to a low of 35.0 days between kills in the wet season of 2003–2004. A mean kill rate of 11.6 days between kills equates to 2.6 cattle killed in a 30-

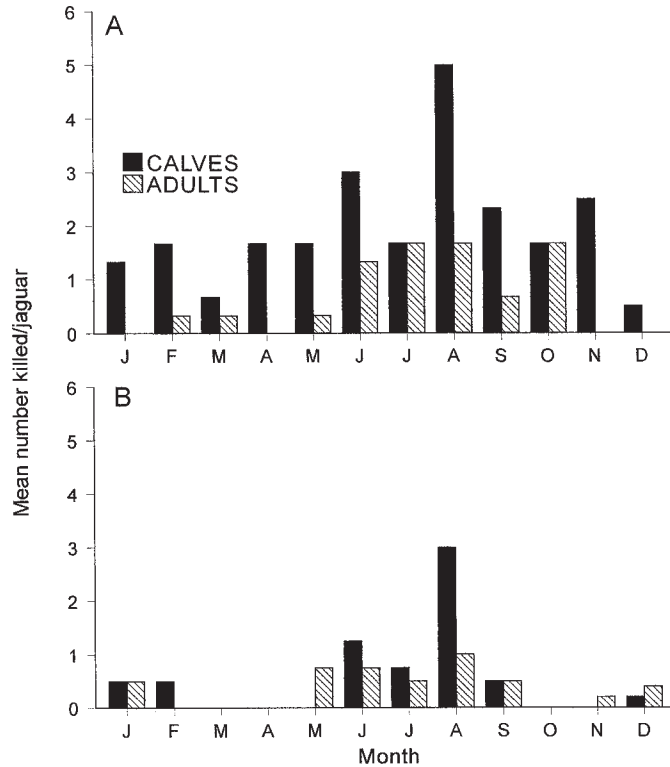


FIG. 2.—Mean number of calves and adult cattle killed per radiocollared jaguar during each month in A) 2002, and B) 2003, in the southern Pantanal, Brazil.

day period, and a mean of 35.0 days is equivalent to 0.9 cattle killed in a 30-day period.

Jaguar kill rates on caiman changed from 25.8 days between kills in the wet season of 2001–2002 to 11.6, 8.6, 14.6, and 16.7 days between kills in the dry season of 2002, wet season

of 2002–2003, dry season of 2003, and the wet season of 2003–2004, respectively. Jaguar kill rates on peccaries increased from a rate of 33.0 and 31.3 days between kills in the wet season of 2001–2002 and dry season of 2002, respectively, to 23.6 days in the wet season of 2002–2003, steadily increasing to 12.7, 11.0, and 8.5 days between kills in the dry season of 2003, wet season of 2003–2004, and the dry season of 2004, respectively.

Time to the next kill.—We found that the amount of time elapsed from killing one prey item to killing the next prey item increased with increasing body size of the prey (Fig. 3). After killing and consuming a very small or small prey item, a jaguar generally killed again in a shorter time interval as compared to when it killed large and very large prey. Among the set of models testing for the effects of prey size, season, season-year, and sex on the time interval to the next kill, the best-performing model retained an additive effect of prey size, sex, and season and an individual random effect of jaguar ID on time to the next kill (Table 5). The model explained 35.7% of the overall AIC_c weight and outperformed the following best models by only 0.619 AIC_c points. In addition, 3 other models shared some weight in explaining the variability in time to the next kill (Table 5; w_i (SY +re(ID)) = 0.262, w_i (PS + SY +re(ID)) = 0.251, and w_i (SEX + SY +re(ID)) = 0.131). However, these models were nested, thus we discussed only the model that retained all of the covariates of interest and that contained all of the useful statistical information, and this happens to be the best-performing model (Table 5). The best-performing model showed that most covariate effects on the time interval to the next kill were not significant. Females (i.e., $\beta_{\text{SEXfemale}}$) and males (i.e., $\beta_{\text{intercept}}$, which stands for a baseline effect of males on time to the next kill) did not exhibit significant differences in the time interval to the next kill:

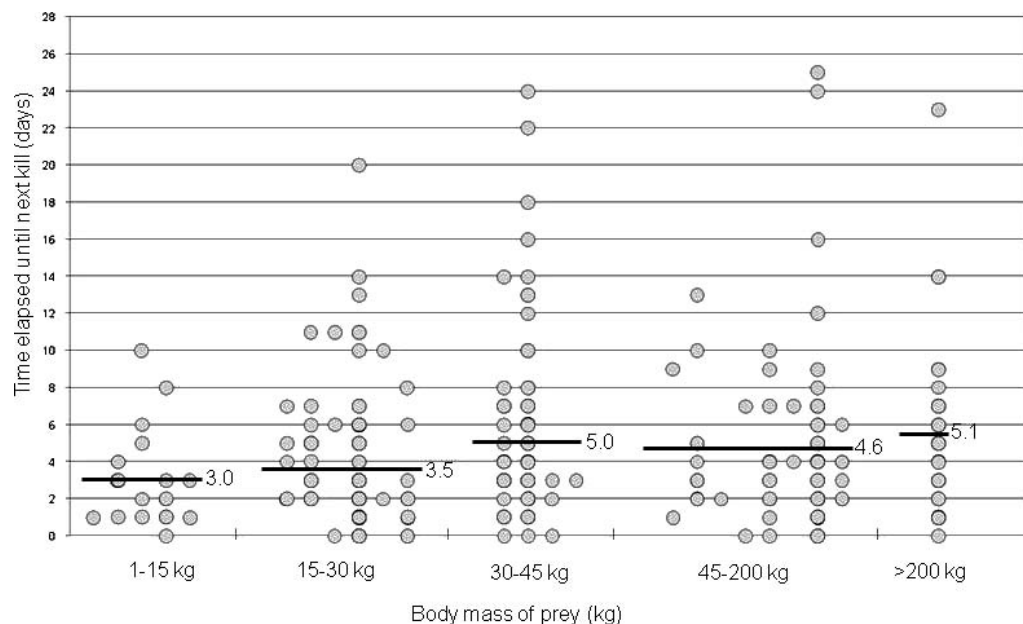


FIG. 3.—Time elapsed (days) until the next kill by a jaguar in relation to the body size of the prey, in the southern Pantanal, Brazil, 2001–2004. Circles show time intervals between known consecutive kills for different body sizes of prey; horizontal bars and numbers indicate mean values.

TABLE 5.—Selection results for models testing for the effects of sex (SEX), season-year (treated either as a factor SY or continuously SYc), prey species (PS), and identity (ID) on the time to the next kill. All models except the model testing for an effect of ID alone (generalized linear model without random effect) are generalized linear mixed models (see text for details) controlling for individual heterogeneity via an individual random effect (re(ID)).

Model covariates	AIC _c	df.	Δ _i	exp(-0.5 × Δ _i)	w _i
PS + SEX + SY+ re(ID)	1,812.623	11	0.000	1.000	0.357
SY+ re(ID)	1,813.242	6	0.619	0.734	0.262
PS + SY+ re(ID)	1,813.327	11	0.704	0.703	0.251
SEX + SY+ re(ID)	1,814.633	7	2.010	0.366	0.131
PS + SYc + re(ID)	1,835.543	6	22.920	0.000	0.000
SYc + re(ID)	1,837.030	1	24.407	0.000	0.000
SEX + SYc + re(ID)	1,838.336	3	25.713	0.000	0.000
PS + re(ID)	1,850.838	5	38.215	0.000	0.000
PS + SEX + re(ID)	1,851.819	6	39.196	0.000	0.000
NO MODEL + re(ID)	1,851.945	1	39.322	0.000	0.000
SEX + re(ID)	1,852.881	2	40.258	0.000	0.000
ID	1,862.700	9	50.077	0.000	0.000

$\beta_{\text{intercept}} = 3.5735$ (95% CI = 2.401–4.746; $t = 3.049$, $P = 0.002$) and $\beta_{\text{SEXfemale}} = 0.1253$ (95% CI = -0.428–0.679; $t = 0.226$, $P = 0.827$). Only a baseline effect of the first class of prey species (1–15 kg) had a significant effect on the time interval to the next kill; all other classes of prey size did not significantly influence the time to the next kill. The wet season of 2001–2002 was the only other covariate level that significantly influenced the time to the next kill: $\beta_{\text{SYwet2001-2002}} = 5.1853$ (95% CI = 4.337–6.034; $t = 6.112$, $P < 0.001$). We found that variability in the time to the next kill across individuals was rather small ($SD = 0.0029$, residuals = 4.1098).

Time at a kill site.—The length of time a jaguar stayed at a kill site increased with increasing body mass of prey (Fig. 4). The larger the prey, the longer a jaguar generally stayed at the carcass, suggesting that they used a large portion of the carcass. Model fit was dominated by a single top model (Table 6), a model that retained an additive fixed effect of prey size, sex, and season-year and an individual random effect on the time interval at a kill site. We found no significant differences between males and females: $\beta_{\text{intercept}} = 13.452$ (95% CI = 9.593–17.312; $t = 3.485$, $P = 0.0005$) and $\beta_{\text{SEXfemale}} = -3.765$ (95% CI = -5.878–-1.652; $t = -1.7821$, $P = 0.1179$). The model did reveal a significant effect of prey size for prey > 200 kg ($\beta_{>200\text{kg}} = 13.355$, 95% CI = 8.797–17.912; $t = 2.930$, $P = 0.0036$), and of dry seasons in 2003 ($\beta_{\text{SYdry2003}} = 6.826$, 95% CI = 4.266–9.386; $t = 2.667$, $P = 0.008$) and 2004 ($\beta_{\text{SYdry2004}} = 22.857$, 95% CI = 14.699–31.015; $t = 2.802$, $P = 0.005$) on the time at the kill site. We also found that variability in the time at a kill among individual jaguars was rather small ($SD = 0.0016$, residuals = 18.873). Although we could not document the amount of each carcass consumed by jaguars, we assumed that the successive locations of a jaguar at a carcass site were related to feeding, guarding, and perhaps prey caching.

Timing of predation events.—When we examined the frequencies of the times in which jaguars made a kill in relation to the frequency of GPS locations obtained, the timing of jaguar kills was not significantly different among the 4 time periods. Of 48 cattle that were killed, 17%, 31%, 33%, and 19% of kills occurred during the day, evening, night, and morning, respectively ($\chi^2_3 = 2.66$, $P = 0.45$). Among 74 peccaries killed, 24%, 20%, 30%, and 26% of kills were during the day, evening, night, and morning, respectively (χ^2_3

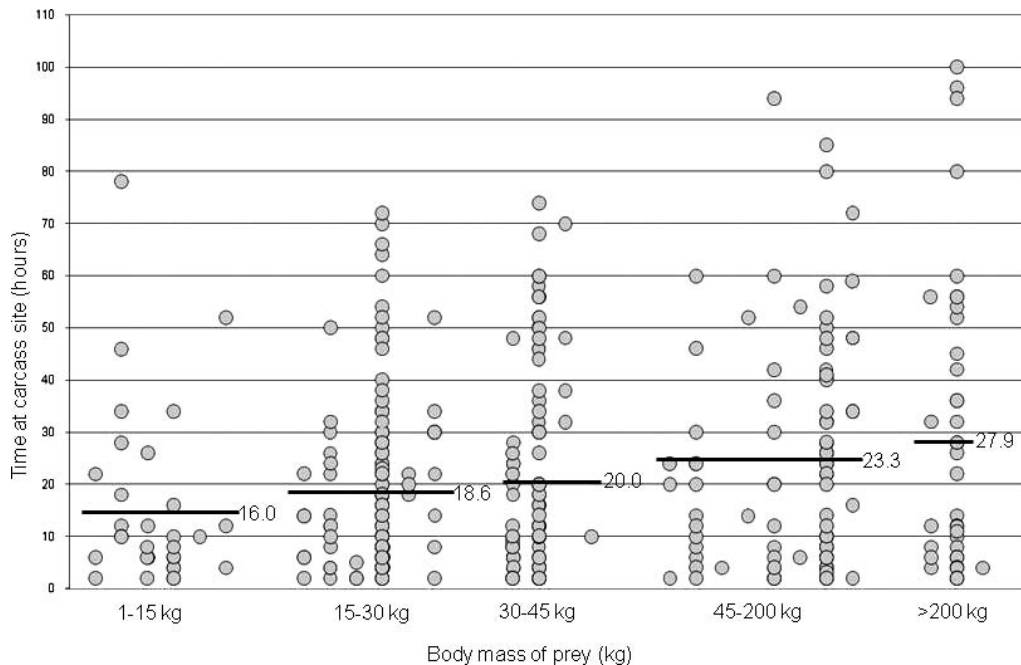


FIG. 4.—Length of time (h) a jaguar stayed at a kill site in relation to the body size of prey, in the southern Pantanal, Brazil, 2001–2004. Circles show length of time jaguars stayed at a kill site of different body sizes of prey; horizontal bars and numbers indicate mean values.

TABLE 6.—Selection results for models testing for the effects of sex (SEX), season-year (treated either as a factor SY or continuously SYc), prey species (PS), and identity (ID) on the time at a kill site. All models except the model testing for an effect of ID alone (generalized linear model without random effect) are generalized linear mixed models (see text for details) controlling for individual heterogeneity via an individual random effect (re(ID)).

Model covariates	AIC _c	df.	Δ_i	$\exp(-0.5 \times \Delta_i)$	w_i
PS + SEX + SY + re(ID)	3,699.166	11	0.000	1.000	0.959
PS + SY + re(ID)	3,705.469	11	6.303	0.043	0.041
SEX + SY + re(ID)	3,717.561	7	18.395	0.000	0.000
SY + re(ID)	3,721.408	6	22.242	0.000	0.000
PS + SYc + re(ID)	3,721.414	6	22.248	0.000	0.000
PS + SEX + re(ID)	3,724.423	6	25.257	0.000	0.000
PS + re(ID)	3,726.730	5	27.564	0.000	0.000
SEX + SYc + re(ID)	3,736.266	3	37.100	0.000	0.000
SYc + re(ID)	3,736.633	1	37.467	0.000	0.000
SEX + re(ID)	3,743.283	2	44.117	0.000	0.000
NO MODEL + re(ID)	3,745.516	1	46.350	0.000	0.000
ID	3,749.400	9	50.234	0.000	0.000

= 2.35, $P = 0.50$). Of 69 caiman killed by jaguars, 26%, 29%, 25%, and 20% of kills occurred during the day, evening, night, and morning, respectively ($\chi^2_3 = 1.44$, $P = 0.69$). For all species combined ($n = 250$ kills), jaguars made 24%, 28%, 27%, and 21% of these kills during the day, evening, night, and morning, respectively ($\chi^2_3 = 2.84$, $P = 0.42$).

DISCUSSION

Most studies of jaguar diets to date are based on the analysis of scats or carcasses found opportunistically. In contrast, we monitored jaguar movements every 2 h and essentially followed them to document what they were killing. Although this sampling was not perfect because we may have missed some small prey that were consumed in <2 h, this method provided a less-biased representation of kill rates, particularly of large prey. Therefore, the kill rates presented could be considered a minimum estimate, although we did locate remains of several small prey (e.g., birds, caiman lizard, coati, small anaconda, and armadillo); they constituted a low proportion of biomass killed and consumed. We also recognize that our level of inference may be most applicable to prey > 45 kg in size because carcasses of small prey could be less detectable due to their ease of transport following the kill, scavengers removing the kill, carcass persistence (decomposition), and ease of dismemberment of the carcass.

The importance of different prey varies among jaguar populations (Oliveira 2002). Although we documented prey remains, we found similarities with studies examining jaguar feeding patterns using scats. In Venezuela jaguars fed on capybaras and collared peccaries, but fed on caiman less than expected (Polisar et al. 2003). White-lipped peccaries were important to jaguars in southwestern Brazil (Crawshaw et al. 2004). In Mexico Núñez et al. (2000) reported that white-tailed deer (*Odocoileus virginianus*) comprised the majority of jaguar diets, but diets in Guatemala were dominated by

armadillos and coatis (Novack et al. 2005). In the northern Pantanal Dalponte (2002) found that capybaras comprised the bulk of jaguar diets. Dalponte (2002) and Oliveira (2002) reported that local variation in prey consumption by individual jaguars likely reflects local patterns of prey occurrence and distribution. We found that individual jaguars killed prey differentially, indicating either individual preferences among jaguars or variation in availability or vulnerability of prey species in each jaguar home range, or a combination of these. Overall, jaguars appeared to kill peccaries, deer, and feral hogs preferentially when compared to their frequency in photographs from remote cameras; killed cattle less than expected; and killed giant anteaters, tapirs, and agoutis in proportion to their abundances.

Although jaguars are extremely powerful, they kill a variety of prey ranging from <5 to >100 kg in size. The length of time between consecutive kills and the time a jaguar remained at a kill site were influenced largely by prey size. As prey size increased jaguars remained longer at those kills and delayed killing again for a longer time interval. We also found that jaguars did not select specific time periods to kill their prey, suggesting kills were made throughout the day and night. This result was not surprising given the mosaic of vegetation providing ambush cover for jaguars. This kill distribution also could reflect the activity patterns of the prey and behavioral flexibility by jaguars to hunt during the day, not just at night.

The proportion of peccaries killed by male and female jaguars differed, perhaps due to the movement patterns of peccaries. Peccary home ranges can be extensive, especially during flooding (Fragoso 1998), and may facilitate predation by more-mobile male jaguars that also travel across larger home ranges (Cavalcanti and Gese 2009). Alternatively, male jaguars with their larger body size might be more adept at killing peccaries without injury. The increase in jaguar kill rates on peccaries suggested an increasing reliability on peccaries as prey, either due to availability or selection. The increased use of peccaries could have important implications not only on the dynamics of the predator-prey system in the Pantanal but also on jaguar-livestock conflicts because jaguar predation on cattle appeared to decrease as predation on peccaries increased.

Jaguar predation on caiman peaked during the wet season when caiman were widely dispersed across the landscape due to high water levels and therefore available to more jaguars. In addition, egg laying also occurs during the wet season (Coutinho and Campos 1996), making female caiman less mobile and possibly more vulnerable to jaguars. Jaguar predation on caiman might have been expected to increase during the dry season when only a few sites contained water and caiman were congregated. However, the dry season also was the livestock calving season, thereby increasing the availability of vulnerable calves. Jaguars appeared to switch to this resource at that time. This inverse relationship between jaguar predation on cattle and caiman was a result of the annual cycles in rainfall patterns. Following the rainy season water levels receded in the Pantanal, and caiman moved with

these levels and predation declined. Simultaneously, as water levels receded cattle were moved into these areas for grazing, and predation on cattle increased. The fluctuation of water levels was the major driver in this ecosystem dictating the availability and vulnerability of prey species, including cattle.

Although jaguars killed a variety of native prey, cattle comprised a major part of their kills. The importance of cattle to jaguars varies among populations. In some areas jaguar predation on cattle is not a serious problem. In Mexico Núñez et al. (2000) found that jaguars did not kill livestock. Rabinowitz (1986) tracked 2 jaguars that traveled near cattle without causing problems. In the northern Pantanal cattle were important in terms of biomass (Schaller and Crawshaw 1980), but jaguar kill rates were not determined. Dalponte (2002) indicated that capybaras and cattle represented the base diet of jaguars in the northern Pantanal. Crawshaw and Quigley (2002) found that 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. When Crawshaw and Quigley (2002) found 17 kills by homing in on radiocollared jaguars, they found 29% (5) were cattle and 41% (7) were white-lipped peccaries, similar to our findings. However, because our study took place during 2 of the more extreme years in terms of rainfall, we reported the frequency of cattle among jaguar kills as ranging between 49% and 19%, reflecting the driest and wettest weather conditions during our study. Our data on the age of cattle killed by jaguars are similar to those of other studies. In Venezuela jaguars attacked young cattle (1–2 years of age) more often than adults (Farrell 1999; Hoogesteijn et al. 1993; Scognamillo et al. 2002). In northeastern Argentina cattle between 1 and 3 years of age 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 method used. When jaguar kills are found opportunistically bias may exist in the size of prey one is able to find.

Although every jaguar we monitored killed cattle, we observed considerable individual variability among cats in the proportions of native prey and cattle killed. Although some cats had >50% of their kills as cattle, for other jaguars this proportion was <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 (Hoogesteijn and Mondolfi 1992; Rabinowitz 1986) might not be valid for our area. Annual variation in kill rates more likely reflected the differences in availability or vulnerability of cattle and alternative prey; for 1 female jaguar (female 2) for which we had data spanning both years, 43% of her kills were cattle in 2002 ($n = 70$ kills), decreasing to 7% of her kills as cattle in 2003 ($n = 45$ kills).

Some studies indicated that livestock-depredating cats are more likely to be males or subadults (Chellam and Johnsingh 1993; Rabinowitz 1986; Saberwal et al. 1994; Stander 1990), but other studies reported that adults were more likely to kill

cattle (Bowns 1985; Esterhuizen and Norton 1985). Due to our limited sample size we were unable to conclude whether sex or age of a jaguar made it more prone to kill cattle. Some studies suggested that the majority of livestock killers were wounded (Fox and Chundawat 1988; Hoogesteijn et al. 1993; Rabinowitz 1986). In Venezuela the majority of cats (53–75%) killed for depredation control previously had sustained severe wounds (Hoogesteijn et al. 1993). In our study all radiocollared cats that killed cattle were in excellent physical condition at the time of capture. Rabinowitz (1986) suggested that once a jaguar preyed on cattle, it continued to treat cattle as a main source of food. Examination of data from 2002 suggested that climatic conditions might have played a stronger role in jaguar prey selection than individual preference or propensity to kill livestock, and 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 migrated from the area (peccary), were concentrated around water (caiman), or were reduced in number. Concurrently, due to low water levels cattle were distributed throughout the ranch and available to all radiocollared jaguars.

Given the dynamic nature of cattle operations in the Pantanal, it is likely that some degree of jaguar predation on cattle always will occur. The level of rainfall in any given year appeared to be the most influential factor affecting individual jaguar kill rates on cattle by determining the availability of cattle on the landscape. Husbandry practices also could have had an influence on jaguar predation as calves were generally born over a 4- to 5-month time span, increasing the time period of vulnerability to predation. Native ungulates usually flood a predator by having a short birth pulse, thereby decreasing the length of time young are exposed or vulnerable to predation (Estes 1976; Rutberg 1987; Skogland 1991). Shortening the birth pulse and increasing the number of pregnant cows within a cattle operation could, in theory, reduce overall predation losses within individual jaguar territories by flooding an individual cat with far more prey than can be killed, assuming a type III functional response (Holling 1959).

Our study provided insights on several aspects of jaguar foraging ecology and behavior, illustrating the opportunistic nature of jaguars that appeared to take advantage of a constantly changing environment where food resources vary both temporally and spatially. We found that jaguar predation on cattle varied not only seasonally but also annually, with consequences to both the ranchers and jaguars (i.e., retaliatory persecution). Like other large carnivores, jaguars may target livestock at higher proportion during periods when native prey are less accessible. Although some people might advocate removal of cattle to reduce conflicts between jaguars and humans, high stocking rates of cattle could be supporting a high density of jaguars in the Pantanal (Soisalo and Cavalcanti 2006). We also recognize that the effects of high stocking rates of cattle on the distribution and abundance of native prey is unknown.

Although the Pantanal is considered important for jaguar conservation (Sanderson et al. 2002), characteristics of the area make conservation of jaguars and the alleviation of jaguar–livestock conflicts 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), other factors directly and indirectly affect jaguar conservation. Jaguars killing livestock creates a conflict with ranchers from an economic perspective. Instead of trying to curtail jaguar depredation on livestock through preventive measures, both ranchers and authorities may need to recognize that cattle comprise a major part of the diet of jaguars and invest in alternative management actions. Cattle are a prey item with the largest available biomass in the area, but also are the most vulnerable (mainly calves). Authorities need to recognize the cost associated with grazing cattle in an area where jaguars exist in considerable numbers (Soisalo and Cavalcanti 2006). Creative solutions in the form of tax benefits, special lines of credit, or a regional increase in beef prices may be needed to conserve jaguars. In contrast, ranchers may need to focus on increasing the production of their herds, or curtail losses via herd management and improved husbandry practices (Hoogesteijn et al. 1993).

Recently, an effort in the Pantanal was initiated to alleviate jaguar–livestock conflicts in the form of a compensation program (Silveira et al. 2006). Although such programs have been implemented worldwide (Naughton-Treves et al. 2003; Saberwal et al. 1994; Swenson and Andr n 2005), they have many weaknesses. Unverified losses, fraudulent claims, bureaucratic claim processes causing lengthy time delays, compensation below 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-M ller 2008). A more recent approach that has been proposed as an alternative to compensation programs is “performance payments” (Nyhus et al. 2005; Zabel and Holm-M ller 2008). Rather than compensating ranchers for the negative aspect of jaguars (i.e., the economic losses), governments and conservation organizations might consider making payments that are conditional on jaguar abundance in an area (Ferraro and Kiss 2002; Zabel and Holm-M ller 2008). By focusing on the number of jaguar offspring or the annual density of jaguars in a particular area, these payments would be solely for a particular conservation goal. However, the problem extends beyond economics, with a cultural aspect that could be more difficult to address. Cultural traditions in the Pantanal are deeply ingrained among the local inhabitants. Jaguar hunts often are viewed as an act of bravery within the community. These cultural traditions, coupled with the characteristics of the area and the lack of enforcement by wildlife authorities, contribute to the illegal shooting of these cats (S. M. C. Cavalcanti, pers. obs.).

The conservation of jaguars in the Pantanal entails the complex task of integrating ecological, economic, and sociocultural aspects in the planning of effective management

not only to decrease economic losses by cattle ranchers but also to improve the local human perceptions of jaguars. To that end, it will be important to devise educational tools that bring ecological knowledge to the local community and make them active participants for conserving this charismatic predator for future generations. In addition, knowledge of predator–prey relationships will be important in guiding future management decisions and conservation plans for this large keystone predator. Continued research will be needed to provide objective and reliable data to elucidate the relationships between humans, livestock, and jaguars throughout Central and South America.

RESUMEN

Los jaguares (*Panthera onca*) a menudo cazan el ganado, resultando en conflicto con los humanos. Hasta la fecha, las tasas y los patrones de depredaci n por jaguares no han sido bien documentados. Nosotros estudiamos la ecolog a de forrajeo de los jaguares en un  rea con ganado y presas nativas, y documentamos las tasas de depredaci n, las caracter sticas de las presas muertas, los patrones de depredaci n, y la influencia del tama o de las presas en la duraci n en los sitios de ataque y en el intervalo de tiempo entre ataque. Entre octubre del 2001 y abril del 2004, monitoreamos 10 jaguares equipados con collares con un sistema de posicionamiento global (GPS, por sus siglas en ingl s). Recogimos 11.787 puntos GPS e identificamos 1.105 agrupaciones de localidades como sitios de uso concentrado (por ejemplo, los sitios de ataque, sitios de reposo, guardidas). De estos, encontramos los restos de presas en 415 sitios de ataque y documentamos 438 partes de presa. Los ataques se componen del 31,7% ganado (9,8% adultos y 21,9% terneros), el 24,4% caim nes (*Caiman crocodilus yacare*), el 21,0% pecar es (principalmente *Tayassu pecari*), el 4,1% cerdos silvestres (*Sus scrofa*), el 3,9% ciervos de los pantanos (*Blastocercus dichotomus*), el 3,2% osos hormigueros gigante (*Myrmecophaga tridactyla*), el 2,0% capibaras (*Hydrochoerus hydrochaeris*), el 1,6% corzuelas colorada (*Mazama americana* y *M. gouazoubira*), y otras especies de aves, mam feros y reptiles. Jaguares individuales difirieron en la proporci n de cada especie que mataron, as  como la proporci n de presas nativas y ganado matados por los felinos. Si bien todos los 10 felinos mataron el ganado, 5 mataron un alto porcentaje de ganado (>35% de los mata), mientras que 3 mataron poco ganado (<15%). Los machos (27%) y las hembras (35%) mataron el ganado en proporciones similares. En contraste, los jaguares machos mataron a una mayor proporci n de pecar es que las hembras, mientras que las jaguares hembras mataron m s caim nes que los machos. El promedio de la tasa de depredaci n de todos los jaguares fue de 4,3 d as \pm 4,4 *SD* consecutivos entre ataques conocidos, sin diferencia estad stica en las tasas de mata entre los 10 felinos. El intervalo de tiempo al siguiente ataque por los jaguares aument  con el aumento del tama o de las presas. La cantidad de tiempo que los jaguares pasaron con un cad ver tambi n aument  al aumentar el

tamaño de la presa. Las tasas de depredación de pecaríes por los jaguares aumentó constantemente durante los 4 años del estudio. En contraste, las tasas de depredación del ganado disminuyeron durante el mismo período. Las precipitaciones y los niveles de agua posteriores sobre el Pantanal fueron el principal impulsor de las tasas de depredación de temporada del ganado y de los caimanes por jaguares. Al aumentar los niveles de agua, la depredación en los caimanes se hizo en forma más extensiva en el paisaje. Por el contrario, al bajar los niveles de agua, el caimán se hizo menos abundante, y el ganado fue trasladado a los pastos, por lo que se aumentó su disponibilidad para más jaguares.

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