

Evaluation of Potential Factors Predisposing Livestock to Predation by Jaguars

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ABSTRACT Depredation of livestock by large carnivores is an important but poorly understood source of human–carnivore conflict. We examined patterns of livestock depredation by jaguars (*Panthera onca*) and pumas (*Puma concolor*) on a ranch–wildlife reserve in western Brazil to assess factors contributing to prey mortality. We predicted jaguars would kill a greater proportion of calves than yearling and adult cattle and that proximity to suitable habitat would increase mortality risk. We further speculated that exposure to predation risk would promote livestock grouping and increased movement distance. We recorded 169 cattle mortality incidents during 2003–2004, of which 19% were due to predation by jaguars and pumas. This level of mortality represented 0.2–0.3% of the total livestock holdings on the ranch. Jaguars caused most (69%) cattle predation events, and survival in allotments was lower for calves than for other age classes. Forest proximity was the only variable we found to explain patterns of livestock mortality, with predation risk increasing as distance to forest cover declined. Due to low predation risk, cattle movement patterns and grouping behavior did not vary relative to level of spatial overlap with radiocollared jaguars. The overall effect of predation on cattle was low and livestock likely constituted an alternative prey for large cats in our study area. However, selection of calves over other age cohorts and higher predation risk among cattle in proximity to forest cover is suggestive of selection of substandard individuals. Cattle ranchers in the Pantanal region may reduce cattle mortality rates by concentrating on losses due to nonpredation causes that could be more easily controlled. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2379–2386; 2007)

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

Vulnerability of livestock to predators may be influenced by such environmental and socio-ecological factors as abundance and distribution of natural prey, habitat characteristics, and husbandry practices (Kolowski and Holekamp 2006). In theory, if predation on a given prey species is opportunistic, individual prey should exhibit limited anti-predator responses and, thus, have high vulnerability to predation (Fernández-Juricic et al. 2004). Vulnerability to predation should be more pronounced on substandard individuals because they are conspicuous and less able to escape or repel predators (Lima and Dill 1990, Curio 1993). It follows that predators should kill a disproportionate number of juveniles of a particular species when adults are

more difficult to capture and kill (Temple 1987). However, predators also may impose sublethal effects on prey, such as increased gregariousness and movement distances, in response to increased perceived predation risk (Boonstra et al. 1998, Berger et al. 2001, Creel et al. 2005). Clearly, the assessment of potential sublethal effects of predation on livestock, concurrent with the study of factors causing direct livestock depredation, are important for understanding the full impact of large carnivores on livestock.

Jaguars (*Panthera onca*) are the largest felids occupying the Americas. In recent decades, extensive fragmentation of jaguar habitat and expansion of human activities into such areas has increased both jaguar depredation on livestock as well as conflict with humans (Rabinowitz and Nottingham 1986, Weber and Rabinowitz 1996). However, there has been limited assessment of the magnitude of jaguar use of livestock as prey or of factors predisposing livestock to depredation by jaguars. For instance, the demonstrated preference by jaguars for forested habitats in close association with standing water is attributed to increased wild prey vulnerability to predation in such habitats (Crawshaw and Quigley 1991, Quigley and Crawshaw 1992). Similar patterns may apply to jaguar selection of domestic prey. Inappropriate husbandry practices and wild prey availability and vulnerability are factors reported to influence vulnerability of livestock to depredation by jaguars, particularly among calves (Quigley and Crawshaw 1992, Hoogesteijn et al. 1993, Polisar et al. 2003). It follows that development of conceptual models of livestock predation by jaguars will remain incomplete without more detailed empirical work examining how the above factors affect livestock vulnerability to predation.

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We examined patterns of livestock depredation by jaguars (and to a lesser extent puma [*Puma concolor*]) to assess the main factors contributing to mortality risk. Specifically, we assessed jaguar–livestock interactions by monitoring survival of domestic cattle and evaluating how predator space use affected mortality risk as well as by measuring livestock behavioral responses to predation risk. Consistent with the hypothesis that close contact with jaguars within suitable habitat favors increased mortality risk, we predicted that 1) jaguars would kill a greater proportion of livestock calves relative to yearlings and adult cattle, and 2) proximity to suitable habitat, such as forest and permanent water bodies, would increase overall mortality rates. Furthermore, we speculated increased exposure to predation risk would promote livestock grouping and increase movement distances.

STUDY AREA

We conducted our study in the southern part of the Pantanal region of the Mato Grosso do Sul state in Brazil from February 2003 to December 2004. The Pantanal is a floodplain covering approximately 140,000 km² of land in Brazil, on the borders of Bolivia and Paraguay. The Pantanal is characterized by an annual regime of flooding and low land relief. Landscape in the region is characterized by a mosaic of rivers, ponds, swamps, seasonally inundated grasslands and woodlands, and nonflooding forests. The study site was a 150-km² cattle ranch–wildlife reserve, San Francisco ranch, located in the southern region of the state (20°05'S and 56°36'W). Three major habitat types occurred on the ranch: 1) open areas, with grasslands composed mainly of grass species interspersed with palm trees such as the carandá (*Copernicia alba*) and acuri palms (*Attalea phalerata*) and commercial rice fields; 2) closed woodlands, the cerradão, constituting a one-story forest with trees such as the ipê (*Tabebuia* sp.) lacking clear vertical stratification, and a grass understory that is flooded during wet season; and 3) semi-deciduous forests having vertical differentiation, including ipê and acuri palms (Dubs 1994). Average annual precipitation at the study site between 1988 and 2004 was 1,336.3 mm, with most of the rain falling between October and April.

The ranch had approximately 5,000 head of cattle that included mainly *Bos indicus* cebú race (nelore) and the breed Montana. Cattle were kept in fenced allotments in elevated areas of permanent pastures and routinely rotated between allotments to avoid overgrazing. Vegetation inside allotments was mostly comprised of introduced grass species with few patches of semi-deciduous forests left inside allotments to provide shade. After the rice season (Feb–Jun), part of the herd was left to feed on rice fields. In addition, some lowland areas of cerradão were used for livestock grazing during the dry season. Calving period occurred from September to December. Data on livestock causes of death at the ranch were recorded between 1991 and 2002, with annual depredation by large felids (jaguar and puma) estimated at 11% ($n = 667$) of all livestock mortality (R.

C. Coelho, San Francisco Ranch, unpublished report). In relation to total livestock holdings for the period ($n = 56,408$ head; $\bar{x} = 4,700 \pm 495.39$ [SD] head/yr) the average annual rate of livestock depredation by cats in the ranch was $0.13 \pm 0.11\%$ and death by other causes (e.g., accident, snake, disease, parturition problems, flood, and unknown natural causes) was $1.06 \pm 0.25\%$ (R. C. Coelho, unpublished report).

METHODS

During March 2003–October 2004, we captured 11 jaguars (5 F and 6 M) and 3 pumas (2 F and 1 M) and fitted them with radio-collars. Animal handling procedures were approved by the Brazilian Environment Institute (IBAMA; permit no. 02027.007013/03-81). We fitted immobilized animals with very high frequency radiocollars (Advanced Telemetry Systems, Isanti, MN and Telonics, Inc., Mesa, AZ). We monitored radiocollared animals during March 2003–December 2004 and obtained locations 3 times per week from the ground using standard triangulation techniques (Samuel and Fuller 1996) and weekly via fixed-wing aircraft. We used only independent locations (i.e., >24 hr apart) in analyses (Grassman et al. 2005). We deemed 8 jaguars (5 F and 3 M) to be residents based on their long-term occupation of the study area; the female pumas had territories adjacent to the intensive study area. Despite intensive search, we never relocated or found tracks of the male puma postcapture and, thus, considered the male puma a transient. In addition, 1–2 transient pumas and 2 young uncollared jaguars were also known to be present on the study area. Thus, we monitored 8 collared jaguars in the context of predation on livestock. Note that, although predation incidents attributed to transient pumas were recorded during our study, for all analysis of space use we included only data on collared jaguars. We calculated 95% and 50% kernel home-range sizes using the Animal Movement Extension in the program ArcView Geographic Information System (GIS) 3.2 (Hooge et al. 1999), using least-squares cross validation (Worton 1995). This allowed us to determine home and core areas, respectively. We included in our analysis only home ranges that we found to reach an asymptote at ≥ 30 locations. We determined accuracy of ground and aerial telemetry by location via blind observation of transmitters placed throughout the study area; mean error associated with aerial telemetry was 131 ± 47 m ($n = 10$) and from the ground was 206 ± 168 m ($n = 10$).

To survey depredation events or other mortality, we recorded mortalities for the entire ranch during 2003–2004. To estimate survival and mortality causes of livestock we conducted daily visits of 15 allotments where animals had been held intensively for most of year. These allotments contained one-third of all livestock holdings in the ranch (approx. 2,000 head), and comprised an area of 7.24 km², with individual allotments averaging 0.72 ± 0.46 km². Allotments were adjacent to each other and separated by wire fences. The distance of allotment fences to permanent

forest averaged 211 ± 371 m ($n = 15$). Allotments contained roughly similar amounts of patches of forest. Each allotment contained a herd comprised of one age–sex class and 12 age–sex class herds were rotated among allotments. We studied 3 different classes of herds separated by sexes: weaned calves 6–12 months, yearlings 13–24 months, and adult animals >25 months. During the study, all dead cattle were recovered within 48 hours of death, with the exception of one newborn calf in 2004. For the purpose of our survival analysis, we considered each cattle herd the experimental unit and we observed herds during several time intervals of unequal lengths. Therefore, for each herd we recorded information on time in the allotment (d), survival status (no. of deaths), and habitat type where the herd was located (i.e., pasture, cerradão, rice field).

Livestock found dead were necropsied and we collected information on gender, age, and precise location using a Global Positioning System (GPS) unit; we later used GPS locations to estimate habitat type and proximity to nearest forest and water. We concluded predation by cats if we observed ≥ 2 of the following: signs of bites on carcasses of cattle, presence of tracks and scats near kill sites, or signs of a trail where prey had been carried or dragged. To determine cause of death for nonpredation mortality, a veterinarian at the ranch examined animals within 2 days of recovery. Because it was not always possible to perform necropsies on carcasses, we classified mortalities into 2 proximate causes: cat predation (jaguar and puma) and other (i.e., accident, snake, disease, poison, parturition problems, flood, and unknown natural causes). Previous field observations of cattle moving and staying away from the interface between allotment fences and permanent forest ≤ 5 days after a jaguar attack (F. C. C. Azevedo, Instituto Pró-Carnívoros, personal observation) suggested potential influence of predation risk by jaguars on cattle movement and gregarious behavior. Thus, to evaluate cattle location relative to known locations among collared cats, we located each cattle herd weekly inside each allotment within 2 days after we had located collared cats. We determined cattle locations based on position of the majority of the herd using a GPS unit. For each cattle location, we recorded information on habitat type, grouping behavior (grouped or ungrouped), and size of allotment.

Data Analysis

Predation impact.—To assess the impact of predation for the entire ranch, we compared frequency of predation to nonpredation incidents using a chi-square goodness-of-fit test, including all events of mortality recorded during 2003–2004. To assess predator selectivity for cattle for the entire ranch, including allotments not visited daily by research personnel, we performed a chi-square goodness-of-fit test, using each predation event during 2003–2004 as the experimental unit. We investigated whether the recorded frequency of predation on different livestock age–classes deviated significantly from their known availability. We also investigated whether livestock depredation varied between jaguars and pumas. Mortalities between predator species

were differentiated through presence of tracks or telemetry signals near carcasses. For these analyses, we divided cattle into 4 age class groups not separated by sexes: 1) calves <4 months; 2) calves 4–12 months; 3) yearlings 13–24 months; and 4) adults >24 months. We based information on cattle availability and age class for the entire ranch on known numbers of cattle provided by San Francisco ranch. We considered all analyses of predation impact statistically significant when $P < 0.05$. Due to lack of previous data on differential predation regarding cattle age classes, probability levels were 2-tailed.

Survival.—We estimated survival and cause-specific mortality rates of cattle within allotments based on 2 main assumptions: 1) within each interval daily survival and age-specific mortality rates were constant and 2) all animals within an age–sex class had the same probability of survival and mortality (Heisey and Fuller 1985). We recorded cattle survival for a cumulative total of 9,200 animals (213.1 ± 71.0 cattle/allotment). We calculated annual survival and cause-specific mortality rates for each cattle age-class using program MICROMORT (Heisey and Fuller 1985). We defined tracking days as the total number of animals within each allotment multiplied by the number of days of observation of each time interval. Unless otherwise noted, estimates of survival rates are accompanied by 95% confidence intervals. Note that cattle of different ages and genders were kept in different allotments at different times, therefore potentially influencing predation risk exposure among groups. However, given that all allotments were located in the same general vicinity, we assumed that cattle were exposed comparably to predators and, thus, that differences in mortality patterns between groups were reflective of differential predation risk.

To assess relationships between survival and selected explanatory variables, models of cattle mortality were generated using Poisson regression (Zar 1999) using PROC GENMOD in SAS 8.02 (SAS Institute, Cary, NC). Using this procedure, the dependent variable is a rate and a Poisson distribution is the basis for statistical inference (Selvin 1995). We evaluated the relationship between daily predation rate and independent variables including age class and sex. In our predation risk models, we calculated the dependent variable from observations of cattle inside each allotment during different time intervals; thus, each sample unit in our regression analysis was number of deaths offset by number of tracking days for each cattle herd during the interval. We estimated parameters of each model using maximum likelihoods and we compared model fit using Akaike's Information Criterion with small-sample correction (AIC_c ; Anderson et al. 2000). In addition we described influence of variables on predation rates using rate ratios (rate ratio = e^{coeff}) representing the ratio of predation rates as a function of variation in independent variables (Hosmer and Lemeshow 2000).

Vulnerability to predation.—We used logistic regression to investigate the importance of habitat factors such as forest and water on cattle mortality risk. We used cause of

Table 1. Livestock availability and number of mortality incidents ($N=169$) for the entire area of San Francisco ranch, in the Pantanal region of Brazil, during 2003–2004.

Livestock age class	Availability			Predation	Cause of death		
	\bar{x}	SD	% of total		% of class	Other	% of class
Ad (>2 yr old)	3,414	205.7	53.3	4	0.1	44	1.2
Yearlings (13–24 months)	1,522	41.0	23.7	6	0.3	37	2.4
Calves (4–12 months)	753	230.5	11.7	12	1.5	27	3.5
Calves (0–3 months)	709	166.8	11.0	10	1.4	29	4.0
Total	6,398	150.6	32	0.5		137	2.1

mortality (predation vs. other causes) as dependent variable. We compared distance of locations of dead cattle relative to nearest forest and water. To assess the extent that proximity to suitable habitat affected livestock vulnerability to predation, we performed simple correlation analyses using distance of locations of depredated cattle versus nearest forest and water. For comparison, we also examined distance to forest and water among cattle dead from other causes. We tested data for normality using the Kolmogorov–Smirnov test for goodness-of-fit (Dytham 2003). When variances were comparable, we used t -tests; otherwise we used nonparametric Mann–Whitney tests.

Space use.—To describe spatial distribution of livestock relative to collared cats, we used cattle locations to construct home ranges (95% fixed kernel [FK]) and core use areas (50% FK), using the animal movement extension in program ARCVIEW GIS 3.2 (Hooge et al. 1999). For this analysis, we pooled locations of separate allotments. We transposed jaguar home ranges for the entire period of study onto a grid (FK) and assigned specific levels of utilization (0–95%) to each area within the home range (Roloff et al. 2001, Oakleaf et al. 2003). We then overlaid cattle locations and determined levels of overlap to infer potential jaguar predation risk at each cattle location. To determine cattle movement patterns and grouping behavior in relation to jaguar home range areas, we assessed livestock locations at various predation risk levels (Oakleaf et al. 2003). We assumed predation risk increased with proximity to core jaguar use areas.

Cattle gregarious behavior and movement.—We used logistic regression (Hosmer and Lemeshow 2000) to identify factors influencing cattle grouping behavior relative to proximity to jaguars. Grouping behavior (grouped, ungrouped) was the dependent variable, and we considered cattle as grouped whenever we located the majority of animals from a herd moving or standing in close (i.e., <2 m) proximity during visual observations. Each observation trial lasted ≥ 30 minutes, between 0600–0800 hours. Because food resources inside each allotment were equally spaced we assumed that grouping was a response to increased perceived predation risk (Hebblewhite and Pletscher 2002). As independent variables we used habitat type (categorical variables: open areas [pastures and rice fields] vs. closed woodland [cerradão]) and jaguar use level (categorical variable: no jaguar use, 1–50% FK use, 51–80% FK; 81–95% FK).

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

RESULTS

Predation and Cattle Populations

For the entire study period and total ranch area, we recorded 169 cattle mortality incidents. Predation mortality for all age classes accounted for 19% of all deaths and was less common than nonpredation mortality ($\chi^2 = 8.91$, $df = 3$, $P = 0.03$). Jaguars and pumas killed 0.2% ($n = 12$) and 0.3% ($n = 20$) of the total livestock holdings on the ranch for 2003 and 2004, respectively, whereas mortality due to other causes represented 0.7% ($n = 44$) and 1.5% ($n = 93$) for each year, respectively. Based on the number of cattle killed by cats during period of study and considering all livestock age classes, livestock depredation rates differed significantly between jaguars and pumas ($\chi^2 = 11.73$, $df = 3$, $P = 0.001$), with jaguars being responsible for most (68.8%, $n = 22$) cattle predation. Whereas jaguars preyed upon all cattle age classes, pumas selected only calves aged <12 months. Among all cattle killed by cats, we observed selectivity towards the 2 younger cattle age classes ($\chi^2 = 40.01$, $df = 3$, $P = 0.001$); cattle that were >12 months were preyed less than expected (Table 1).

Survival

We recorded livestock survival during 43 time intervals (40.4 ± 47.4 [SD] d/interval). The annual survival rate was 0.86 (95% CI = 0.80–0.93), 0.97 (95% CI = 0.94–0.99) and 0.96 (95% CI = 0.94–0.99), for calves, yearlings, and adults, respectively. We recorded 34 cattle deaths inside the 15 allotments, representing 20.1% of all cases of mortality

Table 2. Cause-specific mortality rates of cattle tracked inside allotments on San Francisco ranch, Brazil, during January–December 2004.

Age class	Cumulative no. of animals	\bar{x}	SD	Deaths	%	Annual cause-specific mortality rate			
						Predation	95% CI	Other	95% CI
Calves	1,261	180	75	20	1.58	0.047	0.005–0.089	0.087	0.037–0.137
Yearlings	6,421	229	68	6	0.09	0.004	0.000–0.011	0.029	0.002–0.057
Ad	1,518	190	69	8	0.53	0.004	0.000–0.012	0.030	0.008–0.052

on the ranch during the study period. We found that 8 deaths (23.5%) were due to predation, with jaguars being proximally responsible for most kills ($n = 7$). For all 3 age classes, mortality rates due to nonpredation causes were likely higher than from predation (Table 2). The predation risk model that best explained patterns of cattle mortality due to predation included only the variable for age class. Model-averaged coefficient estimate and unconditional standard error for the variable age (-9.806 ± 0.452) indicated a strong age effect on livestock mortality risk ($P < 0.001$; Table 3). The rate ratio for the age variable indicated that among yearlings predation risk declined by 89% ($e^{-2.23} = 0.11$) in comparison with calves, whereas adults were 79% less likely to be depredated ($e^{-1.549} = 0.21$).

Habitat and Vulnerability to Predation

Our analysis of the importance of habitat factors in cattle mortality for the entire ranch suggested that forest was the prevalent variable explaining cause of mortality ($P = 0.006$; Table 4). The habitat-related odds-ratio for the best model (0.997; 95% C = 0.995–0.999) indicated that probability of a death from jaguar predation increased as distance to forest declined. The number of locations of cattle killed by cats decreased with increased distances from both forest ($r = -0.82$, $P \leq 0.001$) and water ($r = -0.89$, $P \leq 0.001$). We observed the same pattern for locations of cattle dying of nonpredation causes in relation to either forest ($r = -0.80$, $P = 0.049$) and water ($r = -0.83$, $P = 0.003$). However, when comparing the average distances to forest, locations of cattle killed by cats (213.3 ± 188.5 m, $n = 32$) were closer to forest ($t_1 = 2.68$, $P = 0.008$) than were nonpredation mortalities (318.2 ± 204.5 m, $n = 137$). In contrast, distances between depredated (348.8 ± 292.0 m, $n = 32$) and nondepredated (320.2 ± 207.6 m, $n = 137$) deaths were similar relative to distance to water (Mann–Whitney $U = 2,498.5$, $P = 0.962$).

Table 3. Factors influencing mortality of cattle in allotments on San Francisco ranch, Brazil, during January–December 2004.^a

Model _{<i>i</i>}	Coeff	K_i	Δ_i	w_i	95% CI	<i>P</i> -value
age	-9.766	3	0.00	0.609	-10.566–-8.966	<0.001
age + sex	-9.824	4	1.08	0.356	-10.845–-8.804	<0.001
sex	-10.591	2	5.84	0.003	-11.571–-9.611	<0.001

^a For each model i , K_i is the no. of parameters in the model, Δ_i is the change in Akaike's Information Criterion with small-sample correction (AIC_c) between the model and the model with the lowest AIC_c (best model), and w_i is the Akaike wt.

Space Use

Our spatial analysis suggested the degree of cattle-to-jaguar static interaction was low within the study area. Considering the total estimated home range size for the 8 resident jaguars within the ranch (112.2 km², 95% FK) and our study area (150 km²), the overlap with cattle home range was only 16.4%. When analyzing overlap between jaguar core areas (50% FK) and cattle space use within allotments (95% FK), overlap was only 2.4%. We observed no overlap between cattle core areas (50% FK) and jaguar home-range areas (95% FK).

Our analysis of cattle gregarious behavior suggested habitat type was the prevalent variable explaining grouping behavior ($P = 0.006$; Table 5). Of all cattle locations recorded during the study ($n = 278$), 69.8% were from ungrouped animals in open habitat. The odds-ratio for the model (0.404; 95% CI = -0.28 to 1.09) indicated that cattle grouping in open habitat was 60% less likely to occur than in closed habitat. Our results showed that among factors influencing cattle movement, the best model included only differential jaguar use between cattle locations ($F = 6.38$, $P = 0.012$). The model-averaged coefficient estimate (1.15 ± 1.03) suggested that this variable was important to cattle movement (Table 6). Variables representing days between locations, jaguar use level at initial location, and jaguar use level at final location of cattle did not affect cattle movement (all $R^2 < 0.05$). The average movement distance of cattle during tracking was $1,213.4 \pm 1,482.5$ m per day.

DISCUSSION

Predation and Survival of Cattle Populations

Our results indicate that the overall impact of large felid predation on cattle was low in our study area. This rate (0.5%) was lower than that reported for most other large felid livestock depredation studies (Mizutani 1993, Butler 2000, Madhusudan 2003, Patterson et al. 2004). Considering the estimated daily energetic needs of the jaguar population in the study area (34 g/d/kg of cat; Emmons 1987, Polisar et al. 2003), depredated livestock represented only 0.56% (9,634 kg) of the standing crop of cattle (approx. 1,865,000 kg; Azevedo and Murray 2007). Therefore, cattle predation rate was markedly low, indicating that cats did not subsist on cattle during the period of study. Similar conclusions were suggested for other studies on carnivores (Mizutani 1993, Polisar et al. 2003, Patterson et al. 2004). In contrast, losses due to nonpredation causes were 4 times higher (2.14% of total livestock holdings), implying that although the overall mortality rate for cattle in

Table 4. Logistic regression models of variables found to be significant in predicting causes of cattle mortality (predated vs. other causes) on San Francisco ranch, Brazil, during January–December 2004, as ranked by Akaike's Information Criterion with small-sample correction (AIC_c), where other causes is the reference cell. Odds ratios (OR) and corresponding 95% confidence intervals are provided.^a

Model _{<i>i</i>}	OR ₁	OR ₂	95% CI ₁	95% CI ₂	K_i	Δ_i	w_i	<i>P</i> -value
Constant + forest	0.997		0.995–0.999		2	0.00	0.61	0.006
Constant + forest + water	1.000	0.997	0.999–1.002	0.995–0.999	3	1.42	0.30	0.017
Constant only	0.411		0.150–0.67		1	5.47	0.04	<0.001
Constant + water	1.012		1.000–1.02		2	7.08	0.02	0.513

^a For each model i , K_i is the no. of parameters in the model, Δ_i is the change in AIC_c between the model and the model with the lowest AIC_c (best model), and w_i is the Akaike wt. Model significance was determined by the likelihood ratio test.

Table 5. Logistic regression models of variables found to be significant in predicting cattle grouping behavior (grouping vs. ungrouping) on San Francisco ranch, Brazil, during January–December 2004 as ranked by Akaike's Information Criterion with small-sample correction (AIC_c), where grouping are the reference cell. Odds ratios (OR) and corresponding 95% confidence intervals are provided.^a

Model _{<i>i</i>}	OR ₁	OR ₂	95% CI ₁	95% CI ₂	K_i	Δ_i	w_i	<i>P</i> -value
Constant + habitat ^a	0.404		–0.28–1.09		2	0.00	0.77	0.006
Constant + habitat ^a + cat use level	0.428	1.011	–0.27–1.13	1.00–1.02	5	3.24	0.15	0.033
Constant only	0.411		0.15–0.67		2	4.98	0.06	<0.001
Constant + cat use level	1.012		1.00–1.02		4	8.23	0.01	0.392

^a Design coded with open habitats as reference (i.e., cattle are 0.40 times more likely to be ungrouped in closed habitats than in open habitats). For each model i , K_i is the no. of parameters in the model, Δ_i is the change in AIC_c between the model and the model with the lowest AIC_c (best model), and w_i is the Akaike wt. Model significance was determined by the likelihood ratio test.

the study area was low (2.64% of total livestock holdings), nonpredation causes constituted a more important factor in cattle death (Mizutani 1993, Cozza et al. 1996, Patterson et al. 2004, Graham et al. 2005). Our results strongly suggest that cattle likely constituted an alternative prey, which were killed opportunistically by predators in the study area (Oakleaf et al. 2003, Polisar et al. 2003, Patterson et al. 2004).

Similarly to patterns of mortality for the entire ranch, cattle survival rates within allotments indicate that livestock mortality was low and mortality risk from nonpredation causes was higher than predation risk. In support of our first prediction, predation risk was highest among the younger age class and these results are consistent with those observed previously for livestock (Hoogesteijn et al. 1993, Anderson et al. 1998, Oakleaf et al. 2003, Polisar et al. 2003). Overall, predation rates were likely not sufficient to cause anti-predator responses in cattle. However, selective calf predation may suggest that jaguar predation was limited by prey size and that selection for young or small individuals reflected difficulties in capturing larger prey (e.g., see Temple 1987).

Habitat and Space Use Patterns

Under the assumption that cattle would be killed in predator-suitable habitat, we expected to see increased predation in proximity to forest and water. This expectation was borne out given that more calves were killed in proximity to forest, likely due to differential mortality risk of juveniles when in proximity to predator hiding cover (Berger et al. 2001, Oakleaf et al. 2003). Others have also found forested habitats to be important in increasing vulnerability of calves to predation by jaguars (Quigley 1987, Quigley and Crawshaw 1992), but our results diverge

from most other jaguar depredation studies in that water had apparently no influence on livestock mortality risk. The high availability of ephemeral water bodies that persist throughout the first months of the dry season in the Pantanal region likely reflected the lack of influence of permanent water sources on the vulnerability of cattle to predation by jaguars.

Habitat overlap can influence predator selectivity of prey (Meriggi and Lovari 1996), and the clear lack of overlap between jaguars and livestock in this study suggests that

Table 6. Factors influencing cattle movement, as ranked by Akaike's Information Criterion with small-sample correction (AIC_c) on San Francisco ranch, Brazil, during January–December 2004.^a

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

^a For each model i , K_i is the no. of parameters in the model, Δ_i is the change in AIC_c between the model and the model with the lowest AIC_c (best model), and w_i is the Akaike wt. Model jag change refers to the amount of change in jaguar use levels between cattle locations; model d refers to days between locations; model use final refers to cat use level at final location; model use initial refers to cat use level at initial location.

predation risk generally was low in the allotments. These findings imply that jaguar presence probably had limited direct influence on cattle grouping behavior and that number of cattle depredated and cattle–carnivore interactions also failed to be influential. The low predation risk may also explain lack of cattle movement in response to exposure to higher predation risk. Similar justification has been offered to explain cattle behavior in ranges occupied by other large carnivores (Oakleaf et al. 2003). Note, however, that our movement models had low predictive power and therefore predation risk likely was not sufficient to influence cattle movement patterns or grouping behavior.

MANAGEMENT IMPLICATIONS

The information on jaguar predation we provided is relevant to understanding livestock predation by jaguars and pumas. We suggest that large felids in our area were unlikely to rely extensively on cattle as prey and the overall effect of cats on cattle was not significant. Cattle losses to predators were so low that the ranch should concentrate on losses due to nonpredation causes that could be more easily controlled to minimize overall mortality rates. Clearly, additional efforts are needed to further evaluate how sublethal effects associated with different intensities of perceived predation risk might influence predator's prey selection in the study area. Furthermore, a continuous monitoring of jaguar and puma densities and their selection of habitats will contribute to a better understanding of the patterns of livestock depredation by jaguars and pumas and how these cats respond to variations in the availability of cattle within the studied area.

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LITERATURE CITED

- Anderson, C. R., M. A. Ternent, D. S. Moody, M. T. Brusino, and D. F. Miller. 1998. Grizzly bear–cattle interactions on two cattle allotments in Northwest Wyoming. Wyoming Game and Fish Department, Cheyenne, USA.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. *Journal of Wildlife Management* 64:912–923.
- Azevedo, F. C. C., and D. M. Murray. 2007. Spatial organization and food habits of jaguars in the southern region of Pantanal, Brazil. 2007. *Biological Conservation*. 137:391–402.
- Berger, J., J. E. Swenson, and I. Persson. 2001. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039.
- Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs* 68:371–394.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Butler, J. R. A. 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology* 38:23–30.
- Cozza, K., R. Fico, M. L. Battistini, and E. Rogers. 1996. The damage–conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation* 78:329–336.
- Crawshaw, P. G., Jr., and H. Quigley. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology* 223:357–370.
- Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and C. Michael. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387–3397.
- Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. *Advances in the Study of Behavior* 22:135–238.
- Dubs, B. 1994. Differentiation of woodland and wet savanna habitats in the Pantanal of Mato Grosso, Brazil. Dissertation, University of Zürich, Edinburgh, United Kingdom.
- Dytham, C. 2003. Choosing and using statistics: a biologist's guide. Second edition. Blackwell, Oxford, United Kingdom.
- Emmons, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavior Ecology and Sociobiology* 20:271–283.
- Fernández-Juricic, E., J. Jokimäki, J. C. McDonald, F. Melado, A. Toledano, C. Mayo, B. Martín, I. Fresneda, and V. Martín. 2004. Effects of opportunistic predation on anti-predator behavioural responses in a guild of ground foragers. *Oecologia* 140:183–190.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human–predator correlates, prey losses and patterns of management. *Biological Conservation* 122:159–171.
- Grassman, L. I., M. E. Tewes, N. J. Silvy, and K. Kreetiyutanont. 2005. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in the north-central Thailand. *Journal of Zoology* 266:45–54.
- Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800–809.
- Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668–674.
- Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program. U.S. Geological Survey, Alaska Biological Center, Gustavus, USA.
- Hoogesteijn, R., A. Hoogesteijn, and E. Mondolfi. 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. *Symposium of The Zoological Society of London* 65:391–407.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.
- Kolowski, J. M., and K. E. Holekamp. 2006. Spatial, temporal, and physical characteristics of livestock depredation by large carnivores along a Kenyan reserve border. *Biological Conservation* 128:529–541.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 69: 619–640.
- Madhusudan, M. D. 2003. Living amidst large wildlife: livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, South India. *Environmental Management* 31:466–475.
- Meriggi, A., and S. Lovari. 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33:1561–1571.
- Mizutani, F. 1993. Home range of leopards and their impact on livestock on Kenyan ranches. *Symposium of The Zoological Society of London* 65: 425–439.

- Oakleaf, J. K., C. Mack, and D. L. Murray. 2003. Effects of wolves on livestock calf survival and movements in central Idaho. *Journal of Wildlife Management* 67:299–306.
- Patterson, B. D., S. M. Kasiki, E. Selembo, and R. W. Kays. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119:507–516.
- Polisar, J., I. Maxit, D. Scognamillo, L. Farrel, M. E. Sunquist, and J. F. Eisenberg. 2003. Jaguars, pumas, their prey base and cattle ranching: ecological interpretations of a management problem. *Biological Conservation* 109:297–310.
- Quigley, H. 1987. Ecology and conservation of the jaguar in the Pantanal region, Mato Grosso do Sul, Brazil. Dissertation, University of Idaho, Moscow, USA.
- Quigley, H., and P. G. Crawshaw, Jr. 1992. A conservation plan for the jaguar (*Panthera onca*) in the Pantanal region of Brazil. *Biological Conservation* 61:149–157.
- Rabinowitz, A. R., and B. G. Nottingham. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology* 210:149–159.
- Roloff, G. J., J. J. Millsaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for rocky mountain elk. *Journal of Wildlife Management* 65:889–914.
- Samuel, M. D., and M. R. Fuller. 1996. Wildlife telemetry. Pages 370–418 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. Fifth edition, revised. The Wildlife Society, Bethesda, Maryland, USA.
- Selvin, S. 1995. *Practical biostatistical methods*. Duxbury Press, Belmont, California, USA.
- Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology* 68:116–125.
- Treves, A., and K. U. Karanth. 2003. Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491–1499.
- Weber, W., and A. Rabinowitz. 1996. A global perspective on large carnivore conservation. *Conservation Biology* 10:1046–1054.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Woodroffe, R. 2001. Strategies for carnivore conservation: lessons from contemporary extinctions. Pages 282–312 in J. Gittleman, K. Funk, D. Macdonald, and R. Wayne, editors. *Carnivore conservation, conservation biology series 5*. Cambridge University Press, Cambridge, United Kingdom.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794–800.
- Zar, J. Z. 1999. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.

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