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**ORIGINAL ARTICLE**

**FACTORS AFFECTING JAGUAR AND PUMA PREDATION ON LIVESTOCK IN COSTA RICA**

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**Keywords**

Conflict;  
Felids;  
Ranchers;  
Livestock;  
Jaguar;  
*Panthera*;  
*Puma*;  
Cattle.

**Abstract**

Throughout their range, wild felids in the Americas prey on livestock and this sometimes leads to retaliatory killing. Recently, conservation and research programs focused on such conflicts have recommended mitigation and prevention measures to producers, but these programs sometimes lack guidelines to direct implementation. We developed an index of risk of felid predation on cattle based on data from 52 ranches in Northwest Costa Rica. We evaluated the following as potential indicators of risk: climate, proximity to protected areas, distance to riparian forest, and wildlife occurrence as landscape factors, and cattle management efforts, and average livestock weight as anthropogenic factors. As a result, the index was defined as a hierarchical classification of these variables that provides a planning tool to identify and address the vulnerability of livestock at cattle ranches to felid predation events.

**Introduction**

Livestock-felid conflicts occur worldwide. In Africa, lion (*Panthera leo*) predation on domestic animals is associated with the reduction of their historical range, and mostly driven by human-induced activities [1]; similar issues are reported for felids in Asia (e.g. snow leopards (*Uncia uncia*) [2]), Europe (lynx [*Lynx lynx*][3]), and the Americas (jaguars (*Panthera onca*) [4, 5] and pumas (*Puma concolor*) [6, 7]).

In Latin America, the causes and patterns of predation on livestock by wild felids are associated with landscape and anthropogenic factors [8]. The biophysical aspects that potentially increase the occurrence of human-felid conflicts include dense forested areas, proximity to natural vegetation, prey availability, distance to wilderness areas, water sources, and roads [9, 10]. These factors have been considered in previous systematic analyses as the drivers of the issue [11–13]. In Costa Rica, researchers have

highlighted the importance of investigating the causes of livestock-felid conflicts and have also identified potential drivers of these conflicts, including spatial and temporal distribution of wild cats, landscape metrics, and livestock management, as critical for designing conservation actions [14, 15].

Despite the numerous factors that have been described in the past, there is still a lack of hierarchical understanding of conflicts, and this limits the implementation of effective solutions needed to reduce and mitigate conflict. Indeed, in Central American countries where the resources designated to conservation are limited [16], conservationists and decision makers need tools to prioritize areas where livestock-felid conflicts occur [8, 17–19]. Researchers have identified differences between sites where the frequency of livestock predation is higher than others [2], hence observing inherent conditions that make these sites hotspots of depredation [20].

In Costa Rica, livestock-felid conflicts have occurred historically, and in the past the jaguar was classified as a pest [15]. Hence, the configuration of the landscape, as well as the combined effect of the expansion of livestock activity, illegal hunting of natural prey, and lack of environmental education of local citizens, have increased negative interactions between humans and wild felids [15, 21].

In this study, we developed a planning tool called “*Predation risk index*”. The index is a combination of the associated driving factors of human-felid conflicts, resulting in an estimate of the probability of felid predation on livestock. This tool is an attempt to provide a more objective classification of livestock-felid conflicts in order to improve the decision-making process [22]. With this index, we theorize that landscape features and anthropogenic variables lead to the occurrence of conflicts at multiple hierarchical levels, and that depredation behavior is context dependent [8, 23].

## Methods

### *Study area*

The study area is located in northwest Costa Rica, including part of the adjacent Chorotega and North Huetar regions (11° 7.7'N and 11° 5.1'N, 85° 58.5'W and 84° 40.4'W). The Chorotega region represents 30% of the country's cattle production [24]. Average annual rainfall is nearly 1,400 mm in the plains, which contain the rivers Tempisque and Bebedero, and about 1,950 mm in the hillside areas of the Peninsula de Nicoya [25]. The North Huetar region provides 31% of the country's cattle production [26], rolling with moderate to steep slopes in the mountainous parts, but also flat, floodable plains and marshlands; annual precipitation average is 2010 mm [27]. The entire study area is 17,592 km<sup>2</sup> and includes 1,040 km<sup>2</sup> of different protected areas with a great variety of wild cats and prey [15].

We visited 52 livestock farms from January to December 2009. These farms were all located within an area covered by a previous project on conservation of felids and their prey on cattle farms [15], and all had reported livestock predation events. Field visits for data collection were conducted no more than two weeks after a predation event. We used only confirmed records of jaguar and puma attacks; attacks by coyotes (*Canis latrans*), dogs (*Canis familiaris*), or any other carnivores were excluded from our analyses. We combined all kills because ranchers could not really distinguish between those of jaguars versus pumas.

At each field visit, coordinates of the predation site were registered using GPS (Garmin MAP® 60CSx), and configured in geographical coordinates WGS84. Pertinent information about the landscape and human-related aspects related to livestock management were taken from previous fieldwork [15].

### *Landscape variables*

The landscape variables selected to construct the risk index were: climate seasonality, proximity to protected areas (e.g., national parks, biological reserves), the nearest riparian forest and, qualitatively, wildlife occurrence as indexed by hunting activities. *Climate seasonality*, as a proxy for how the climate can affect the number of predation events [28], was included because at some point, precipitation determines the seasonal distribution of potential prey, and consequently the shifting movements and foraging behavior of predators [29]. Climate seasonality was calculated by using the annual mean number of rainy days per month (Meteorological Institute of Costa Rica). *Proximity to protected areas* is the distance from the nearest protected areas with jaguar and/or pumas populations, and is based on the assumption that national parks, forest reserves, wildlife sanctuaries, among others, protect remaining populations of wild cats. Thus, neighborhoods near these areas are more likely to have predation events [14, 20, 30–32], and we recorded distances to generate a gradient of predation distances from the nearest protected area. *Nearest riparian forest* is defined as the spatial distance from each predation event to the nearest riparian forest structurally connected to protected areas and was derived from a National GIS database by using river and vegetation coverage (Technological institute of Costa Rica). This variable describes the way that vegetative coverage provides shelter and facilitates ambush predatory behavior of pumas and jaguars [15, 20, 27, 33]. Natural vegetation cover is closely linked with the movement of wildlife, in this case riparian forests serve as corridors and connectors between protected areas and farms with livestock [27]. *Wildlife occurrence* is a description of all potential prey species for jaguars and pumas in the area that were hunted by locals and reported to us when asked. The species selected as potential prey were based on previous studies and expert consultation [30–39], and included *Tayassu pecari* (White lipped peccary), *Pecari tajacu* (Collared peccary), *Odocoileus virginianus* (White-tailed deer), *Canis latrans* (Coyote), *Cuniculus paca* (Paca), *Nasua narica* (Coati), *Dasyopus novemcinctus* (Nine banded armadillo), *Dasyprocta punctata* (Agouti), *Sylvilagus* spp. (Rabbit), *Crax rubra* (Curacao) and *Penolope purpuracens* (Crested guan).

### *Anthropogenic variables*

We also included variables that provide a human-effect proxy for the risk index: herd management and cattle weight. *Herd management* is important because a high percentage of predation on livestock relates to different kinds of management related to livestock use (e.g., milk, beef, reproduction; 7, 17]. Herd management is classified in different subcategories according to the percentage of events related to this variable, placing the different types of managements into gradual categories from least (feedlot) to most (extensive/free-range) risk of predation. *Cattle Weight* is the average weight of all cattle in the herd, and based on the hypothesis that livestock predation is allometric to felid body size [28]; that is, at some average weight, cattle exceed the threshold of

likely prey because larger animals are better able to repel predators [29]. This variable was collected from direct interviews and field visits with ranchers, and the animals' weight average was 173 kg, with a maximum of at least 400 kg and a minimum of 20 kg.

### *Data analysis*

A Pearson correlation coefficient was used to assess the association among variables. Statistical analyses were implemented with software R. 2.10.1[40]. QGIS 1.8. Lisboa [41] software was used to assess spatial patterns and variables related to predation events.

### *Predation Risk*

Given the likelihood of predation risk occurrence, which is the result of a threat (big cat presence nearby) and the vulnerability determined by landscape and anthropogenic variables [7, 15, 17, 20, 28], the risk index is a comprehensive attempt to understand and systematize the circumstances under which livestock herds are more vulnerable to predation events [38]. Each variable was partitioned into 5 different categories and assigned values of 0 – 4, where 0 is very low risk, 1 is low risk, 2 is medium risk, 3 is high risk and 4 is very high risk. An equation ( $RI = \sum Vi/n$ ) can be used to calculate the risk, where  $Vi$  is the value of risk assigned to each variable and  $n$  the number of variables used to construct the index, obtaining an average  $RI$ , rounded to the nearest unit. The landscape variable, *Wildlife occurrence*, was incorporated here by assuming that the presence of species most preferred by jaguars and pumas would result in lower predation risk for livestock as opposed to when they were not present in the area.

## **Results**

### *Landscape variables*

The seasonality in the Huetar Norte and Chorotega regions showed a pattern of association with peaks of predation (Pearson coefficient -0.69, CI= -25-90,  $p = 0.012$ ). Monthly variation in rates of predation was significant ( $\chi^2 = 23.53$ , 11 df,  $p = 0.01$ ), with increasing rates of predation during the driest months of the year, reaching the highest rates from January and May (Fig. 1). More than 56% of the predation events occurred at ranches 0 to 5 km from the nearest protected area (Fig. 2). The percentage of predation events continued to decline as distance from the nearest protected area increases ( $\chi^2 = 104.87$ , 4 df,  $p = 2.2^{-16}$ ). Similarly, 75% of predation events occurred at ranches nearest to riparian forests (<0.3 km), and predation events decreased significantly at farms farther from riparian forests (Fig. 3;  $\chi^2 = 193.3$ , 4 df,  $p = 2.2^{-16}$ ).

### *Anthropogenic variables*

The frequency of predation events was highest (65%) at ranches where livestock was managed over extensive areas (Fig. 4;  $\chi^2 = 193.3$ , 4 df,  $p = 2.2^{-16}$ ). In these cases,

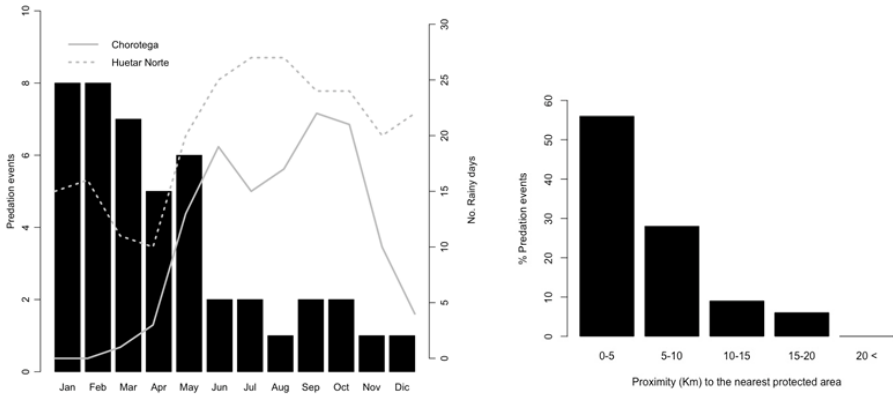


Figure 1 (left): Monthly relationship between the number of rainy days and the number of livestock predation events by large felids, Northwest Costa Rica.

Figure 2 (right): Percentage of livestock predation events by large cats, relative to the proximity of Protected Areas, Northwest Costa Rica.

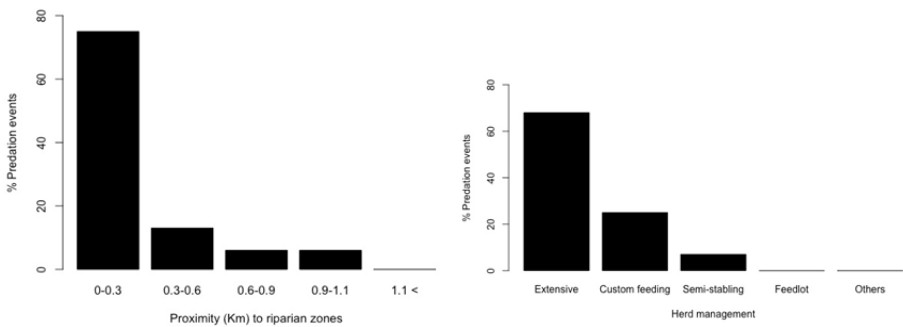


Figure 3 (left): Percentage of livestock predation events by large cats relative to the proximity of riparian forest, Northwest Costa Rica, 2009.

Figure 4 (right): Percentage of livestock predation events by large cats relative to type of herd management, Northwest Costa Rica.

livestock is almost free ranging, in contrast with custom feeding management (25% of predation events) and semi-stabling (7% of predation events) management, which demands closer interactions of ranchers with livestock [15]. With respect to livestock weight, most predation events (48%) occurred at ranches where average weights ranged from 50-100 kg, and no reports of predation events occurred where average weights were >400 kg (Fig. 5;  $\chi^2 = 62.3$ , 4 df,  $p = 9.526^{-13}$ ).

*Predation risk*

A table of risk index (Table 1) was constructed using results from our analyses and from reviewed literature within the range of the puma and the jaguar. As an example, livestock on a ranch with 0-7 rainy days per month (Risk 4), 0-5 km from the nearest protected area (4), <0.3 km from the nearest riparian forest (4), with free-ranging cattle (4) averaging < 100kg (4), and with none of the specified prey animals in the area (4) would be at the highest risk (4).

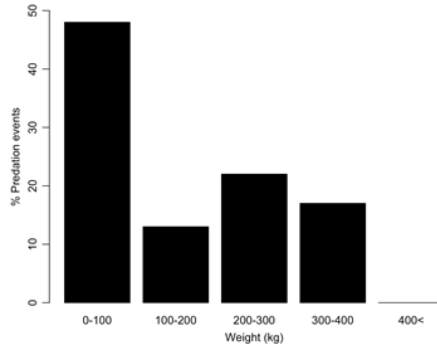


Figure 5: Percentage of livestock predation events by large cats relative to weight classes, Northwest Costa Rica.

Table 1: Thresholds to determine the hierarchical classification of livestock ranches, based on the potential predation risk by jaguars and pumas in Costa Rica.

Predation risk	Risk Index Value				
	Very low 0	Low 1	Medium 2	High 3	Very High 4
<i>Landscape variables</i>					
Climate seasonality (# Rainy days per month)	> 28	21 – 28	14 – 21	7 – 14	0 – 7
Proximity to the nearest protected area (km)	> 20	20 – 15	15 – 10	10 – 5	5 – 0
Nearest Riparian forest (km)	> 1.1	1.1 – 0.9	0.9 – 0.6	0.6 – 0.3	< 0.3
Wildlife occurrence	* Group I	** Group II	*** Group III	**** Group IV	Other prey species
<i>Socio-economic variables</i>					
Herd management	Others	Feedlot	Semi-stabling	Custom feeding	Extensive
Cattle weight (kg)	<400 kg	300 – 399	200 – 299	100 – 199	>100 kg
<b>Risk value (<math>\Sigma Vi/n</math>)</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>

\**Tayassu pecari, Odocoileus virginianus*  
 \*\* *Canis latrans, Pecari tajacu*  
 \*\*\* *Cuniculus paca, Nasua narica, Dasypus novemcinctus*.  
 \*\*\*\* *Dasyprocta punctata, Sylvilagus sp., Crax rubra, Penelope purpuracens*

## Discussion

In our areas, our results suggest that during the driest months livestock and other potential prey tend to cluster near water sources, which may help maximize the foraging success of pumas and jaguars. In contrast, researchers found the opposite trend in tropical lowlands of Guatemala, where the attacks of jaguar and puma on cattle tend to increase in the wettest months of the year, because predators are more difficult to detect by livestock and people [11]. A major conundrum concerning livestock depredation in Costa Rica is that jaguars and pumas are rare species, and their remaining populations are mostly in protected areas [14]. The proximity of livestock ranches to these particular areas favors the occurrence of predation events, and indeed, the presence of natural forests plus the presence of rivers increase the probability of these events [10, 12]. Dense forest coverage likely serves as refuge for felids, for stalking cover, and as passages that help predators move between farms and protected areas [6, 7].

However, cattle management techniques are a controllable factor affecting depredation rates. Similarly, livestock density and condition (i.e., average weight) are also management aspects that can be controlled to reduce depredations. Finally, control of poaching of wild species on adjacent lands can likely decrease livestock losses [28]; farmers having depredation problems often (68%) report that poachers usually roam near their property, likely causing the loss of natural prey for the wild felids in the area and thus encouraging them to feed on domestic animals [15].

The implementation of planning methodologies for human-wildlife conflict prevention requires a clear understanding of particular problems in order to prioritize resources and make significant progress towards conservation goals [18, 42 – 44]. Due to the complexity of livestock predation events, it is necessary to use key variables in a systematized way as an instrument for wildlife managers and conservationists [45]. The use of the risk index provides information to help diagnose rural land use, especially when surrounded by protected areas. It also allows for actions by agricultural and environmental institutions responsible for the development and implementation of conservation measures to assess whether the risk of loss of livestock and domestic animals is imminent.

The risk index is a practical tool that should be applied in a logical manner (e.g., Fig. 6). The first step alludes to environmental and agricultural agencies that need to collect information necessary for understanding the nature of the conflict based on previous experiences; this is centrally important since government agencies are in charge of implementing policies and enforcing the law [20], and they have field personal that are familiar with the local issues. The application of the index and identification of the different levels of risk is critical, since the conflict resolution process should always be based on a diagnostic phase which must be efficient and effective in terms of the predictability of the conflict [7, 22].

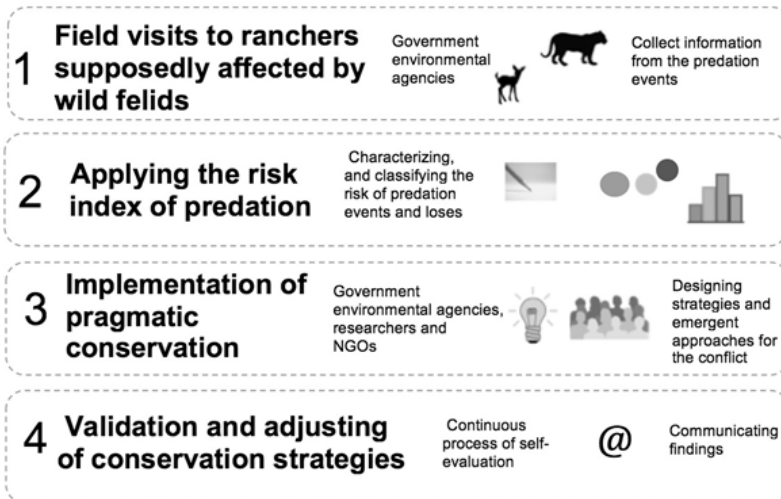


Figure 6: Conceptual application of the predation risk index.



## Conclusions

The occurrence of predation events on livestock is not a random event. The existence of livestock–felid conflicts is the result of a combination of a set of landscape and anthropogenic variables. Because of this, a comprehensive understanding of the conflict is needed, and a hierarchical classification of these variables can be applied as a tool to manage conflicts where the financial resources are limited to classify and predict predation events.

According to our data, as well as other studies within the range of these predators, the most important landscape variables are proximity to the nearest protected area, the existence of riparian vegetation and climate seasonality. Anthropogenic factors such as herd management is important in terms of mitigation and prevention because these are the factors that we can directly manage in order to reduce conflict.

Finally, this approach should be used as a flexible tool in which the user can add or modify variables in order to better understand and mitigate livestock-felid conflicts. The index is a preliminary approach that was derived from field data that provides demonstrated useful results in terms of planning. However, we suggest that this research can be replicated and the tool improved for use in other regions outside Northwest Costa Rica.

## Acknowledgements

The authors thank the U.S. Fish and Wildlife Service for financial support in the early stages of this project, as well National University of Costa Rica (Project 0452 – 13). Thank you also to Aleckey Chuprine, Francisco Morazán and all the volunteers and students who collaborated in the fieldwork

## References

Five “key references”, selected by the authors, are marked below (Three recommended (●) and two highly recommended (●●) papers).

1. ● Patterson, B.D., Kasiki, S.M., Selempo, E., and Kays, R.W. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. *Biological Conservation* 119:507–516.  
<http://dx.doi.org/10.1016/j.biocon.2004.01.013>
2. Jackson, R.M., Ahlborn, G., Gurung, M., and Ale, S.B. 1996. Reducing livestock depredation losses in the Nepalese Himalaya. In *Proceedings of the Seventeenth Vertebrate Pest Conference*, pp241–247.
3. Odden, J., Herfindal, I., Linnell, D.C., and Andersen, R. 2008. Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *J. Wildlife. Manage* 72:276–282.  
<http://dx.doi.org/10.2193/2005-537>
4. Azevedo, F.C., & Verdade, L.M. 2012. Predator-prey interactions: Jaguar predation on caiman in a floodplain forest. *J. Zoology* 286:200–207.  
<http://dx.doi.org/10.1111/j.1469-7998.2011.00867.x>
5. Palmeira, F.B., Crawshaw, P.G., Haddad, C.M., Ferraz, K.M., and Verdade, L.M. 2008. Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biological Conservation* 141:18–125.  
<http://dx.doi.org/10.1016/j.biocon.2007.09.015>

6. Zarco-Gonzalez, M.M., Monroy-Vilchis, O., Rodriguez-Soto, C., and Urios, V. 2012. Spatial Factors and Management Associated with Livestock Predations by *Puma concolor* in Central Mexico. *Human Ecology* 40:631–638.  
<http://dx.doi.org/10.1007/s10745-012-9505-4>
7. Rosas-Rosas, O.C., Bender, L.C., and Valdez, R. 2008. Jaguar and Puma Predation on Cattle Calves in Northeastern Sonora, Mexico. *Rangeland Ecology & Management* 61:554–560.  
<http://dx.doi.org/10.2111/08-038.1>
8. Leite, R., & Galvao, F. 2002. El jaguar, el puma y el hombre en tres áreas protegidas del bosque atlántico costero de Paraná, Brasil. In Medellín, R., Equihua, C., Chetkiewicz, C., Crawshaw, P., Rabinowitz, A., Redford, K., Robinson, J., Sanderson, E., and Taber, A. (eds), *El jaguar en el nuevo milenio*, Wildlife Conservation Society, México. pp 238–250.
9. Bradley, E. H., & Pletscher, D. H. 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. *Wildlife Soc Bull* 33:1256–1261.  
[http://dx.doi.org/10.2193/0091-7648\(2005\)33\[1256:AFRTWD\]2.0.CO;2](http://dx.doi.org/10.2193/0091-7648(2005)33[1256:AFRTWD]2.0.CO;2)
10. Kaartinen, M., Luoto, M., and Kojola, I. 2009. Carnivore-livestock conflicts: Determinants of wolf (*Canis lupus*) depredation on sheep farms in Finland. *Biodiversity Conservation*, 18:3503–3517.  
<http://dx.doi.org/10.1007/s10531-009-9657-8>
11. ● Soto-Shoender, J.R., & Giuliano, W.M. 2011. Predation on livestock by large carnivores in the tropical lowlands of Guatemala. *Oryx* 45:561–568.  
<http://dx.doi.org/10.1017/S0030605310001845>
12. ● Michalski, F., Boulhosa, P., Faria, A., and Peres, C.A. 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: Determinants of large felid depredation on livestock. *Animal Conservation* 9:179–188.  
<http://dx.doi.org/10.1111/j.1469-1795.2006.00025.x>
13. ●● Rosas-rosas O.C., & Valdez, R. 2010. The role of landowners in jaguar conservation in Sonora, Mexico. *Conservation Biology* 24:366–371.  
<http://dx.doi.org/10.1111/j.1523-1739.2009.01441.x>
14. Salom-Pérez, R., Carrillo, E., Sáenz, J.C., & Mora, J.M. 2007. Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. *Oryx* 41:51–56.  
<http://dx.doi.org/10.1017/S0030605307001615>
15. Amit, R., Rojas, K., Alfaro, L.D., and Carrillo, E. 2009. Conservación de felinos y sus presas dentro de fincas ganaderas. National University of Costa Rica Tech Rep. pp 100.
16. Galetti, M., Giacomini, H.C., R. S. Bueno, R.S., Bernardo, C.S., Marques, R.M., Bovendorp, R.S., Steffler, C.E., Rubim, P., Gobbo, S.K., Donatti, C.I., Begotti, R.A., Meirelles, F., Nobre, A., Chiarello, G., and C. A. Peres. 2009. Priority areas for the conservation of Atlantic forest large mammals. *Biological Conservation* 142:1229–1241.  
<http://dx.doi.org/10.1016/j.biocon.2009.01.023>
17. Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., and Eisenberg J. F. 2003. Jaguars, pumas, their prey base, and cattle ranching: Ecological interpretations of a management problem. *Biological Conservation* 109:297–310.  
[http://dx.doi.org/10.1016/S0006-3207\(02\)00157-X](http://dx.doi.org/10.1016/S0006-3207(02)00157-X)
18. Hoogesteyn R., & Hoogesteyn, A. 2008. Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation? *Oryx* 42:132–138.  
<http://dx.doi.org/10.1017/S0030605308001105>
19. Rabinowitz, A. 1986. Jaguar predation on domestic livestock in Belize. *Wildlife Soc. Bull.* 14:170–174.

20. Zarco-González, M. M., Monroy-Vilchis, O., and Alaníz, J., 2013. Spatial model of livestock predation by jaguar and puma in Mexico: conservation planning. *Biological Conservation* 159:80–87.  
<http://dx.doi.org/10.1016/j.biocon.2012.11.007>
21. Burgas, D., Byholm, P., and Parkkima, T. 2014. Raptors as surrogates of biodiversity along a landscape gradient. *J. Applied Ecology* 51:786–794.  
<http://dx.doi.org/10.1111/1365-2664.12229>
22. Treves, A., Wallace, R. B., Naughton-Treves, L., and Morales, A. 2006. Co-Managing Human–Wildlife Conflicts: A Review. *Human Dimension Wildlife* 11:383–396.  
<http://dx.doi.org/10.1080/10871200600984265>
23. Miller, J. R. B., Ament, J. M., and Schmitz, O. J. 2014. Fear on the move: Predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *J. Animal Ecology* 83:214–222.  
<http://dx.doi.org/10.1111/1365-2656.12111>
24. Retana J., & Rosales, R. 2001. Efecto de la variabilidad climática sobre la producción bovina de carne en la Región Chorotega de Costa Rica. *Tópicos Meteorológicos y Oceanicos* 8:55–59.
25. Enquist, C.A. F. 2002. Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *J. Biogeography* 29:519–534.  
<http://dx.doi.org/10.1046/j.1365-2699.2002.00695.x>
26. Ministerio de planificación de Costa Rica. 2014. Región Huetar Norte, plan de desarrollo 2030.  
<<https://documentos.mideplan.go.cr/alfresco/d/d/workspace/SpacesStore/72e8292f-97f9-465c-a5edc2c4b442a55c/Region%20Huetar%20Norte.pdf?guest=true>>. Accessed 14 April 2016.
27. McCain, C.M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *J. Biogeography* 31:19–31.  
<http://dx.doi.org/10.1046/j.0305-0270.2003.00992.x>
28. Zanin, M., Sollmann, S., Torres, N.M., Furtado, M.M., Jacomo, A.T., Silveira, L., and De Marco, P. 2015. Landscapes attributes and their consequences on jaguar *Panthera onca* and cattle depredation occurrence. *Eur. J. Wildlife Restauration* 61:529–537.  
<http://dx.doi.org/10.1007/s10344-015-0924-6>
29. Khorozyan I., A. Ghoddousi, A., Soofi, M., and Waltert, M. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation* 192:268–275.  
<http://dx.doi.org/10.1016/j.biocon.2015.09.031>
30. Rabinowitz A. & Notthingham, B. 1986. Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology* 210:149–159.  
<http://dx.doi.org/10.1111/j.1469-7998.1986.tb03627.x>
31. Rabinowitz, A., & Zeller, K. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation* 143:939–945.  
<http://dx.doi.org/10.1016/j.biocon.2010.01.002>
32. Zeller, K. 2007. Jaguars in the new millennium data set update: The state of the jaguar in 2006. *Wildlife Conservation Soc.*, New York. pp77.
33. Weckel, M., Giuliano, W., and Silver, S. 2006. Cockscomb revisited: jaguar diet in the Cockscomb Basin Wildlife Sanctuary, Belize. *Biotropica* 38:687–690.  
<http://dx.doi.org/10.1111/j.1744-7429.2006.00190.x>
34. Newby, J. R., Mills, S., Ruth, T.K., Pletscher, D.H., Mitchell, M.S., Quigley, H.B., Murphy, K.M., and DeSimone, R. 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biological Conservation* 159:230–239.  
<http://dx.doi.org/10.1016/j.biocon.2012.10.018>

35. ●● Carrillo, E., Fuller, T.K., and Saenz, J.C. 2009. Jaguar (*Panthera onca*) hunting activity: effects of prey distribution and availability. *J. Tropical. Ecology* 25:563–567.  
<http://dx.doi.org/10.1017/S0266467409990137>
36. Harmsen, B.J., Foster, R.J. Silver, S.C, Ostro, L.E.T. and Doncaster, C.P. 2010. The ecology of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize. In *Biology and Conservation of Wild Felids*. Oxford University Press, pp.403–416.
37. Aranda, M. 1996. Distribución y abundancia del jaguar *Panthera onca* (Carnivora: Felidae) en el estado de Chiapas México. *Acta Zoológica Mexicana* 68:45-52.
38. Hernández-Saintmartín, H., Rosas-Rosas, O.C., Palacio-Núñez, J., Tarango-Arámbula, L., Clemente-Sánchez, F., and Hoogesteijn A. 2013. Activity Patterns of Jaguar, Puma and Their Potential Prey in San Luis Potosi, Mexico. *Acta Zoologica Mexicana* 29:520–533.
39. Chinchilla, F. 1997. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*) y el manigordo (*Felis pardalis*) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. *Revista Biología Tropical* 45:1223–1229.
40. R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. Vienna, Austria.<https://www.cran.r-project.org/>> Accessed June 15 2010.
41. Quantum GIS Development Team. 2015. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project.<http://qgis.org/en/site/>> Accessed April 15 2016.
42. Foschiatti, A.M. 2004. Vulnerabilidad Global y Pobreza. Consideraciones conceptuales. *Geográfica Digital* 2:1–20.
43. Schroeder, R.L., Medellín, R.A., Ramírez, O. and Rojo, A. 2009. Planes de Manejo de las Unidades de Manejo para la Conservación de la Vida Silvestre (UMA). *Investigación Ambiental* 1:136–142.
44. Ojasti, J., & Dallmeier, F. 2000. Manejo de fauna silvestre neotropical. Washington, D.C. Smithsonian Institution. pp290.
45. De Azevedo, F., & Murray, D. 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation* 137:391–402.  
<http://dx.doi.org/10.1016/j.biocon.2007.02.022>