Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock

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Abstract

Most large carnivore species are in global decline. Conflicts with people, particularly over depredation on small and large livestock, is one of the major causes of this decline. Along tropical deforestation frontiers, large felids often shift from natural to livestock prey because of their increased proximity to human agriculture, thus increasing the likelihood of conflicts with humans. On the basis of data from 236 cattle ranches, we describe levels of depredation by jaguars *Panthera onca* and pumas *Puma concolor* on bovine herd stocks and examine the effects of both landscape structure and cattle management on the spatial patterns and levels of predation in a highly fragmented forest landscape of southern Brazilian Amazonia. Generalized linear models showed that landscape variables, including proportion of forest area remaining and distance to the nearest riparian forest corridor, were key positive and negative determinants of predation events, respectively. We detected clear peaks of depredation during the peak calving period at the end of the dry season. Bovine herd size and proportion of forest area had positive effects on predation rates in 60 cattle ranches investigated in more detail. On the other hand, distance from the nearest riparian forest corridor was negatively correlated with the number of cattle predated. The mean proportion of cattle lost to large felids in 24 months for the region varied according to the herd class size (<500: 0.82%; 500–1500: 1.24%; >1500: 0.26%) but was never greater than 1.24%. The highest annual monetary costs were detected in large cattle ranches (>1500 head of cattle), reaching US$ 885.40. Patterns of depredation can be explained by a combination of landscape and livestock management variables such as proportion of forest area, distance to the nearest riparian corridor, annual calving peak and bovine herd size.

Introduction

Carnivores often limit the number of their prey, thereby altering the structure and function of entire ecosystems (Schaller, 1972; Terborgh *et al*., 2002; Treves & Karanth, 2003). Moreover, species with large spatial requirements, such as top predators, play indispensable roles in the long-term maintenance of diversity (Terborgh, 1992). As a result, socio-economically viable options that ensure the persistence of carnivore populations is of central concern to conservation biologists interested in top-down regulation of natural ecosystems (Gittleman *et al*., 2001). In this context, human–carnivore conflicts pose an urgent challenge to carnivore conservation, especially in recent deforestation frontiers where the requirements of carnivore populations are often at odds with those of human activities.

Most large carnivore species are experiencing global declines driven almost entirely by human activities and/or conflict with humans. African lion *Panthera leo*, spotted hyena *Crocuta crocuta*, tiger *Panthera tigris*, African wild dog *Lycaon pictus*, Florida panther *Puma concolor coryi* and gray wolf *Canis lupus* had drastic reductions in their original geographic ranges, being largely restricted to reserves or protected areas (Fergus, 1991; Mizutami, 1999; Rasmussen, 1999; Seidensticker, Christie & Jackson, 1999; Smith, Brewster & Bangs, 1999).

Human–carnivore conflicts arise for several reasons. The large home ranges of carnivores often draw them into recurrent competition with humans, particularly in areas associated with extensive livestock management. Indeed, many large carnivore species are specialized on either natural or domesticated ungulate prey, and some individuals seek and readily kill large livestock when opportunities arise (Meriggi & Lovari, 1996; Karanth, Sunquist & Chinnappa, 1999; Polisar *et al*., 2003).

Large felids have been brought into increasing proximity and conflict with humans by the rapid conversion and fragmentation of their natural habitats. Attacks on livestock in deforestation frontiers are occurring more frequently (Crawshaw, 2003) as carnivores respond to these problems by expanding their diets to include livestock (Woodroffe, 2001). Neotropical cats, mostly jaguars *Panthera onca*, have been reported to kill livestock throughout South and Central America where they co-occur in close proximity (Schaller & Crawshaw, 1980; Mondolfi & Hoogesteijn, 1986; Rabinowitz, 1986; Quigley & Crawshaw, 1992; Crawshaw, 1995; Sáenz & Carrilo, 2002; Conforti & de Azevedo, 2003; Polisar *et al*., 2003). Pumas *Puma concolor*, are also blamed for monetary losses due to depredation on livestock (Yáñez *et al*., 1986; Iriarte, Johnson & Franklin, 1991; Cunningham *et al*., 1995; Mazzolli, Graipel & Dunstone, 2002; Conforti & de Azevedo, 2003; Polisar *et al*., 2003).

Although the threats of habitat loss and fragmentation are severe, one of the most important causes of mortality in adult carnivores is hostility from humans (Woodroffe & Ginsberg, 1998), and this takes place in both protected and unprotected areas. A number of carnivore species are vulnerable to deliberate persecution, firearm culling or poisoning, accidental deaths from roadkills and other unintended sources of mortality. A summary of several studies estimated that the greatest proportion of adult mortality in mountain lions (75%) resulted from conflicts with humans (Weaver, Paquet & Ruggiero, 1996).

Faced with these issues, the development of effective conservation strategies for large carnivores depends on resolving conflicts between people and predators. The success of any strategy will depend on an ability to reduce carnivore impacts on human lives and livelihood to a level that people will accept, without reducing predator populations to unviable levels (Woodroffe & Frank, 2005). As a starting point, there is a need to determine whether there are regions with high levels of depredation, the habitat configuration, attributes and other characteristics of areas with higher numbers of attacks, and the attitudes of ranchers and other stakeholders towards predators.

In this study, we describe levels of depredation by jaguars *P. onca* and pumas *P. concolor* on bovine livestock based on a large number of cattle ranches in a region of southern Amazonia where we lack any knowledge on the status of jaguar populations (Sanderson *et al*., 2002). This study is unusual in its cross-scale approach in that it examines how the spatial variation in the probability of felid attacks is affected by both landscape-wide and local variables. The study area has a livestock population including over 1.69 million bovine cattle (IBGE, 2004) and ranches suffer frequent attacks by large felids. The usual retaliation response of ranchers to felid attacks is lethal control through direct persecution by professional jaguar/puma hunters wielding firearms and assisted by a pack of hounds. Hence, we assessed the depredation levels in a deforestation frontier and the landscape and management variables influencing these rates.

Study area and methods

This study was conducted in the region of Alta Floresta, a prosperous frontier town located in northern Mato Grosso, and one of the most important agro-pastoral municipal districts of the entire Brazilian Amazon (09°53′S, 56°28′W; Fig. 1). A Landsat time series shows that this once entirely

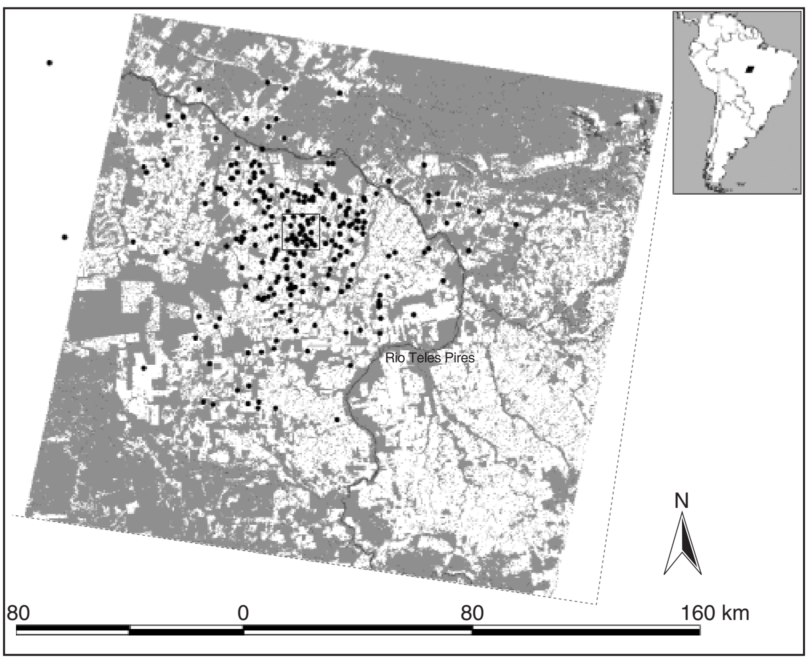

Figure 1 Location of the southern Amazonian study region of Alta Floresta, northern Mato Grosso, Brazil, showing the 236 ranchers surveyed. Grey and white areas represent forest and non-forest cover, respectively, on either bank of the Teles Pires river. The town of Alta Floresta is located at the centre of the square.

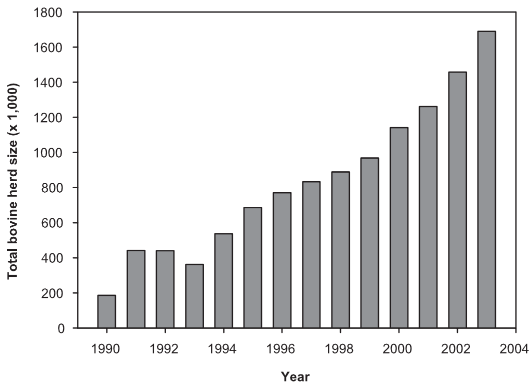

Figure 2 Total bovine herd size in the Alta Floresta region (1990–2003).

forested region has been subjected to very high deforestation rates since the early 1980s. As of 2003, only 37% of the pre-frontier forest cover of 1975 remained in the Alta Floresta region south of the Teles Pires river. The conversion of primary forest by cattle ranchers into a dominant matrix of managed pastures resulted in a hyper-fragmented landscape, where remaining forest fragments continue to be disturbed by logging, wildfires and hunting (Michalski & Peres, 2005; Peres & Michalski, 2006). The total bovine herd in the Alta Floresta region of 54 668 430 km^2 (including Alta Floresta, Apiacás, Carlinda, Nova Bandeirantes, Nova Monte Verde and Paranaíta) has increased linearly from 1990 to 2003 ($r^2 = 0.952$, $P < 0.001$; Fig. 2) with a mean annual growth of 115 694 over this period. The total herd size in 2003 was 1 690 007, following more recent increases of 196 075 cattle from 2001 to 2002, and 232 805 cattle from 2002 to 2003 (IBGE, 2004). The most recent estimate of the total number of cattle for the town of Alta Floresta alone (657 834 in 2003) indicates a ratio of 17 cattle per human inhabitant (IBGE, 2004). The Alta Floresta land title distribution and colonization programme, which dates from the late 1970s, assured that a wide range of land property sizes were available for sampling. These included small cattle ranchers (mean ± SD property size = 526.8 ± 960.0 ha, range = 16.9–4356.0 ha, $n = 19$), medium ranchers (mean ± SD = 1772.5 ± 2689.0 ha, range = 38.7–12 000 ha, $n = 22$) and large ranchers (mean ± SD = 7678.5 ± 6580.9 ha, range = 2300–26 620 ha, $n = 21$). The land tenure system was designed so that small properties were usually nearer the town whereas large properties were further away. All 236 properties included in the study were active cattle ranches located within a 110 km radius of the town of Alta Floresta. These were accessible via paved or unpaved roads, the Teles Pires river, or both. Locations of all ranches sampled were plotted onto a 2004 Landsat ETM+ image using global positioning system coordinates obtained *in situ*.

As a key prerequisite, all candidate sampling sites that had been visited were associated with at least one local informant, usually a long-term resident, cattle manager or landowner, who was (1) willing to be interviewed, (2) had local information regarding the details of cattle management practices, (3) worked within the ranch with the cattle herd and (4) had been living in the cattle ranch or close to it for at least 2 years (mean ± SD = 12.4 ± 8.0 years; $n = 205$ respondents).

From June to September 2001, May to July 2002 and October 2003 to December 2004, we conducted 236 interviews in different properties (Fig. 1). Property characteristics, including bovine herd size, livestock management practices, history of carnivore depredation in the previous 24 months, levels of tolerance toward large cats and levels of receptivity of non-lethal methods that could be used to control depredation levels, were recorded. In all cases, interviews were aided by colour plates in field guides, photographs of the two large felid species, and photographs of tracks of each species and of bovine carcasses resulting from attacks in which the species identity of the predator was known (Pitman *et al.*, 2002).

The predation events reported here were pooled together for pumas and jaguars because the carcass remains resulting from kills by these two large felids could not always be unambiguously distinguished *in situ* by the interviewees.

All estimates of depredation reported here were related to a 24-month period before the interview date. Our interview-based sampling protocol was independently validated by monitoring 23 forest sites (9.7% of all ranches interviewed) in relation to the presence and abundance of large felids and occurrence of predation events within these sites. We monitored each of these sites continuously for 2–4 months using both line-transect censuses and a photo-trapping protocol (F. Michalski & C. A. Peres, unpubl. data) and subsequently repeated our interviews 1 year thereafter. On the basis of the number of predation events reported at these 23 sites, we conclude that our interview data are reliable: respondents never falsely reported the presence of large felids and the number of predation events reported were similar to those obtained *in situ*. We also have high-levels of confidence on the interview data based on our long-term familiarity with local landowners during at least 4 years of fieldwork (F. M. and C. A. P.) and over 10 years of veterinary assistance and research activity in this region (A. F.).

A suite of landscape variables were extracted from the Landsat (ETM + 227/067 – 12 June 2004) image using ArcView 3.2. Following a two-stage unsupervised classification of this image, it was possible to unambiguously resolve eight mutually exclusive land cover classes including close-canopy forest, open-canopy forest, lightly disturbed forest, highly disturbed forest, managed and unmanaged pasture, bare ground and open water. The image was georeferenced using a 1996 satellite image as a base with an accuracy of 0.33 pixels, each with a spatial resolution of 15 m.

For each property where interviews were conducted, we measured the straight-line distance to Alta Floresta (D_{AF}), defined as the distance from the geometric centre of the town to the point where we conducted the interview (usually the central open area of the property).

The age of the ranch (AGE) was obtained both directly from the interview data and indirectly on the basis of a biannual time-series analysis with ETM Landsat images dating from 1984 to 2004. This was defined as the number of years since the surrounding open-habitat matrix was formed by rapid and extensive clearcutting of adjacent primary forest areas.

The proportion of forest pixels (FOR) was used to quantify forest 'quantity' and was calculated using two different approaches. We initially calculated the proportions of pixels of closed-canopy and open-canopy forest occurring within 10 concentric area rings, with a constant width of 10 km, from the geometric centre of the town of Alta Floresta. Secondly, we calculated the proportions of closed-canopy and open-canopy forest areas contained within a circular buffer of 5 km centred at the locations where ranch interviews were conducted.

The monthly peak frequency of cattle attacks ($n = 184$ reported months) was obtained as a summary of all interviewees that were able to provide specific information on months with pulses of depredation higher than the background monthly average observed throughout the year in their ranches. Monthly calving peaks are defined as a summary variable for those ranches that specifically reported data on calving frequency over time. In Alta Floresta, cattle ranches often manipulate the timing of cattle reproductive activity through either deliberate exposure of receptive cows to uncastrated bulls or artificial insemination.

As an independent measure of patch connectivity, we conducted a cost surface (CS) analysis using ArcView 3.2 following the methods described in Michalski & Peres (2005). The CS considers a diffusion coefficient described by the pixel-specific habitat resistance to large felid dispersal from the nearest source areas of forest. For a number of reasons, we assumed that these were located in the large blocks of continuous forest to the north and south of Alta Floresta, and assigned the lowest CS weight (1) to areas of either closed-canopy or open-canopy forest, followed by lightly disturbed forest and highly disturbed forest (3) and unmanaged scrubby pastures (5). The highest CS weight (20) was assigned to non-forest pixels (water, managed pasture and bare ground) that are rarely traversed by jaguars and pumas. We then calculated the overall CS value based on a Euclidean distance function. However, the CSs were based on the shortest non-linear cost distance (or accumulated travel cost) from each cell to the nearest source cell, rather than the linear distance between a patch and a source. CSs thus took into account both the length of connecting pixels available for animal movement along the path of least resistance and the habitat quality of those pixels for jaguars and pumas. Small CS values represent low dispersal costs from source areas to well-connected patches, usually through suitable riparian forest corridors, and high values represent high dispersal costs to poorly connected or unconnected patches, usually through non-forest areas.

Cattle herd size ($\log_{10}$) is defined as a measure of the total bovine herd stock obtained from interview data. The presence of maternity pasture is a binary variable obtained through interview and describes an area to which pregnant cows were translocated to give birth. These protected maternity areas were closely monitored by ranch staff, and were usually near the ranch headquarters or main house and far from the nearest forest edge.

Staffing ratio (Sqrt) is a measure obtained from the interview data and defined as the number of cattle managers and ranch hands employed in a given property per 100 cattle.

Distance to riparian corridor (Sqrt) is a landscape metric extracted in ArcView 3.2 from the classified 2004 Landsat ETM + image, and described as the straight-line distance from interview sites (usually a central point in the ranch) to the nearest riparian corridor linking forest patch areas >1000 ha.

We controlled for high levels of inter-dependence between landscape and ranch management variables by performing a Pearson's correlation matrix, and excluding those variables that were intercorrelated by $r > 0.85$. In order to investigate the local likelihood of predation events, we performed generalized linear models (GLMs) with a LOGIT link function by assuming a binomial error distribution in the response variable and including five variables describing the landscape structure of each ranch (distance to Alta Floresta, age of the ranch, proportion of forest pixels within a 5 km buffer, CS value and distance to the nearest riparian corridor), which resulted in eight different models. After testing all main effects and all possible interactions among the variables, we used a supervised stepwise procedure to select the most parsimonious minimum model based on Akaike's information criterion (AIC). We used stepwise backward regression models with elimination at $P = 0.15$ to retain the best predictors of bovine depredation rates. The Durbin–Watson D statistic, eigenvalues and analysis of variance were used to assess the goodness of fit of the multiple regression models.

We further examined the proportion of interviews reporting predation (binary variable) during the 2 years before interviews in relation to the proportion (%) of closed-canopy and open-canopy forest within each of the 10 concentric rings from the geometric centre of the town of Alta Floresta. The effects of monthly rainfall and monthly calving frequency on monthly peaks of cattle attacks were assessed using correlation analysis.

The monetary costs reported by interviewees ($n = 62$) in terms of cattle revenues lost was calculated according to three classes of herd size and in relation to the proportion of estimated total assets in terms of the cattle stock. The estimated cost in US dollars (exchange rate date of 8 September 2005) is a minimum conservative value considering mean transaction prices reported by interviewees in the region for the local market value of young calves (US$ 128.23) because this was the most frequent age class of cattle attacked by large cats.

Results

Occurrence of predation events

Although the predation events reported here were pooled together for pumas and jaguars, we estimate that 72% of all

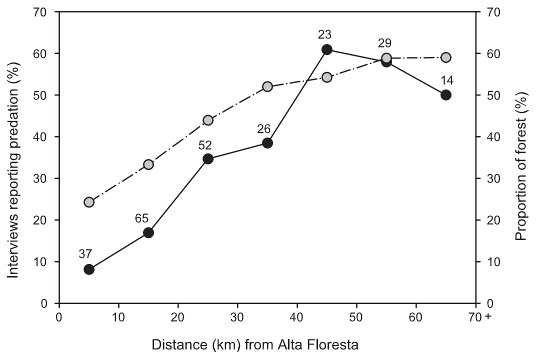

Figure 3 Interviews reporting predation (%) on bovine herd (●) and percentage of forest (◎) remaining within each 10-km wide variable-area concentric ring from the geometric centre of the town of Alta Floresta (see text). Number of ranches surveyed are indicated above ●.

Table 1 Summary of the 'best model' of probability of predation events on bovine livestock at 234 Amazonian cattle ranches based on GLMs with AIC model selection

		Landscape variables[b]			
	Percentage[a]	CORR	FOR	D_{AF}	CORR:D_{AF}
Predation	30.8	−4.240**	0.035*	−0.388	0.533*
		(1.451)	(0.016)	(0.342)	(0.250)

Standard errors are shown in parentheses.
[a]Predation rate in terms of the percentage of all interviewed ranches (n=234) reporting problems.
[b]Binomial GLM coefficients are indicated below each independent variable retained in the best model (CORR, Sqrt distance to the nearest riparian corridor; FOR, percentage of forest pixels within a 5 km buffer; D_{AF}, Sqrt distance from Alta Floresta; CORR:D_{AF}, only significant interaction obtained from all possible interactions). Significant values: *$P<0.05$; **$P<0.01$.
GLMs, generalized linear models; AIC, Akaike's information criterion.

predation events were caused by jaguars on the basis of our own personal observations and a sub-sample of interviews ($n = 47$) where we were able to establish unequivocally the predator species identity. A small sub-sample of interviewees ($n = 4$) was unable to quantify the exact number of animals preyed by each felid species, but they concluded that the majority of bovine kills were associated with jaguars.

We initially examined the trends in predation occurrence, treated as a binary variable, across all interviews ($n = 236$). The proportion of properties reporting at least one predation event by large cats on their bovine herds increased with both the distance from Alta Floresta and the proportion of forest area (%) remaining in each concentric zone. The proportion of interviews reporting predation and the proportion of remnant forest were therefore greater in areas farther from the town centre (Fig. 3).

GLMs were performed to tease apart the relative importance of different landscape variables on the occurrence of predation events. The final AIC model selection indicates that the probablity of predation events was markedly higher in properties closer to riparian corridors linking areas larger than 1000 ha and containing a higher proportion of closed- and open-canopy forest areas within a 5 km buffer around the interview site. The only significant interaction between any given landscape variable was that between distance to the nearest riparian corridor and distance to Alta Floresta, suggesting that the effects of proximity to corridors increased in less forested areas (Table 1).

Monthly variation in calving and predation events

Peaks in felid attacks on cattle and predation events, as reported by ranchers in the Alta Floresta region, were concentrated during certain months of the year ($n = 184$ reported months). Peak predation was temporally correlated with the monthly peaks ($n = 101$ reported months) in calving activity at different times of the year for a smaller set of properties for which these data on calving were also available ($r_s = 0.770$, $P<0.01$, $n = 12$ months). The monthly frequency of reported calving peaks was also negatively correlated with the mean monthly rainfall in this region ($r_s = -0.763$, $P<0.01$, $n = 12$ months; Fig. 4).

Landscape and management variables affecting depredation rates

We performed a backward multiple regression model incorporating five landscape and ranch variables (bovine herd size, proportion of forest area, presence of maternity pastures, distance to riparian corridors and staffing ratio) in order to tease apart the relative importance of these variables on the number of predation events reported across different ranches ($n = 60$) during the 24 months before the interviews. Predation rates were positively affected by bovine herd size and the proportion of forest area within a 5 km buffer, and negatively affected by distance from the nearest riparian corridor linking large (≥1000 ha) forest patches (Table 2).

Revenue lost in the Alta Floresta region

The proportion of cattle lost to large cats in each ranch property size class was measured according to the total bovine herd size and calculated on the basis of data obtained from 62 properties. The US$ revenue lost was calculated according to the mean price of calves in the region reported during the interviews (Table 3). We believe that this approach is the most realistic representation of this region given that the mean age class distribution of felid attacks (in 54 properties for which the mean age of the victims was reported) shows that most cattle killed (66.7%) were very young calves (0–5 months), followed by calves aged 6–10 months (20.4%) and 11–15 months (9.3%), and only rarely cattle older than 15 months (3.7%).

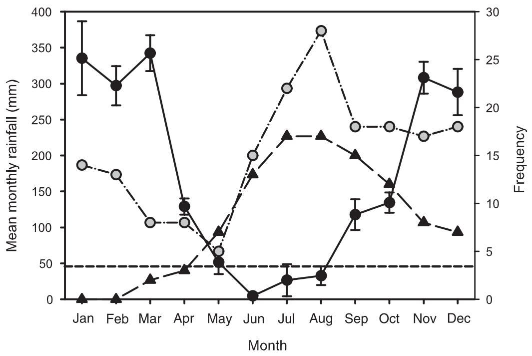

Figure 4 Mean (±SE) monthly rainfall (1998–2004) (●) (source: CEPLAC/SUPOR/SEPES), reported peaks in cattle attacks by large felids (n=184) (◎) and monthly calving frequency (n=101) (▲) in the Alta Floresta region.

The percentage of interviews reporting predation increased with the increase in herd size (<500 cattle: 57.9%; 500–1500: 72.3%; >1500: 85.7%), but the mean proportion of the total cattle herd lost (%) was higher in medium-sized cattle ranches (500–1500 cattle; 1.24%), followed by small ranches (<500 cattle; 0.82%), and finally the large cattle ranches (>1500 cattle; 0.26%). According to the information obtained through our survey, the highest monetary costs were detected in large cattle ranches reaching US$ 1770.80 in a 2-year period (Table 3).

Retaliation measures and acceptance of non-lethal control methods

According to a range of formal and anecdotal accounts of jaguar and puma mortality obtained over the year (2003–2004), an estimate of 110–150 animals are killed annually through direct persecution by professional jaguar/puma hunters, ranch staff or poisoned carcasses. However, according to 62 interviews for which questions on control methods were answered, 53.2% of the landowners were interested in implementing non-lethal methods to control depredation levels in their ranches. Only 32.3% of the landowners responded that they were not interested in any non-lethal method to control depredation and 14.5% did not know or were undecided.

Discussion

To our knowledge this study is based on the largest number of sites where the occurrence of large felid predation has been quantified in any tropical forest region across a wide range of property sizes, bovine herd sizes, management practices and landscape context. Our study indicates that the proximity of large felids to agro-pastoral land uses in tropical deforestation frontiers increases the rates of livestock depredation and human–wildlife conflicts. In general, however, the number of ranches succumbing to at least one predation attack from large felids was relatively small (30.8%, n = 234). Our analysis also revealed a strong trend in the spatial variation of predation events in that a greater proportion of kills took place in ranches that are still embedded in large forest areas or located at greater distances from the geometric centre of the main market town, or both. The same pattern has also been observed in southern Brazil, where areas closer to conservation units and farther from urban centres show a clear correlation between jaguar attacks and proximity to forest borders (M. R. P. L. Pitman, pers. comm.). It is not surprising, therefore, that the distribution of interviews reporting more frequent predation events were located in areas distant from the town centre, especially because the distribution of undisturbed forest areas reflects the same radial pattern, with large forest areas still remaining to the north and south of the Landsat image.

Geographic ranges of the world's large carnivores have experienced major contractions, many species often becoming confined to areas that are either sparsely settled by humans or well protected (Linnell, Swenson & Andersen, 2001; Woodroffe, 2001). Moreover, jaguars, the species that most frequently preyed on cattle in the Alta Floresta region (72%, n = 47 interviews), require habitats that have a dense forest cover, access to water and a sufficient natural prey base (Hoogesteijn & Mondolfi, 1992). In Alta Floresta this occurs only in fairly large remnants of relatively undisturbed forest (F. Michalski & C. A. Peres, unpubl. data).

Our study reveals that there is a clear seasonal variation in depredation peaks, which is strongly correlated with the annual calving peak, both peaks co-occurring at the end of the dry season. In the Venezuelan Llanos, there is also a temporal correlation between depredation and calving peaks (Scognamillo *et al*., 2002; Polisar *et al*., 2003). As observed by Butler (2000) and Kays & Patterson (2002), during the dry season in Africa, lions increase predation rates on livestock close to the few water sources remaining, where they can find and kill prey converging on water, limited food sources and vegetative cover. In our study, there was no lack of vegetative cover and no evidence of natural prey populations becoming limited during the dry season, but perennial bodies of water such as forest streams likely attracted a larger number of livestock which may have facilitated higher rates of predation attacks closer to riparian corridors, particularly in ranches lacking proper herd management and infrastructure facilities, including permanent sources of drinking water for cattle all year round.

Landscape variables were key determinants of the local predation probability in the Alta Floresta region. Distance to the nearest riparian corridor, proportion of forest area within a 5 km buffer of the ranch headquarters, and interaction between distance to the corridor and distance to Alta Floresta were important predictors of the occurrence of predation events. On the other hand, age of the ranch, CS connectivity values and distance to Alta Floresta *per se* were not significant predictors of predation events, probably because we pooled together the jaguar and puma depredation data. These species are known to differ in their habitat preferences. Pumas are more capable of moving across less

Table 2 Stepwise multiple regression model showing the effects of landscape and ranch management variables on the number of predation events reported by local interviewees at 60 ranches for a period of 24 months

Effect	Coefficient	SE	Standard coefficient	Tolerance	*t*	*P*
$\log_{10}$ herd size	0.279	0.086	0.362	0.998	3.254	0.002
Forest area (%) within a 5 km buffer	0.010	0.005	0.250	0.864	2.096	0.041
Distance to riparian corridor (Sqrt)	−0.261	0.130	−0.241	0.863	−2.013	0.049

Variables listed here are those retained by the model using a backward elimination procedure at $P = 0.15$. Variables excluded from the models are not listed.

Table 3 Summary of monetary costs incurred at 62 ranches during a 24-month period according to three herd size classes in the Alta Floresta region

Herd class	*n*	Property size (ha) (mean ± SD)	Number of heads of cattle (mean ± SD)	% Pred[a]	Per cent lost[b] (mean ± SD)	Revenue lost (US$)
<500	19	526.8 ± 960.0	269.3 ± 159.8	57.9	0.82 ± 1.12	290.2 ± 327.9
500–1500	22	1772.5 ± 2689.0	843.7 ± 351.5	72.3	1.24 ± 1.68	1393.0 ± 2491.9
>1500	21	7678.5 ± 6580.9	6661.2 ± 4064.0	85.7	0.26 ± 0.40	1770.8 ± 2948.9

n indicates the number of ranches surveyed in each size class.
[a]Pred, percentage of interviews reporting predation.
[b]Mean (± SD) proportion of the total cattle herd lost (%).

forested areas than jaguars. In a long-term study in the Cerrado and Pantanal regions of Brazil, pumas showed high rates of the use of Cerrado and scrub habitats, being capable of ranging across highly disturbed areas, such as pasture and croplands (Silveira, 2004). In contrast, jaguars did not use any of these highly disturbed habitats in the same study area. Likewise, puma depredation in the Venezuelan Llanos appears to be less limited by proximity to forest than jaguar depredation (Polisar *et al.*, 2003). Thus, even older, more established ranches surrounded by a greater proportion of open areas and those farther from source areas could also have been visited by pumas attracted by cattle. Jaguars select habitat types non-randomly in comparison with availability in the Morro do Diabo State Park. In this study, radio-tracked jaguars strongly selected against open pasture (Cullen *et al.*, 2005). In our study, only distance from the town of Alta Floresta failed to explain the probability of predation events, unless the interactions with distance to riparian corridors and proportion of forest cover are taken into account.

In terms of rates of predation events, herd size and the proportion of remaining forest area were positively correlated with the number of animals killed. González (1995) also noted that the level of depredation caused by jaguars was positively related with herd size and forest cover. Also, our study shows that the distance to riparian corridors was negatively correlated with the probability of predation and the number of cattle killed, showing that the proximity of corridors linking large forest areas can increase ranch depredation rates.

Maternity pasture and staffing ratio were excluded from the model possibly because of the following reasons: (1) all ranches containing maternity pastures protect the calves for only 30–35 days after birth; (2) staffing ratio was negatively related with depredation rates, but because ranchers usually hire more workers in larger ranches, the herd size effect predation rates was stronger than that of the staffing ratio. Young calves (0–5 months) accounted for over two-thirds of all kills and were more susceptible to large felid attacks than any other age class. The premature release of calves from maternity pastures apparently failed to reduce depredation rates. Bulls, steers and cows intimidate the predators because they are usually more aggressive and better armed (with horns) than the younger animals (Sunquist & Sunquist, 1989). In addition, calves are characterized by their extreme curiosity and limited defensive behaviour, which leave them more exposed to predation. In the Llanos of Venezuela, young animals also comprised the bulk of jaguar predation on livestock (Hoogesteijn, Hoogesteijn & Mondolfi, 1993). This was confirmed in more recent studies in the Venezuelan Llanos (Polisar *et al.*, 2003) and in the Brazilian Pantanal (Boulhosa, 2000; Dalponte, 2002).

We found a low proportional loss in ranch revenues sacrificed to herd losses in a 24-month period. The mean percentage of cattle lost varied from 0.82% in small cattle ranches to 1.24% in mid-sized ranches and 0.26% in large ranches. Jackson *et al.* (1994) concluded that livestock losses to cats are generally low and less than 1–3% of total stock per year. In New Mexico, puma predation affects less than 1% of the ranches (Evans, 1983). Hoogesteijn *et al.* (1993) compared cattle mortality to predators on three Venezuelan ranches; in one of these ranches, they found that losses to large cat predation accounted for only 6% of all losses or deaths due to any other cause. On another ranch, cat predation accounted for 31% of calves lost. In southern Brazil, estimates of annual stock losses to pumas represent only 0.27% or US$ 1890 in a 2-year period of study (Mazzolli *et al.*, 2002). A study with 42 rural properties surrounding Iguaçú National Park in southern Brazil revealed that only 11 properties (28.2%) reported predation incidents, but the total annual financial loss considering all properties did not exceed US$ 3000, which represented only 0.4% of the total livestock holdings (Conforti & de Azevedo, 2003). In the northern Brazilian Pantanal, the total economic loss in cattle herds due to jaguar depredation represented only 0.3% (US$ 12 913.96 in a 5-year period) from the total economic value of cattle herds from all ranches surveyed (US$ 4 317 663.00) (Boulhosa, 2000). Another jaguar predation study at two sites in the same region of the Brazilian Pantanal reported an annual livestock loss due to jaguar predation of US$ 28 500, representing 0.84% of the total livestock holdings (Dalponte, 2002).

Although the mean proportion of cattle herds lost did not exceed 1.24% for 24 months in medium-sized ranches (500–1500 heads of cattle), the Alta Floresta region essentially functions as a population sink for large felids because of the number of jaguars and pumas killed by landowners (or their sub-contracted bounty hunters). During a 1-year period (2002–2003) in the Alta Floresta region, a minimum of 75–90 large felids were killed within an area that spans some 34 200 km^2 (Michalski & Peres, 2005). During the following year (2003–2004) this number increased to a minimum of 110–150 jaguars and pumas killed. This amounts to a mean annual rate of 0.31 large cats killed per 100 km^2, or 0.56 large cats killed per 100 km^2 of forest (because only 55.8% of this region is forested), which must be a significant fraction of the standing cat populations in the Alta Floresta region. These estimates are highly conservative and included quantitative reports independently sourced from five professional jaguar hunters, and the main photography shop in the town of Alta Floresta, which often develops colour photos of proud jaguar/puma hunters (or ranch hands) exhibiting their trophies.

In conclusion, our study indicates that stable coexistence of people and large felids in typical tropical deforestation frontiers such as Alta Floresta is a challenge for conservation biologists because of the severity of carnivore–human conflicts. However, we suggest that future research projects and support programmes among ranchers, especially those in medium-sized properties (500–1500 heads) which showed higher relative losses, should be implemented to offer technical advice on cattle management to minimize predation events. This study highlights that over half the interviewees would be interested in implementing non-lethal control methods in their ranches to reduce depredation levels. These non-lethal methods can include the use of electric fences, maternity pastures in areas closer to the main pasture compartments of the ranch containing young calves protected for at least 3 months, a herd management policy that routinely places older animals in areas closer to the forest and younger animals closer to the ranch headquarters, and provision of drinking water to prevent cattle from dry season excursions to forest streams along riparian corridors. Through these actions, an effective and positive contribution can be made to the conservation of large neotropical felids.

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