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Habitat correlates of jaguar kill-sites of cattle in northeastern Sonora, Mexico

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Abstract: Predation on cattle by the endangered jaguar (*Panthera onca*) can be a serious ecological and economic conflict. We investigated habitat characteristics of kill sites of cattle in Sonora, Mexico, from 1999 to 2004 to see whether habitat management or cattle distribution could be used as effective nonlethal methods to limit predation. Kill-sites were positively associated with oak, semitropical thornscrub, and xeric thornscrub vegetation types, whereas they were negatively associated with upland mesquite. Sites of cattle kills were also positively associated with proximity to permanent water sources and roads. A model including these relationships fit kill locations well (AUC = 0.933) and correctly classified 93% of all kill-site locations. Because kill-sites were associated with specific habitat attributes, management practices that alter cattle distribution, such as placement of permanent water sources in uplands, herding, and fencing riparian areas characterized by frequent depredations, can be used to minimize co-occurrence of jaguars and cattle and, thus, potentially limit predation without illegal killing of jaguars. These practices could also lead to more uniform use of pastures and, consequently, higher stocking rates, resulting in increased profitability to landowners. Managing habitat attributes that predispose cattle to predation may provide a viable alternative for maintaining both livestock enterprises and a large endangered carnivore in areas of conflict.

Key words: cattle, habitat, human–wildlife conflicts, jaguar, Mexico, predation, Sonora

Jaguars (*Panthera onca*) can be serious predators of livestock (Rabinowitz 1986, Rosas-Rosas and Lopez-Soto 2002, Rosas-Rosas et al. 2008), and cattle ranching is the main rural land use in northeastern Sonora, Mexico, where the northernmost jaguar population in North America occurs (Rosas-Rosas et al. 2008). Cattle ranching is profitable only for some of the largest landowners in Sonora (Rosas-Rosas et al. 2008). But, despite this tenuous profitability, the inherited tradition of cattle ranching is strong, and ranchers continue in livestock enterprises despite droughts, fluctuating beef markets, and predators. Because of tenuous profitability, however, jaguar predation on livestock can be an economic problem that is difficult to overcome, especially for smaller cattle operations (Rosas-Rosas et al. 2008).

Many factors can influence a jaguar's decision to prey on livestock, including its learned behavior, its injuries, lack of appropriate cattle management practices, scarcity of natural prey, weather, and tolerance of humans (Rabinowitz 1986, Crawshaw and Quigley 2002, Polisar et al. 2003, Rosas-Rosas et al. 2008). Although habitat characteristics are frequently recognized as a contributor to vulnerability of cattle to large felid predation (Polisar et al. 2003, Patterson et al. 2004, Azevedo and Murray 2007), they are seldom considered in predation management practices. However, increasing evidence demonstrates strong relationships between vulnerability to predation and specific habitat attributes for both livestock and wildlife. For example, proximity to forest cover has been implicated in predisposing cattle to jaguar predation in Brazil (Azevedo and Murray 2007) and to cougar (*Puma concolor*) predation in Venezuela (Polisar et al. 2003). Similarly, cattle losses to African lions (*Panthera leo*) were associated with tall, dense grass cover adjacent to permanent water sources (Patterson et al. 2004). Identification of habitat attributes that predispose livestock to predation allows for management of these features or livestock distribution to potentially decrease vulnerability, and thus for a habitat-based, nonlethal method of controlling predation.

Jaguars are endangered and protected in Mexico (SEMARNAT 2002). The northernmost breeding population of jaguars in the Americas inhabits the mountainous ranges of the Sierra Madre Occidental in northeastern Sonora, approximately 300 km south of the U.S. border. Illegal killing of jaguars because of livestock predation is the main threat to this population; >11 jaguars have been illegally killed in this area from 1999 to 2004 in response to between 45 and 134 claimed cattle depredations (Rosas-Rosas et al. 2008). Effective management of predation by jaguars on cattle is thus needed both to conserve jaguars in Mexico and to minimize cattle losses. Because habitat conditions often are easier to manage than are populations of endangered species, such as jaguars, understanding and identifying habitat correlates that predispose livestock to jaguar predation in northeastern Sonora is an important step in ameliorating predation conflicts. Our goals were to identify habitat and landscape features associated with successful predation sites of jaguars on cattle and to develop management recommendations that could minimize predation conflicts.

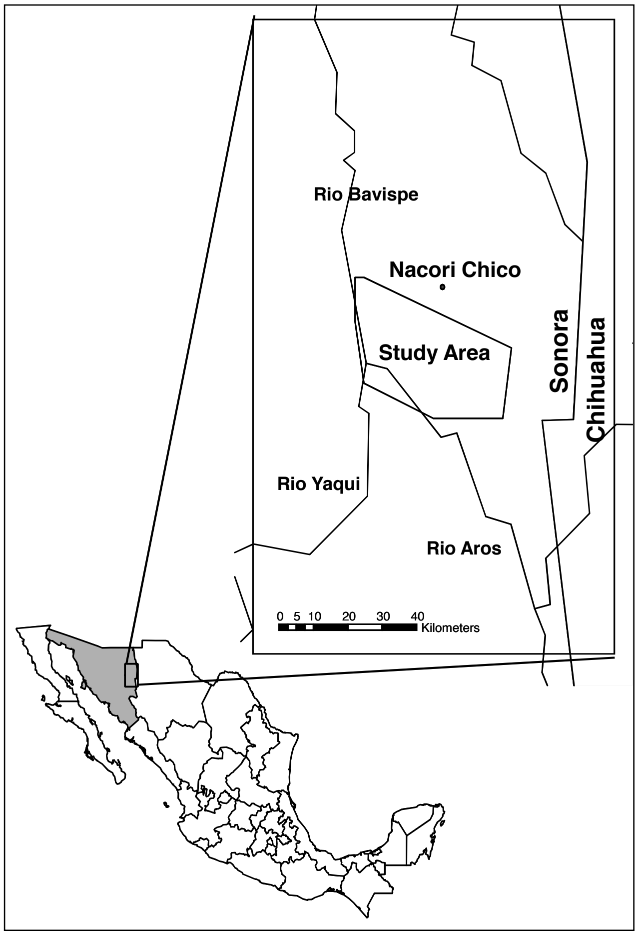

Figure 1. Location of study area in northeastern Sonora, Mexico.

Methods

Study area

Our study area encompassed approximately 400 km² in northeastern Sonora in the northern Sierra Madre Occidental, Mexico (Figure 1), and was located approximately 300 km south of the U.S. border. Topography was rocky and rugged , with several intermittent and perennial streams; elevations ranged from 500 to 1,500 m. Annual precipitation was about 400 mm in the valleys to 1,000 mm in higher elevations. There were 2 main seasons in the study area: a dry season (November to June) and a wet season (July to October). Monsoonal rains characterize the wet season, with scattered rains also present in winter (January to February).

The main vegetation community was semitropical thornscrub (56% of study area), which was comprised primarily of zamota (*Corsetia glandulosa*), mauto (*Lysiloma divaricata*), mesquite (*Prosopis juniflora*), torote (*Bursera* spp.), tarachique (*Dononaea viscosa*), palm trees (*Erythea roezlii*, *Sabal mexicana*), prickly pear (*Opuntia* spp.), palo blanco (*Piscidia mollis*), catclaw (*Mimosa* spp.), cholla (*Opuntia* spp.), organ pipe cactus (*Lemaireocereus thurberi*), and quelite (*Amaranthus palmeri*). Other common vegetation types included mesquite (12%); oak (*Quercus* spp.) forest (8%); xeric thornscrub (3%), which included mesquite, sotol (*Dasylirion wheeleri*), prickly pear, catclaw, cholla, and organ pipe cactus; and tropical deciduous forest (2%; Brown 1982), which included zamota (*Corsetia glandulosa*), mauto (*Lysiloma divaricata*), torote (*Bursera* spp.), tarachique (*Dononaea viscosa*), palm trees (*Erythea roezlii* and *Sabal mexicana*), and palo blanco (*Piscidia mollis*). Natural and induced pastures comprised 6% of the study area.

Eleven cattle ranches comprised our study area, and the total number of cattle within the study site averaged 2,815 (SE = 226) from 1999 to 2004. Ranches were primarily managed for calf production, with calves sold at about 6 months of age. Cattle management practices were similar among ranches and were dependent on rainfall, with cattle being rotated from upland pastures to areas with perennial water sources usually adjacent to perennial riparian areas during the dry season. During the wet season, all cattle freely ranged over upland pastures.

Jaguar kill-locations

We used ranch records and field surveys to assess production, survival, and causes of mortality of cattle calves from June 1999 through December 2004; all predation observed was on calves <12 months old. We conducted daily field surveys to locate calf mortalities throughout all calving areas in the study site. In addition, we located calf mortalities during track, scat, and camera-trapping surveys that were also conducted throughout the study area (Rosas-Rosas et al. 2008). Each year, we walked all trails, washes, roads, and other paths in areas where cattle were located daily during the primary calving period (mid-May through mid-August), and then approximately weekly throughout the remainder of the year. We also had ranch workers looking for dead calves and notifying us when they found a dead calf, so that we could investigate and confirm the cause of death. This approach allowed us to cover all areas being used by cattle and allowed detection of most mortalities. Prompt location of dead calves was crucial to determining the actual cause of death because scavengers quickly located carcasses and modified conditions around the carcass. We were able to locate 82% of predator kills the day following the kill, 10% within 2 days, and the rest (8%) after 3 days (Rosas-Rosas et al. 2008).

We classed mortalities as jaguar predation, cougar predation, abandonment of the calf by the mother following birth, abnormal parturition (the calf dying during or immediately after birth), malnutrition (cow did not nurse the calf sufficiently or did not have enough milk), predators other than jaguar or cougar, disease, and unknown (Rosas-Rosas et al. 2008). We necropsied all dead calves to determine if the animal died before it was fed on by jaguars (i.e., whether it was predated or simply scavenged) and recorded all clinical signs associated with each carcass, as well as the characteristics of the immediate area. Hemorrhaging and consequent dark discoloration in the skin and bones around canine punctures were used to differentiate actual predation from scavenging; if puncture marks and associated hemorrhage were not present, it was unlikely that the animal was alive when fed on or killed by a jaguar. We used predator sign (tracks and scrapes; Aranda 2000), body parts consumed, whether the kill was covered with debris, position of bite marks, presence and location of canine punctures, distance between canine punctures, and other general observations to differentiate between jaguar and cougar kills (Hoogesteijn 2001, Crawshaw and Quigley 2002, Rosas-Rosas et al. 2008).

Modeling kill-locations

We modeled habitat features associated with locations of cattle killed by jaguars using Maximum Entropy 3.1 (MaxEnt; Phillips et al. 2006) to identify habitat attributes associated with areas of increased vulnerability to predation in our study area. Maximum entropy is a machine learning response that utilizes only known occurrences (i.e., presence data, specifically location of kill-sites in our study) and compares environmental correlates at those occurrence sites to the same correlates at 10,000 random locations, rather than with inferred absences, such as those collected from transect-based sampling strategies. Because it uses only presence data, MaxEnt, both eliminates the need for pseudo-absence data, which can bias wildlife-habitat models (Gu and Swihart 2004), and provides a less biased alternative to other approaches that require the generation of known non-use areas (e.g., discriminant analysis, logistic regression, etc; Phillips et al. 2006, Baldwin and Bender 2008*a,b*). Consequently, maximum entropy modeling consistently outperforms other methods of modeling spatial distribution (Elith et al. 2006, Hernandez et al. 2006, Phillips et al. 2006), except possibly those utilizing multiple repeated visitations to the same sampling points that correct for imperfect detection of individuals (i.e., occupancy modeling; MacKenzie et al. 2006, Baldwin and Bender 2008*b*). However, because our presence data (kill-site locations) were not collected from random surveys throughout our study area, results could potentially be influenced by our nonrandom strategy of locating jaguar kills. We feel that such bias, if present, was likely minimal because we located virtually all cattle kills in our study area based on production data from landowners (Rosas-Rosas et al. 2008).

We modeled 6 variables shown or suspected to affect cattle habitat use (Hart et al. 1993, Holechek et al. 2004, Bailey 2005), including elevation, vegetation cover type, distance to roads, distance to permanent water sources (including perennial streams and rivers, springs, ponds, and permanent water developments), slope, and aspect. We used GIS coverages from Geographic Basic Digital Products-2003 (INEGI®, Mexican National Institute of Statistics and Geography) in ArcGIS 9.2 (ESRI, Redlands, Calif., USA) to characterize kill sites with regard to these attributes and to develop input environmental layers for each variable for use in MaxEnt.

We modeled all possible 1 to 6 variable candidate models and compared resultant models using receiver operating characteristic (ROC) plots and the critical ratio test (Pearce and Ferrier 2000 as modified by Baldwin and Bender 2008*a*). We used ROC plots to assess relative performance and to establish thresholds for identifying the likelihood of a site as a location for a kill (Phillips et al. 2006). The ROC is a plot of sensitivity and 1-specificity, with sensitivity representing how well the data correctly predicted presence (kill-sites); specificity provides a measure of correctly predicted random sites (Fielding and Bell 1997). We used the area under curve (AUC) to assist in selecting the most appropriate model (Fielding and Bell 1997, Phillips et al. 2006). This approach provided an index of model accuracy; values ranged from 0.5 to 1.0, with values of 0.5 indicating fit no greater than random, while models with AUC > 0.7 indicating good fit (Swets 1988). We calculated standard errors for AUC values using 30% of the locations as test data.

We compared all possible models, and reported models with the highest AUC value for each subset of habitat variables (i.e., 1 to 6 variable models). Because higher-dimensioned models often have greater AUC even if some variables contribute little to the final model (Baldwin and Bender 2008*a*), we (1) used AUC to select the model with the best fit (highest AUC) from each set of 1 to 6 variable models (to ensure that only models that fit the data well were considered) and (2) compared whether higher-dimensioned models differed statistically from lower (more parsimonious) models. If they did not differ, we selected the most parsimonious (fewer variable) model. For the latter, we used the critical ratio test (Pearce and Ferrier 2000) to compare the most general model (containing all variables) to simpler models to determine if the increase in explanatory value was significant at $\alpha = 0.05$, following Baldwin and Bender (2008*a*). We also derived thresholds for probability as a kill site for test data by maximizing sensitivity and minimizing specificity (Fieldling and Bell 1997, Phillips et al. 2006). We used these thresholds to convert probabilities to binary response (presence-absence) and used the equal test sensitivity and specificity threshold values to calculate successful classification percentages to corroborate results from ROC curves. We corroborated model selection using concordance (percentage successful classification of kill-sites) because a model that poorly classifies the data it was built from is unlikely to have any true predictive ability (Hosmer and Lemeshow 1989).

Last, we constructed response curves to illustrate the effect of significant variables on probability of a site for a kill. Upward trends for variables indicated a positive association, while downward movements represented a negative relationship; and the magnitude of these movements indicated the strength of these relationships.

Results

We confirmed 45 jaguar depredations of cattle (all calves <12 months old) from 85 confirmed or suspected predator kills (Rosas-Rosas et al. 2008). Significantly more (Binomial $P < 0.001$) depredations occurred during the dry season (87%) than during the wet season (13%). Kill-sites averaged 47.7 m (SE = 6.8) from permanent water, 281.3 m (SE 37.1) from roads, 848.0 m (SE = 24.1) in elevation, 25.2 (SE = 1.9) degrees of slope, and 170.4 (15.7) degrees in aspect. We recorded kills in 7 vegetation types: primary oak forest ($n = 18$), semitropical thornscrub ($n = 18$), xeric thornscrub ($n = 3$), disturbed semitropical

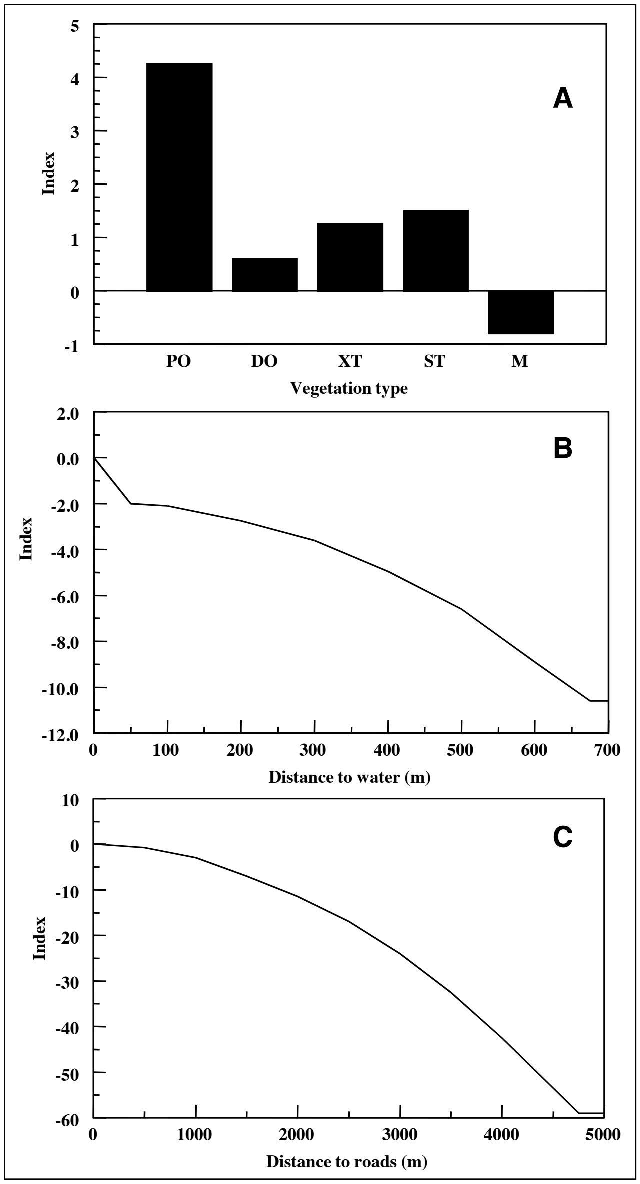

Figure 2. (A) Relationships between vegetation cover type (PO = undisturbed oak forest; DO = disturbed oak forest; XT = xeric thornscrub; ST = semitropical thornscrub; M = mesquite). (B) Distance to permanent water source in meters. (C) Distance to roads in meters with vulnerability of cattle to jaguar predation in northeastern Sonora, Mexico. Vulnerability increases with increasing log contribution to raw prediction score (Index).

thornscrub (*n* = 2), tropical deciduous forest (*n* = 2), mesquite (*n* = 1), and disturbed oak forest (*n* = 1).

Vegetation cover type (AUC = 0.771; SE = 0.069), distance to permanent water (AUC = 0.717; SE = 0.070), and distance to roads (AUC = 0.791; SE = 0.050) were related to kill-site locations, whereas elevation (AUC = 0.569; SE = 0.084), slope (AUC = 0.659; SE = 0.068), and aspect (AUC = 0.507; SE = 0.083) were not. The model including vegetation type, distance to permanent water, and distance to roads provided the most parsimonious fit (Table 1) and fit data well (AUC = 0.933; SE = 0.028; class percentage = 93.3%). Percentage contributions of individual variables to the overall model were: vegetation cover type = 50.0; distance to riparian = 27.2; and distance to roads = 22.8. Cattle vulnerability decreased rapidly to approximately 70 m from permanent water sources, then more gradually with increasing distance from permanent water until vulnerability was essentially 0 at >700 m from permanent water (Figure 2). Vulnerability was highest within 1,000 m of roads (Figure 2). Vulnerability of cattle to jaguar predation was also strongly positively associated with primary oak forest and weakly positively associated with disturbed oak forest, semitropical thornscrub, and xeric thornscrub (Figure 2). Conversely, sites of cattle kills were weakly negatively associated with mesquite, which was characteristic of uplands. Collectively, vulnerability of cattle was greatest adjacent to permanent water sources, especially riparian habitats when associated with patches of undisturbed oak forest and semitropical thornscrub, which comprised a minority of our study area (Figure 3).

Discussion

Most (87%) jaguar predation on cattle occurred during the dry season, usually in riparian habitats in primary oak forest and semitropical thornscrub vegetation types (Figure 2). These sites were characterized by dense vegetation, which provides ideal stalking cover for ambush predators, such as jaguars (Sunquist and Sunquist 1989). In northeast Sonora, cattle ranchers move cattle to pastures adjacent to riparian corridors or pastures with permanent water sources to provide cattle with thermal

Table 1. Best supported 1 to 6 variable models of habitat characteristics associated with sites of successful depredation of cattle by jaguars, area under curve (AUC) and SE of models, model concordance (Con.), and associated probability that the lesser dimensioned models did not differ from the full (6 variable) model.

Model[1]	AUC	SE	Con.	*P*
V, W, R, S, A, E	0.947	0.022	0.96	–
V, W, R, S, A	0.947	0.022	0.96	1.000
V, W, R, S	0.945	0.021	0.93	0.912
V, W, R	0.933	0.028	0.93	0.713
V, W	0.873	0.043	0.82	0.087
W	0.791	0.050	0.82	0.043

[1]V = vegetation cover type; W = distance to permanent water sources; R = distance to roads; S = slope; A = aspect; and E = elevation.

cover, succulent forage, and water during drought conditions and during the dry season. These areas have dense surrounding vegetation and permanent water, habitat characteristics that increase vulnerability to jaguar predation (Figures 2, 3; Hoogesteijn et al. 1993, Azevedo and Murray 2007). These same habitats also are preferred by natural prey of jaguars, including white-tailed deer (*Odocoileus virginianus*), coatimundi (*Nasua narica*), and collared peccaries (*Pecari tajacu*) that further increases the likelihood of presence of jaguars (Rosas-Rosas 2006). While distance to roads was also associated with vulnerability to predation, this effect was weaker than either vegetation type or proximity to riparian habitats. Roads were rare in our study area and generally followed major drainages, so this effect probably represented a response to major drainages, a coarser result than the finer scale response to all riparian areas (Figures 2, 3). More importantly, however, because cattle losses were associated with

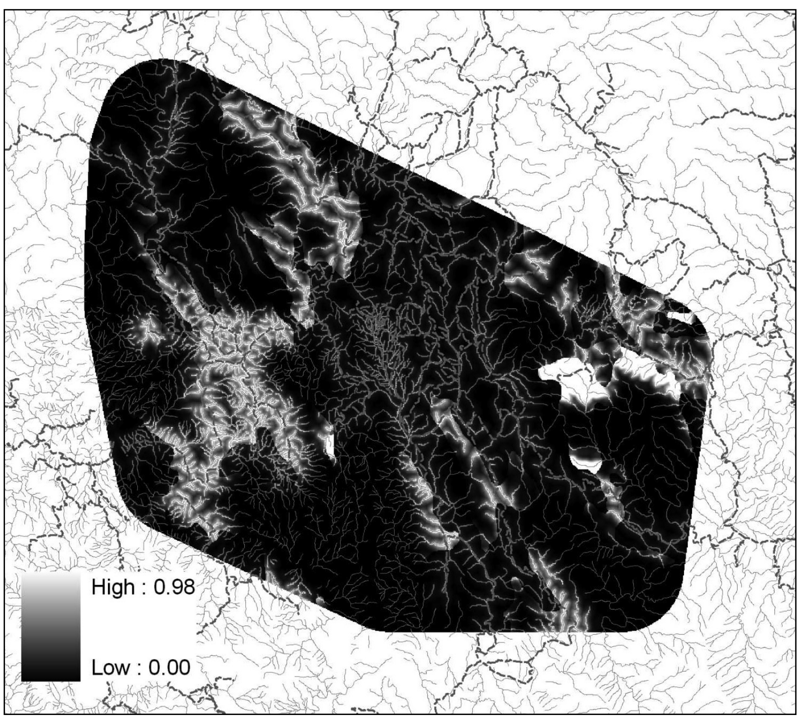

Figure 3. Probability of vulnerability of cattle to jaguar predation in northeastern Sonora, Mexico, study area. Lighter colors represent increasing vulnerability to predation. Streams are presented as light solid lines and roads are bold dashed lines.

specific habitat features in northeastern Sonora, habitat and cattle management can be used to alter cattle use of habitats associated with increased vulnerability and thereby potentially reduce predation.

A cattle management practice that could minimize cattle vulnerability to jaguars is to develop permanent water sources in upland pastures to avoid concentrating cattle near dense riparian cover during the dry season. This would minimize concurrent use of habitats by jaguars and cattle and thus decrease vulnerability to predation (Polisar et al. 2003, Azevedo and Murray 2007). Another alternative cattle management practice that may be effec-tive in northern Sonora is to hire additional ranchhands to herd cattle away from densely vegetated riparian areas during the dry season, particularly during the night when most predation occurs (Rosas-Rosas 2006); this approach was already implemented by some ranchers in our study area to decrease calf losses to all mortality factors. Further, fencing densely wooded riparian areas associated with frequent attacks would also minimize co-occurrence of cattle and jaguars, as successful jaguar depredations were far less common in the more open, adjacent upland habitat types (Figures 2, 3).

Moreover, some of these methods to mitigate jaguar predation have the potential to increase livestock stocking rates and redistribute live-stock grazing, thereby increasing profitability for landowners. Placement of water sources in upland pastures can redistribute cattle away from chronic predation areas, concurrently resulting in more uniform use of pastures (Hart et al. 1993, Bailey 2005). Likewise, herding cattle away from riparian corridors has the potential to alter cattle distribution resulting in more even grazing distribution (Bailey 2005) and, thus, potentially increasing stocking rate while decreasing vulnerability of cattle to jaguar predation. Such actions can increase profitability of ranchers by minimizing losses of cattle to jaguars, increasing individual cattle gains and increasing overall herd size, particularly given that the majority of our study area was comprised of uplands with low vulnerability to jaguar predation (Figure 3).

Factors implicated in increasing vulnerability of cattle to jaguar predation included a lack of permanent water sources in upland pastures, nonregulated calving seasons, lack of constant monitoring of pregnant cows, lack of supplementary food, insufficient ranch hands, drought, and lack of alternative prey (Rabinowitz 1986, Nowell and Jackson 1996, Saenz and Carrillo 2002, Polisar et al. 2003, Hoogesteijn and Hoogesteijn 2008). Solutions to prevent or minimize impacts of these predisposing factors include compensatory payments, translocation of individual felids, electric fences, guard dogs, taste-aversion collars fitted to livestock, and changing species of livestock (Rabinowitz 1986, Nowell and Jackson 1996, Saenz and Carrillo 2002, Schiaffino et al. 2002, Polisar et al. 2003, Hoogesteijn and Hoogesteijn 2008). Many of these solutions are expensive (payments, translocations, electric fencing), inappropriate (changing species of livestock), or difficult to implement (guard dogs, taste aversion collars) for an average cattle rancher in northern Sonora. Consequently, predators, such as jaguars, often are killed simply for being a potential threat to livestock (Rosas-Rosas et al. 2008). Alternatively, altering cattle distribution is a basic range and livestock management practice (Holechek et al. 2004, Bailey 2005) that can also be used to decrease use of areas of higher risk of predation and, thus, potentially limit predation conflicts.

Management implications

Modified habitat and cattle management practices may be able to decrease jaguar predation conflicts in northern Sonora by redistributing cattle away from areas of high vulnerability. Some of these actions, such as establishing water sources in uplands, can also enhance grazing options and, thus, potentially increase livestock associated revenues without the severe legal consequences associated with killing jaguars. Combined with predator control measures that emphasize removing problem jaguars rather than broadcast predator control (Rosas-Rosas et al. 2008), altering habitat attributes that predispose cattle to predation or altering distribution of cattle may provide a viable alternative for maintaining both livestock enterprises and a large endangered carnivore in areas of conflict.

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