

DISSERTATION

HUMAN-CARNIVORE CONFLICT MITIGATION ON RANCLANDS IN THE WESTERN
UNITED STATES AND EASTERN COLOMBIA

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ABSTRACT

HUMAN-CARNIVORE CONFLICT PREVENTION ON RANGLANDS IN THE WESTERN UNITED STATES AND EASTERN COLOMBIA

Conflict between large carnivores and ranching livelihoods is a persistent challenge for carnivore conservation and management. Shifting societal views of large carnivore management at the end of the 20th century led to population recovery and, in some cases, reintroduction to their former range. Working lands, productive areas encompassing a matrix of human land use and natural land cover, are an important part of carnivore range as they provide vital habitat and connectivity between protected areas. However, large carnivores can have direct and indirect impacts to humans and human livelihoods on working lands through livestock depredation, increased labor to mitigate depredations, and in some cases risk to human safety. In the Western United States, the reintroduction of gray wolves (*Canis lupus*) and the recolonization of grizzly bears (*Ursus arctos*) are hailed as species recovery success stories but have been met with resistance from rural ranching communities. Wildlife managers, researchers, and other entities throughout the region seek to reduce livestock producers' burden of living with large carnivores while ensuring sustainable populations. On the plains of Eastern Colombia, jaguars (*Panthera onca*) are recolonizing former range after being nearly extirpated following centuries of conflict over livestock and the pelt trade in the mid-20th century. In Colombia, jaguars depredate livestock, but there is little government support for the implementation of prevention tools and no compensation for losses, leaving non-governmental organizations as the sole implementers of conflict mitigation. In both contexts, wildlife managers require tools and strategies to address

livelihood impacts and incentivize human-carnivore coexistence. Development and evaluation of these methods is important to ensure that limited resources are being utilized effectively. In this dissertation, I examine human-carnivore conflict in the Western United States and Eastern Colombia through three lenses: population trends related to conservation interventions for large carnivores; evaluation of non-lethal conflict reduction tools; and the human dimensions of non-lethal mitigation.

In Chapter 1, I examine jaguar population trends on a working ranch and wildlife tourism destination in Casanare, Colombia. We integrated nine years of camera trap data and tourist photos to estimate jaguar survival, abundance, and probability of tourist sightings through a Barker Robust Design mark-recapture model. We then used spatially explicit capture-recapture to estimate jaguar density and compare it to a 2014 estimate. We found that abundance increased from 5 ± 0.26 individuals in 2014 to 28 ± 2.7 in 2022, and density increased from 1.88 ± 0.87 per 100 km² in 2014 to 3.80 ± 1.08 jaguars per 100 km² in 2022. We estimated survival rate of $78 \pm 0.08\%$ for males and $80 \pm 0.07\%$ for females. The probability of a tourist viewing a jaguar increased from $0 \pm 0.11\%$ in 2014 to $40 \pm 0.18\%$ in 2020 before the Covid-19 pandemic. We provide the first robust estimates of jaguar survival and abundance on working lands. Our findings highlight the importance of productive lands for jaguar conservation and suggest that a tourism destination and working ranch can host an abundant population of jaguars when accompanied by conservation agreements and conflict interventions. Our analytical model that combines conventional data collection with tourist sightings can be applied to other species that are observed during tourism activities.

In chapter 2, I evaluate the effectiveness of diversionary feeding—providing food caches to divert predators away from preying on livestock—to reduce depredations by reintroduced

Mexican wolves in the US states of New Mexico and Arizona. We used data from the Mexican wolf recovery program from 2014-2021 in a Bayesian hierarchical model to evaluate whether diversionary feeding reduced livestock depredations by wolf packs and what factors correlated with depredations. Our model accounted for the non-detection of depredation events, given that some depredations are unencountered or unreported on extensive rangelands. We found that diversionary feeding reduced depredations on average by 0.78 ± 0.03 depredations (43.9%) per pack per year. Prey density was negatively correlated to depredations before diversionary feeding. Minimum pack size and annual livestock density were negatively correlated with depredations after diversionary feeding, while prey density was positively correlated. We estimated a mean of $63 \pm 5.4\%$ of depredations were detected with high variation between packs ($40.4 \pm 7.9\% - 74.0 \pm 5.3\%$). Because detections were only two-thirds of model-estimated depredations in our study, our model could improve compensation and targeting of nonlethal tools to mitigate the financial burden of co-occurrence with wolves by elucidating factors that lead to lower detection and adjusting livestock loss compensation multipliers. Our results indicate diversionary feeding can reduce livestock depredations by wolves on large landscapes in the Western United States but is not a panacea for conflict reduction.

In chapter 3, I examine the context of human tolerance for large carnivores before and after the implementation of electric fencing to reduce depredations by jaguars. Non-lethal mitigation is often implemented under the premise that ranchers' tolerance for large carnivores will increase once losses are reduced or eliminated. However, deep-rooted psychological and cultural factors can be equally, if not more, important for predicting tolerance. We conducted structured interviews in four communities in the Colombian Llanos to characterize conflict, identify predictors of retaliatory killings of jaguars, and evaluate the impact of a fencing intervention to increase

tolerance. The social psychological variables from the theory of planned behavior were a better predictor of intention to kill a jaguar than past and expected livestock losses. The intervention did not increase tolerance, likely because self-selection bias led to a treatment group that was tolerant pre-intervention. Sixty percent of respondents reported moderate to severe livestock losses during year 1, highlighting the urgent need to identify broader mitigation strategies for livestock depredation. Positive attitudes and normative support in favor of retaliatory killings were pervasive, while 24% of respondents were intolerant—having positive attitudes of and intent to retaliate against a jaguar following the next livestock depredation. Our results suggest that a strategy focused only on reducing depredation is unlikely to reduce retaliatory killings, as losses are not the only driver of retaliation. The pervasiveness of livestock losses and support for retaliatory killings demonstrate a need for immediate action to reduce livelihood impacts and consider alternative, bottom-up approaches to conflict mitigation in the area.

My research indicates that wildlife tourism and diversionary feeding are two strategies that can mitigate the livelihood impacts of large carnivore presence. Wildlife tourism on Colombian ranchlands provides tangible economic benefits to landowners to conserve jaguars, other wildlife, and their habitat. We observed an important population increase for the locally threatened jaguar, and conserving jaguar habitat likely has reverberating benefits for ecosystem services and other wildlife through prey hunting prohibitions. Further work is necessary, however, to understand the distribution of costs and benefits from jaguar tourism and population growth in the surrounding community to ensure equitable conservation outcomes. In addition, diversionary feeding proved to be an effective tool to reduce depredations by Mexican wolves in the Southwestern U.S. The integration of non-detection of depredation events in our analysis is an important contribution to carnivore management because it can elucidate uncompensated livelihood impacts which

aggravate intolerance for carnivores. This tool could be applied to other populations of carnivores to mitigate losses and may be more easily deployed than some deterrents. Findings from my third chapter reinforce the importance of understanding the human dimensions of human-carnivore conflict prior to implementing conflict reduction strategies. Interventions based solely on livestock losses may be unsuccessful at reducing retaliatory killings if losses are not the only driver of intolerance of carnivores. Ultimately, human-carnivore conflicts and interventions to prevent them are nested with unique social, cultural, ecological, political, and economic context. The failure of interventions to recognize how carnivore behavior interacts with local human contexts may ultimately exacerbate conflict and lead to counterproductive mitigation strategies.

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Chapter 1 : Tourism-supported working lands sustain a growing jaguar population in the Colombian Llanos¹

Introduction

Large carnivores can play crucial regulatory roles in the ecosystems they inhabit, yet populations of many species continue to decline despite conservation efforts (Ripple et al., 2014). A key strategy for conserving large carnivores is reducing pressures in human-dominated landscapes, given that most suitable habitat occurs outside of protected areas (Crooks et al., 2011; di Minin et al., 2016). Working lands can provide vital, permeable habitat for carnivores (Devlin et al., 2023). However, interactions between large carnivores and humans on private lands may be negative, impacting both carnivores and people (Nyhus, 2016). Conservation scientists and practitioners are interested in developing strategies to promote coexistence with large carnivores (Lute et al., 2018), where carnivore populations are sustained and human livelihoods thrive with minimal conflict (Venumière-Lefebvre et al., 2022).

Whereas local support for carnivore presence on working lands tends to be low due to livestock depredation and safety concerns, value for carnivores at the global scale, especially felids, tends to be high (Macdonald et al., 2022). Successful coexistence with large carnivores requires converting global existence value into tangible financial benefits for local communities (Dickman et al., 2011). Conservationists have explored various funding mechanisms to create value from the presence of large carnivores for rural communities (Dickman et al., 2011; Hyde, Boron, et al., 2022). One such opportunity to promote coexistence locally and generate income for

¹ Adapted from Hyde, M., Payán, E., Barragan, J. *et al.* Tourism-supported working lands sustain a growing jaguar population in the Colombian Llanos. *Sci Rep* **13**, 10408 (2023). <https://doi.org/10.1038/s41598-023-36935-2>

those living with carnivores is wildlife tourism, where tourists pay to observe fauna in their natural habitats.

Because attitudes towards large carnivores are a strong predictor of human behavior towards them (Hazzah et al., 2017; Marchini & Macdonald, 2012), proponents hope that tourism income can sway local communities towards positive perceptions of carnivores while benefiting wildlife populations (Macdonald et al., 2017). Income from wildlife tourism can offset the costs of living with large carnivores, such as livestock depredation (Tortato et al., 2017). Furthermore, wildlife tourism can contribute to conservation through funding anti-poaching patrols, livestock compensation programs, and species recovery and restoration, as well as providing opportunities for scientific research and wildlife monitoring (Buckley et al., 2016; Macdonald et al., 2017). However, wildlife tourism initiatives can have both positive and negative outcomes for wildlife populations (Bateman & Fleming, 2017; Broekhuis, 2018; Mossaz et al., 2015). The success of coexistence strategies like tourism requires understanding and quantifying such impacts (Pereira et al., 2022), and these strategies promote coexistence more effectively when accompanied by efforts to reduce livestock losses and conservation agreements (Miller et al., 2016). Moreover, the presence of tourists with high-quality photography capabilities can have important, albeit underutilized, contributions to wildlife monitoring (Rafiq et al., 2019).

Developing effective coexistence strategies for jaguars is urgently needed. Jaguars are among the most emblematic large carnivores (Thornton et al., 2016). Over half (55%) of remaining populations exist outside of protected areas (Jędrzejewski et al., 2018), hence research and conservation strategies on working lands are of critical importance (Boron et al., 2016). Jaguars have lost nearly half their range in the last 50 years (Quigley et al., 2017). Major threats to their

persistence are habitat loss and fragmentation (Petracca et al., 2014), direct killings to prevent or retaliate for livestock losses, and decline of prey (Quigley et al., 2017).

Understanding jaguar survival rates is critical to their conservation but acquiring accurate population metrics can be difficult and costly (Harmsen et al., 2017). Jaguars are naturally elusive, and densities are low (Jędrzejewski et al., 2018). Longitudinal studies of jaguars are therefore challenging because of the financial and logistical difficulty of long-term monitoring. Across the jaguar's extensive range, only four long-term jaguar population studies have been published (Fragoso et al., 2023; Gutiérrez-González et al., 2015; Harmsen et al., 2017; Srbek-Araujo & Chiarello, 2017). In addition, no published long-term study has addressed survival and abundance on working lands, where densities tend to be lower (Jędrzejewski et al., 2018) and survival is likely more challenging.

Hato La Aurora, a working cattle ranch and private reserve, is the only place in Colombia where jaguar tourism is practiced in the species' natural habitat. Hato La Aurora was formally established as a reserve in 2008, and hunting was prohibited on the ranch since 1979. Because of the killing of jaguars for their pelts (known locally as *tigrilladas*) in the mid-20th century (Payan & Trujillo, 2006), populations were decimated, and no jaguars were observed in Hato La Aurora until 2002. In 2013, Hato La Aurora began working with Panthera Colombia, a felid conservation organization, to monitor the jaguar population and reduce human-jaguar conflict in and around the ranch. Panthera Colombia implemented conservation agreements and electric fences around calving pastures to reduce livestock depredations from jaguars with 19 ranches neighboring Hato La Aurora, totaling 8,558 hectares contiguous to Hato La Aurora and 19,326 hectares nearby (Panthera Colombia, unpublished data).

Here, we present the first longitudinal study and demographic estimates for jaguars on working lands and in Colombia. Our approach estimated survival rates, probability of observation by tourists, and abundance of jaguar populations in Hato La Aurora. We used camera trap data and tourist photos collected between 2014 and 2022 in a Barker Robust Design Model (Kendall et al., 2013). We complemented the robust design analysis by comparing our results with spatially explicit density estimates in 2014 and 2022 from the study area. We hypothesized that jaguar abundance, survival, density, and observation by tourists increased over time as a result of recently implemented conservation efforts.

Methods

Study area

Colombia is the most diverse country by land area (Clerici et al., 2019), harboring 1,941 species of birds (Vélez et al., 2021), 520 mammals (Suárez-Castro et al., 2021), and the third largest population of jaguars (Jędrzejewski et al., 2018). The department of Casanare, located in the country's eastern *Llanos* (plains), is part of the transition zone between the tropical rainforest of the Amazon and the Eastern Andes. The landscape is dominated by seasonally flooded savannahs of the Orinoco basin, which form the largest wetland complex in the country. Casanare is a top destination for wildlife viewing due to open savannahs and abundant populations of mammals and birds. The area has been dominated by extensive cattle ranches since bovine introduction in the 1600s (Huertas-Ramirez & Huertas-Herrera, 2015). However, petroleum exploitation, oil palm plantations, and rice cultivation have increased in the last few decades (Romero-Ruiz et al., 2012).

Hato La Aurora (5° 57' 18.8"N, 71° 29' 0.1"E to 6° 4' 52.6"N, 71° 17' 51.4"E) is a private reserve consisting of 15,000 hectares of tropical savannahs and gallery forests in the department

of Casanare (Figure 1.1). The area receives 1,000-3,000 mm of rainfall each year, with marked dry (December-May) and wet (June-November) seasons (IDEAM, 2014). The principal land use and economic activity is cattle ranching, with some introduced grasses for cattle forage. The surrounding area is comprised principally of extensively managed cattle ranches with riparian forest cover, though rice plantations are increasing in the region.

Camera trapping

We installed a total of 296 camera-traps (models Panthera V3, V4, V5, V7, and Cuddeback 1279 and G-5048) between 2014 and 2022 at a distance of 1.5 ± 0.5 kilometers for the study of medium and large vertebrates (Tobler & Powell, 2013) for a total of 16,790 trap-nights (Table 1.1). Camera-trap grids used the same 24-hour configuration and a quiet period of (30 seconds) between trigger events. No baits were used in any of the studies.

Camera trapping for density estimation (2014 and 2022 surveys) followed standardized recommendations (Tobler & Powell, 2013) and complied with the capture-recapture model assumptions: the population is closed, and all individuals have a possibility of being captured (Otis et al., 1978; White, 1982). In April-May of 2014, we installed 52 double camera stations in a grid covering 152 km² at an average distance of 1.6 ± 0.2 kilometers (see Boron et al., 2016 for detailed survey information). In March-May of 2022, we placed 32 single camera stations (Figure 1.2) in a grid covering 102 km² (Minimum Convex Polygon). We installed Cuddeback models 1279 and G-5048, and Panthera series 6 and 7 cameras at a height of 35-40 centimeters. Cameras remained active for 24 hours per day. We used single stations because long-term monitoring of individuals provided photographic evidence of both sides of most jaguars, enabling individual identification when only one side was photographed. Like in 2014, the average distance between stations was 1.6 ± 0.2 kilometers, which is consistent with recommendations for jaguar density studies (Tobler

& Powell, 2013) and is appropriate when considering jaguar home ranges estimates, since it ensures all individuals can be photo-captured (Morato et al., 2016). According to Colombian regulation, non-invasive camera trap studies do not require permits or approval from an Institutional Animal Care and Use Committee or equivalent.

Auxiliary tourist photographs

Trained guides accompanied groups and ensured compliance with the regulations of the reserve. Jaguar viewing occurred in open vehicles and tour guides were required to maintain a minimum distance of 100 meters, avoid any noises, and not leave the vehicle. We collected tourist photos of jaguars that were observed on an opportunistic basis during the study period. Tourists and guides reported sightings and delivered photos to J. Barragan for identification. Jaguars were uniquely identified by rosettes and spot patterns (Boron et al., 2016). Between 2014 and 2022, we collected 79 direct observations where individuals were identifiable. These sightings occurred primarily during the dry season (December-May) due to access issues in the rainy season and prey species like capybaras (*Hydrochoerus hydrochaeris*) being constricted to available surface water. However, a small number of sightings ($n=9$) occurred during the rainy season. Fifty-six additional sightings were discarded due to a lack of distinguishable photographic evidence.

Barker/Robust Design

We used Barker/RD (Kendall et al., 2013) to estimate survival (S), detection probability by camera trap (p), availability to camera traps given previously in the study area (a'') and previously outside the study area (a'), probability of observation by tourists given alive (R) and probability of being dead but not recovered (R'), and abundance (N) of jaguars in Hato La Aurora. We extracted nine annual primary periods from camera trapping studies, eight of which occurred during the dry season and onset of the rainy season (between February-June) and one which

occurred during the rainy season (July-October). We shortened camera trap studies to four-month secondary periods for closure (Gutiérrez-González et al., 2015), as required by the model (Kendall et al., 2013). Camera trap records from outside of the closed period were removed from analysis. Details of the study periods can be found in Table 1.1.

Detection histories were compiled for each individual. Camera trap data were used for the secondary periods. Tourist photos, which could be collected at any time, were included as auxiliary resightings of jaguars at the end of each primary period in the detection history. The inclusion of tourist photos allowed for measurement of probability of viewing by tourists and increased the precision of survival estimates. We then constructed models using the Barker/RD model in Program Mark (White & Burnham, 1999), allowing for a mixture of detection probabilities (Pledger, 2000) and conditioning on at least one capture (Huggins, 1991) for a primary period. Dead recovery information was not available in our study. We therefore fixed parameters of the probability of dead recoveries (r) to 0 and fidelity (F) to 1 since all observations were within the study area. We also accounted for the variable time interval lengths between primary periods, rescaling all survival parameters to an annual basis. Hypotheses and parameter definitions can be found in Table S1.

We used a stepwise approach to model selection because of the large number of potential models associated with Barker/RD (Doherty et al., 2012; Gutiérrez-González et al., 2015). We began by fitting models of probability of detection (p) to test hypotheses of time and sex variation. We did not test for trap response (c) because of the non-invasive nature of remote cameras and the possibility of the model mistaking trap response for heterogeneity. We tested all models for heterogeneity with two mixtures because of jaguars' territorial nature and the assumption that some individuals' home ranges will only partially overlap with the study area, while others will be

completely within it. We hypothesized that p increased by primary periods because researchers improved camera site identification and placement techniques, and that p varied by sex (Sollmann et al., 2011). We tested for variation in p by primary period, secondary period, sex, and constant detection.

We modeled the availability parameters, which describe whether a jaguar was previously in the study area (a'') or previously outside the study area (a'). We hypothesized that the probability of being previously outside the study area (a') and inside the study area (a'') would be Markovian and be the result of sex and time interactions, whereby males were more likely to emigrate and immigrate than females because of dispersal and territoriality (Kantek et al., 2021). We compared models with no movement, random movement, and Markovian movement.

The resighting parameter in this application of the Barker/RD calculates the probability that each jaguar is observed directly by a tourist that year. We fit models to the probability of resighting (R), testing sex, time, sex and time interaction, linear trend, and constant models. Given the increase in jaguar sightings reported by tourists in the last five years, we hypothesized that resightings increased with time since 2017 and varied by sex, given that males are more likely to use higher risk areas (Conde et al., 2010). Resighting effort is an unaccounted covariate in our study, since tour operators did not record the number of tours, hours of effort, or number of viewers.

Finally, we tested models for survival based on our hypothesis that survival would increase with time. We evaluated models with time variation, time and sex interaction, sex, and constant survival probabilities. Previous studies have applied prey density covariates to the survival parameter of robust design frameworks (M'soka et al., 2016). However, prey data were not available for all years of the study, thus could not be applied to survival. We selected the most parsimonious models using Akaike Information Criterion adjusted for small sample sizes (AICc)

for each hypothesized model (Burnham & Anderson, 2002). We used model averaging for the estimated parameters above and the derived parameter of abundance (N).

Derived parameters from the Delta method

We used the Delta method to calculate population changes over time (Harmsen et al., 2017; Karanth et al., 2006) and identify the source of abundance increases. We used derived parameter estimates of N to calculate the finite rate of change in abundance between sampling periods (λ), as N_{t+1} / N_t . We calculated the number of new recruits in the population in Hato La Aurora as $N_{t+1} - N_t \phi$ where ϕ is survival at time $t+1$ (Karanth et al., 2006).

Spatially explicit capture recapture

We ran density analysis with 2022 data to complement robust design estimates and compare with a density survey in Hato La Aurora in 2014 (Boron et al., 2016). We conducted density analysis fitting SECR models in a maximum likelihood framework (Borchers & Efford, 2008; Efford et al., 2009) in the R package “secr” (Efford, 2020). SECR models identify individuals home range centers based on their spatial locations, then estimate density of these centers across an area that includes the camera grid (Efford, 2004; Royle & Young, 2008). In addition to the standard capture-recapture assumptions, SECR models assume circular and constant home ranges during the survey, randomly distributed home range centers, and that the encounter rate of an individual with a trap decreases with increasing distance from the home range center following a predefined function (Efford, 2004). We used the half-normal detection function where the probability of capture (p) of an individual (i) at a trap (j) decreases with distance (d) from the activity center as: $P_{ij} = g_0 \exp(-d_{ij}^2/2\sigma^2)$. The parameter g_0 is the probability of capture when the trap is located exactly at the center of the home range, and sigma (σ) is parameter of the spatial scale over which detection declines away from the home range center (Efford, 2004). As

appropriate for camera trap data, we deployed the binomial encounter model (or Bernoulli model), enabling individuals to be captured at different camera stations during one sampling occasion (i.e., 24-hour period) but only once at each station (Noss et al., 2013; Royle et al., 2009). Like other felids, jaguars have different behavior and home ranges between sexes, hence we allowed both parameters g_0 and σ to vary with sex of the individuals (Sollmann et al., 2011; Tobler & Powell, 2013) and compared four models using AICc: the null model (SECR.0), a model where g_0 varies between males and females (SECR. g_0), a model where σ varies between males and females (SECR. σ), and a model where both g_0 and σ vary between sexes (SECR.sex).

Results

We recorded 50 individual jaguars from 659 identifiable camera trap records and 79 tourist sightings between 2014 and 2022. We detected 19 females and 31 males, although five individuals (four of which were females) were removed from the analysis because they were not detected within closed-capture time periods.

We ran 26 models in the Barker/RD to explore our hypotheses, three of which summed to 0.76 of model weight (Table 1.2). The most parsimonious model had an AICc weight of 0.32 and constant survival rates for males and females, probability of observation by tourists variable by time, and constant detection over the study period.

Our second most parsimonious model, with 0.24 model weight, differed only by constant probability of observation by tourists. Our third model, with 0.21 model weight, demonstrated evidence of transience, whereby a jaguar was detected once in the study area and never again. Below we present estimates from the top model and model-averaged estimates for our parameters of interest. Model-averaged estimates for all parameters can be found in Table S2.

Survival estimates

Apparent survival was constant throughout the study period (Figure 1.3a), though the third most parsimonious model suggested transience, where an individual was detected once and did not return. Model-averaged estimates suggest a slight difference between males and females. The average survival rate was 0.783 (SE 0.075, 95% CI: 0.603-0.896) for males and 0.798 (SE 0.068, 95% CI: 0.633-0.900) for females. Survival rates given transience were lower, 0.706 (SE 0.199, 95% CI: 0.318-0.934) for males and 0.720 (SE 0.200, 95% CI: 0.322-0.941) for females.

Tourist observation estimates

The probability of observation by tourists varied over time (Figure 1.3D). From 2014-2017, the probability of observation by tourists of both sexes was effectively zero. In 2018, the probability of observation by tourists increased to 0.348 (SE 0.157, 95% CI: 0.121-0.674) for females and 0.342 (SE 0.158, 95% CI: 0.116-0.674) for males. Observation by tourists peaked in 2020 at 0.409 (SE 0.181, 95% CI: 0.137-0.750) for females and 0.403 (SE 0.182, 95% CI: 0.133-0.748) for males. The observation probability dropped to less than half of that value in 2021, at 0.186 (SE 0.083, 95% CI: 0.072-0.400) for males and 0.190 (SE 0.084, 95% CI: 0.074-0.407) for females, before rebounding to 0.273 (SE 0.114, 95% CI: 0.108-0.537) for males and 0.279 (SE 0.115, 95% CI: 0.111-0.542) for females in 2022.

Abundance estimates

Abundance increased more than five-fold over the nine-year period in Hato La Aurora (Figure 1.3B and 1.3C). In 2014, there were estimated 3.00 males (SE 0.017, 95% CI: 2.97-3.03) and 2.63 females (SE 0.557, 95% CI: 0.12-3.36). The maximum estimated abundance in the nine-year period was in 2022, when males reached 14.54 individuals (SE 1.392, 95% CI: 11.81-17.27)

and females reached 14.37 (SE 1.307, 95% CI: 11.81-16.93). The lowest recorded abundance was in 2016, when abundance was only four—1.00 female and 3.41 males (SE 0.0105, 95% CI: 0.98-1.02; SE 0.686, 95% CI: 0.2.06-4.74). Our derived abundance estimates differ from our raw numbers of jaguars, which suggests that we did not observe all jaguars that were present in Hato La Aurora ($p^* < 1$) most years, with the exception of 2018. However, detection was high during the study period: 0.900 for mixture 1 of jaguars whose territory was mostly in the reserve and 0.412 for mixture 2 of jaguars whose territory partially overlapped in the top model.

Recruitment and population growth from derived parameters

The Delta method for estimating derived parameters revealed an increasing population during the study; finite rate of change in abundance (λ) averaged 1.389 for males and 1.822 for females (Figure 1.3C). Notably, the female population had the highest growth between 2016-2017, when it rose to 6.801 because of the arrival of five new females. Male population growth was highest in the intervals of 2014-2015 (2.215) and 2016-2017 (2.000).

Recruitment of both male and female jaguars was highest from 2021-2022, when it was 6.253 for males and 6.699 for females (Figure 1.3C). The lowest recruitment for males (-2.184) occurred between 2017-2018. The lowest recruitment for females (-1.714) occurred between 2015-2016. Life histories of jaguars between 2014-2022 are shown in Figure 1.4.

SECR Density

Trapping effort for spatially explicit capture-recapture (SECR) density in 2022 totaled 1,985 camera trap nights. We recorded 17 individuals (99 capture events at 19 of 32 stations): nine females (49 capture events) and eight males (50 capture events). Seven females and seven males were captured at different stations. The best model was SECR. σ where σ varies between males and females (Table 1.3). SECR. σ produced a density estimate of 3.803 jaguars/100 km² (SE 1.048; 95% CI: 2.238-6.464). The g_0 parameter estimate was 0.018 (SE 0.003; 95% CI: 0.013-0.026). The σ estimate was 2.321 km (SE 0.274;

95% CI 1.842-2.924) for females and 5.091 (SE 1.031; 95% CI: 3.437-7.540) for males. Despite overlapping estimates confidence intervals, the estimated density in 2022 was approximately twice that from 2014 (1.88 ± 0.87 jaguars/100 km²; 95% CI: 0.79-4.48) (Boron et al., 2016). Estimates for σ were also similar for females (females 2014: 2.327, SE 0.693 95% CI 1.315-4.119) and higher for males (males 2014: 1.426, SE 0.129 95% CI 1.195-1.701) than 2014 estimates indicating that the smaller grid size in 2022 did not bias density estimates.

Discussion

Conserving large carnivores requires strategies beyond protected areas (di Minin et al., 2016). Working lands with adequate conservation measures can provide sufficient habitat to sustain resident jaguar populations that are comparable to those of protected areas (Devlin et al., 2023). Promoting coexistence can be facilitated by economic mechanisms like tourism that can ease the livelihood impacts of living with large carnivores. To inform such initiatives, there is a need for rigorous, long-term data collection to understand impacts to carnivore demography (Balme et al., 2009). However, few long-term demographic studies exist for jaguars, hindering the evaluation of conservation efforts (Fragoso et al., 2023). Where such studies exist, they tend to focus on protected areas (Gutiérrez-González et al., 2015; Harmsen et al., 2017; Srbek-Araujo & Chiarello, 2017). Our longitudinal study of jaguars in Hato La Aurora, a working ranch and tourism destination in the Colombian Llanos, suggests that private lands with low-intensity cattle ranching and tourism can sustain an abundant jaguar population if combined with conservation actions such as hunting prohibitions, abundant prey (Soofi et al., 2019), conservation agreements with adjacent ranches (Gutiérrez-González et al., 2015) and depredation reduction strategies in the form of electric fencing of calving pastures.

Our application of the Barker/RD, which integrated tourist photos into nine years of camera trapping data, provided much-needed demographic estimates for jaguars, including the first

survival estimates for jaguars on working lands and in Colombia. The inclusion of tourist photos increased the precision of survival estimates (Kendall et al., 2013) and also allowed for quantification of jaguar sightings. Our estimates indicate that Hato La Aurora supported 28 ± 2.70 individual jaguars on the 15,000-hectare ranch in 2022, which is comparable to that of small protected areas within their range. In the federally protected Cockscomb Basin Wildlife Sanctuary in Belize, for example, estimated jaguar abundance peaked at 31 ± 4.77 individuals in 49,000 hectares (Harmsen et al., 2017), an area more than three times the size of Hato La Aurora. Jaguars in Hato La Aurora had a high survival rate (0.78 ± 0.075), again similar to the highest estimated survival rate from Cockscomb Basin Wildlife Sanctuary in Belize (0.78 ± 0.05) (Harmsen et al., 2017).

Our 2022 density estimate of 3.80 ± 1.08 jaguars/100 km² at Hato La Aurora is consistent with recent density studies of jaguars from other working lands. In the Brazilian Pantanal, Devlin et al. (2023) estimated 4.08 ± 0.73 jaguars/100 km² on multi-use (ranching, conservation, and tourism) landscapes. On a state-run cattle ranch in the Venezuelan Llanos with a long history of conservation, Jędrzejewski et al. (2017) estimated a density of 7.67 jaguars/100 km². The ecological similarity of the Venezuelan Llanos with Hato La Aurora suggests that the Colombian Llanos could host a higher density of jaguars if threats are sufficiently reduced.

The increase in density estimates from 1.88 ± 0.87 in 2014 to 3.80 ± 1.08 jaguars/100 km² in 2022, and the concomitant increase in jaguar abundance from five to 28 individuals, is encouraging for range-wide conservation efforts like the Jaguar Corridor Initiative, which seeks to maintain genetic connectivity between source populations throughout Central and South America (Rabinowitz & Zeller, 2010). This population increase was likely due to the high survival rate of jaguars and the 1.82 annual population growth (λ) of females, which is an important determinant

of demography for long-lived species with low reproduction rates (Robinson et al., 2015). However, the specific causal mechanisms driving the population increase require further investigation. We speculate that the status of Hato La Aurora as a private reserve and the conservation actions (e.g., electric fences for calving pastures and conservation agreements) implemented by Panthera Colombia on smaller, nearby ranches enhanced habitat suitability for jaguars, reduced human hunting of prey, and decreased livestock depredations and therefore retaliatory killings. The distribution of land ownership in the Colombian Llanos, whereby large ranches are often surrounded by smaller parcels, may necessitate a dual approach to coexistence strategies. Actions like electric fencing to reduce depredations on larger ranches like Hato La Aurora may be cost-prohibitive because of the extension of land and size of cattle herds. Similarly, tourism on smaller ranches surrounding Hato La Aurora is challenging due to smaller plots of land and limited infrastructure, but electric fencing of pastures is more feasible. In addition, it is possible that jaguar populations are recovering throughout the region since hunting and pelt exports were outlawed following the inclusion of jaguars in the CITES Appendix I in the 1970s (Payan & Trujillo, 2006). Tourism is the economic mechanism that allows the ranch owners to coexist with jaguars in Hato La Aurora, and therefore is of critical importance to jaguar persistence on the landscape.

Sustaining large carnivores on ranchlands requires minimizing livelihood impacts (Venumière-Lefebvre et al., 2022). Tortato et al. (2017) found that in the Brazilian Pantanal income was over 50 times higher from tourism than the estimated cost of livestock depredation on cattle ranches. In Hato La Aurora, wildlife tourism is the economic vehicle that permits coexistence between livestock systems and jaguars, though the differential between tourism and livestock depredation is lower than that of the Brazilian Pantanal. Hato La Aurora loses on average 100 head

of cattle, and a similar number of foals and pigs, to jaguars and pumas annually (pers. communication). Accurate data on income from tourism and the number of tourists visiting Hato La Aurora were unavailable, but ranch owners report that tourism income is crucial to offset the cost of living with carnivores. The allure of observing a jaguar in the wild raises the attractiveness of tourism in Hato La Aurora—further contributing to the viability of this coexistence strategy.

A challenge to large carnivore tourism, however, is reconciling their elusive nature with tourists' desire for predictable, high-quality sightings (Knight, 2009). Hunting prohibitions can make it easier to see species in tourist areas (Eshoo et al., 2018), and savannahs are ideal observation sites because of visibility (Grünwald et al., 2016). This appears to be the case in Hato La Aurora where our models showed higher probability of observation by tourists in recent years compared to 2014-2017. The probability peaked at 0.409 ± 0.182 in 2020 in the dry season months before the Covid-19 lockdown in March of 2020. The next year, in 2021, tourist sightings declined, which we attribute to lingering Covid-19 travel restrictions. We posit that, since jaguars in Hato La Aurora are not hunted or hazed, they may perceive a safer setting and be less likely to avoid human activity. Alternatively, a contributing factor to increased sightings may also be the knowledge of ranch owners and guides of daily patterns of jaguars. As tour guides came to understand where jaguars may be at peak times, they may have frequented those sites, leading to an increase in sighting probability.

Community science data collected by tourists, such as the photographs analyzed in our study, can have important and low-cost contributions to wildlife monitoring efforts (Rafiq et al., 2019). Our application of the Barker/RD using tourist photos as auxiliary data can be applied to other monitoring programs of large, terrestrial mammals, especially to understand the probability of tourists observing them in the wild. When using tourist data, it would be useful to collect

information on “sampling effort” of tourists by recording the number of people in each tour and the time spent observing wildlife and locations (Rafiq et al., 2019). If using camera traps for robust design modeling, moving stations within and between survey periods may increase total detection probability of individual animals and reduce sex-specific and individual heterogeneity (Gerber et al., 2014; Harmsen et al., 2017).

Replicable and landscape-scale coexistence strategies are necessary for large carnivore conservation. In the case of jaguar tourism, understanding the causal mechanisms behind increased sightings is important to strengthen tourism in Hato La Aurora and beyond. Accompanying studies to assess tourism’s impact on attitudes and tolerance (Ohrens et al., 2021; Van Der Meer & Dullemt, 2021) and local livelihoods (Salerno et al., 2016) are necessary for adaptive management of the industry and to optimize long-term benefits for jaguars. For jaguars in Colombia, prey depletion and the introduction of bovines into jaguar habitat are likely exacerbating conflict. Studies on jaguar diets, quantifying retaliatory killings, evaluating nonlethal strategies to reduce livestock depredation, and the human dimensions of living with jaguars are needed to understand barriers and enablers for human-jaguar coexistence at scale.

Tables and Figures

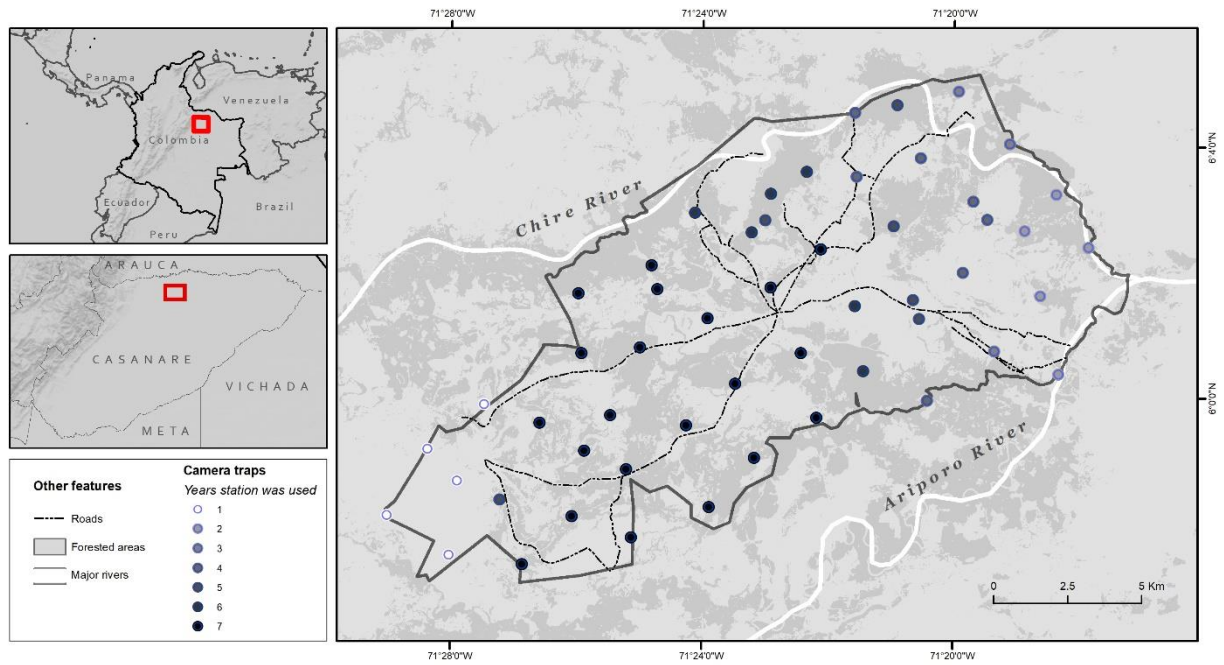


Figure 1.1. Study area map with location and intensity of camera trapping in Hato La Aurora from 2014-2022.

Table 1.1. Camera trapping effort during the study period in Hato La Aurora from 2024-2022.

	Survey periods								
	2014	2015	2016	2017	2018	2019	2020	2021	2022
Months	Mar-Jun	July-Oct	Feb-May	Mar-Jun	Feb-May	Feb-May	Feb-May	Feb-May	Feb-May
# secondary periods	4	4	4	4	4	4	4	4	4
# stations	53	21	30	20	49	20	21	41	41
Camera models	Pantheras	Pantheras	Pantheras	Pantheras	Pantheras	Pantheras, Cuddeback	Cuddeback	Pantheras, Cuddeback	Cuddeback
# trap nights	2616	1401	1753	1489	2440	1210	1296	2106	2479
Total identifiable detections*	76	18	13	26	55	42	95	159	175

*includes camera traps and tourist sightings

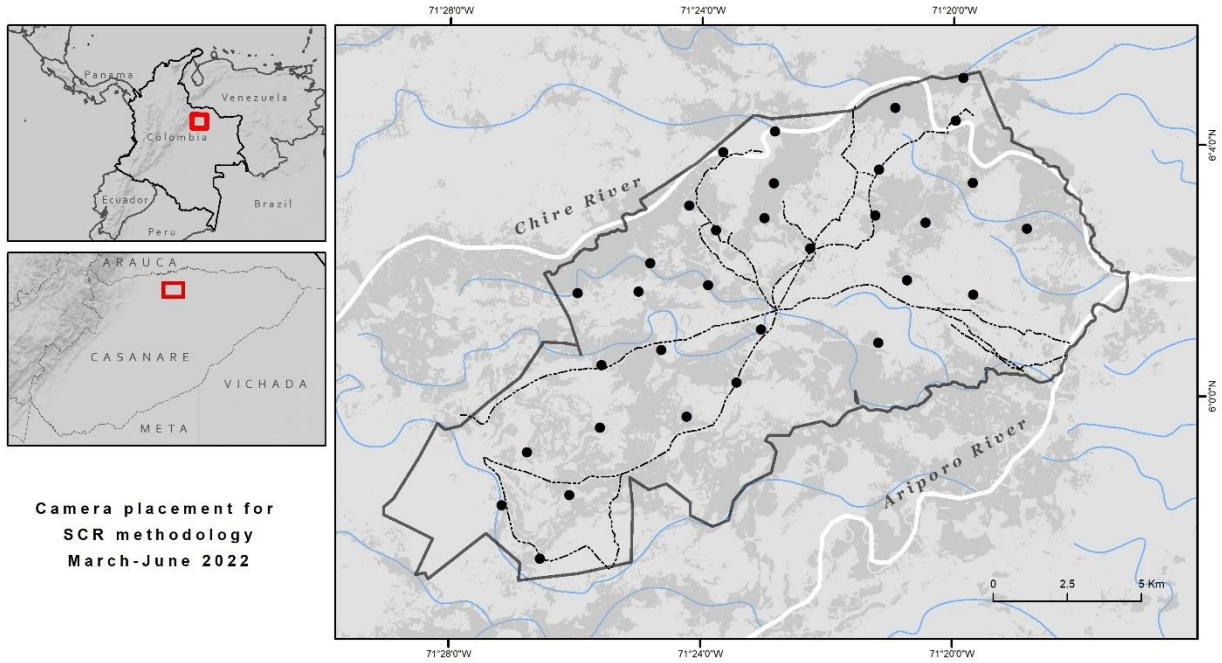


Figure 1.2. Map of camera trap installation for spatially explicit capture-recapture (SECR) in Hato La Aurora in 2022.

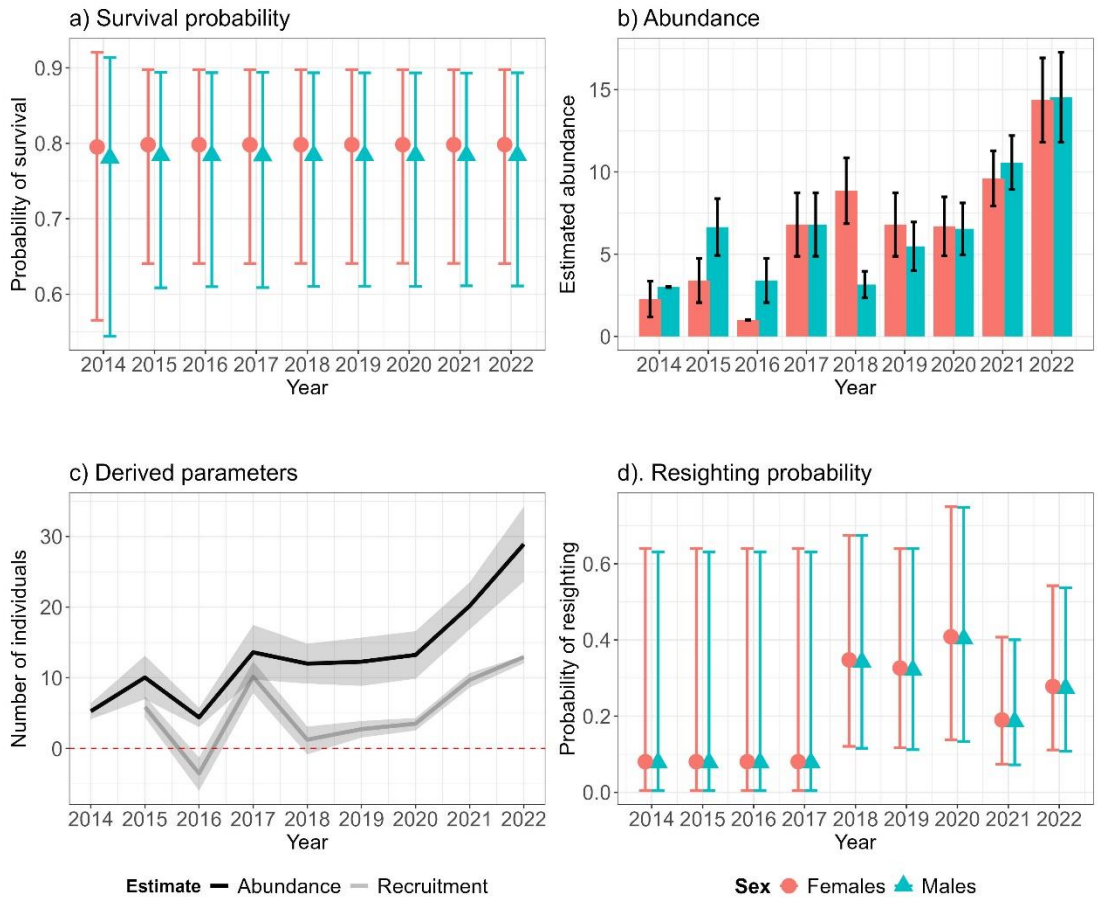


Figure 1.3. a) Model weighted survival probability for male and female jaguars. b) Model weighted derived estimates of male and female jaguar abundances. c) Delta method results for total abundance and recruitment. d) Resighting probability by tourists.

Table 1.2. Model results with the top 10 models from the Barker Robust Design Model.

Rank	Model	ΔAIC	AICc Weight	Model Likelihood	K	-2log(L)
1	S(.) R(year) R'(sex) a"(year) a'(.) p(.) pi	0.00	0.32	1	25	754.35
2	S(.) R(.) R'(sex*year) a"(year) a'(.) p(.) pi	0.54	0.24	0.76	21	764.67
3	S(.) R(year) R'(sex) a"(year) a'(.) p(.) pi TRANSIENCE	0.85	0.21	0.65	31	739.84
4	S(.) R(year) R'(sex) a"(year) a'(.) p(.) pi	2.49	0.09	0.29	26	754.34
5	S(sex) R(sex) R'(sex) a"(year) a'(.) p(.) pi	3.55	0.05	0.17	22	765.27
6	S(.) R(.) R'(year) a"(year) a'(.) p(.) pi	4.15	0.04	0.13	22	765.87
7	S(.) R(sex*year) R'(sex) a"(year) a'(.) p(.) pi	4.62	0.03	0.1	27	753.95
8	S(.) R(T) R'(sex) a"(year) a'(.) p(.) pi	7.92	0.01	0.02	20	774.45
9	S(.) R(.) R'(sex) a"(year) a'(.) p(.) pi	9.03	0.00	0.01	29	753.23
10	S(.) R(.) R'(sex*year) a"(year) a'(.) p(.) pi TRANSIENCE	9.23	0.00	0.01	19	778.13

S=survival, R=observation by tourists, R'=dead but not recovered between primary periods, a''=inside the study area given previously in the study area, a'=previously outside the study area, p=detection probability, pi= heterogeneity.. AICc = Akaike Information Criterion adjusted for small sample sizes; $\Delta AICc$ = difference in AICc values between each model and the model with the lowest AICc; K = number of model parameters;

Table 1.3. Model results from the spatially explicit capture-recapture density analysis.

Rank	Model	AICc value	ΔAIC	AICc Weight	K
1	SECR. σ	490.509	0.00	0.9	5
2	SECR.sex	495.114	4.61	0.09	6
3	SECR.0	499.597	9.09	0.01	4
4	SECR.g0	501.519	11.01	0	5

AICc = Akaike Information Criterion adjusted for small sample sizes; $\Delta AICc$ = difference in AICc values between each model and the model with the lowest AICc; K = number of model parameters; g0 = probability of capture at the home range centre, σ = spatial parameter related to home range size; SECR.g0: g0 varies between males and females; SECR. σ : σ varies between males and females; SECR.sex: both g0 and σ vary between males and females; SECR.0: null model.

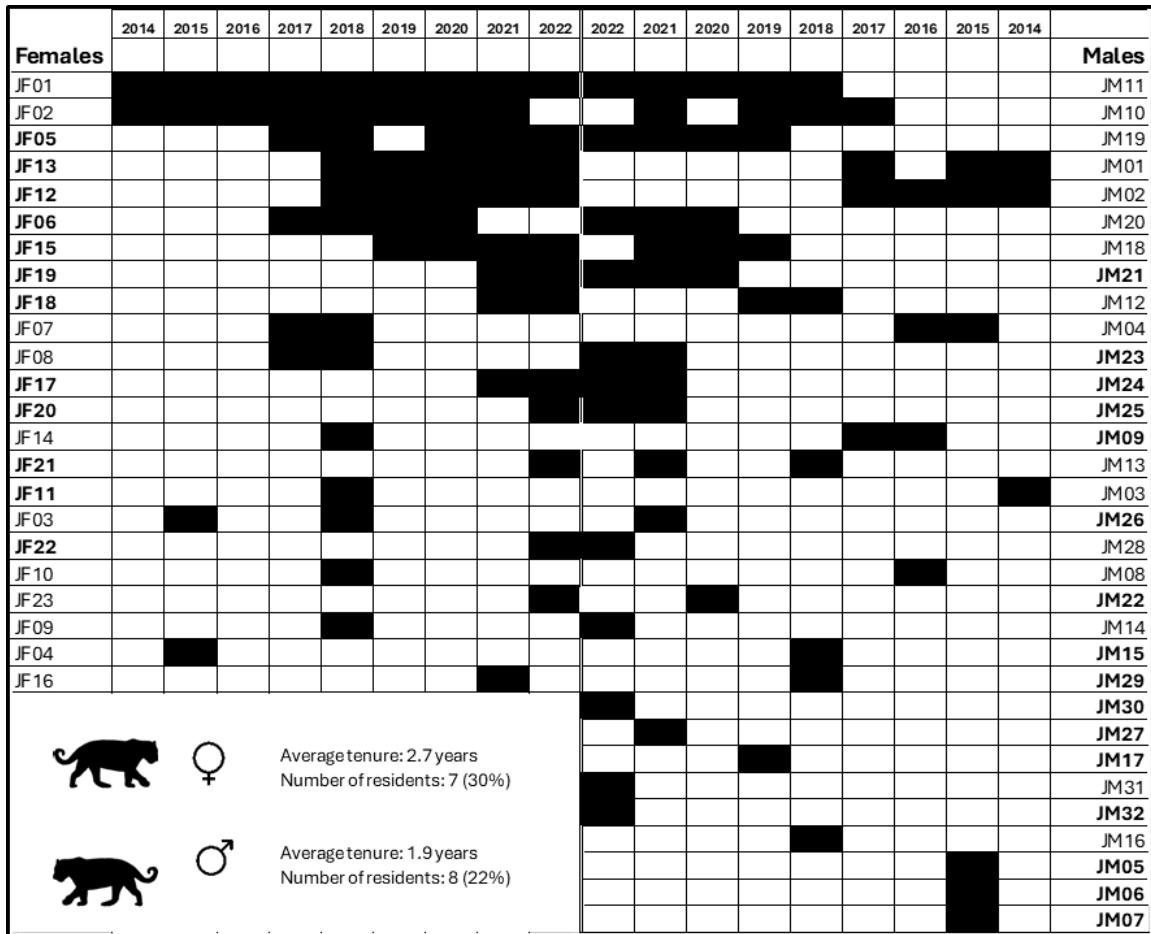


Figure 1.4. Life histories of jaguars detected in Hato La Aurora 2014-2022. Bolded names are jaguars that were born in Hato La Aurora. Icons credit Gabriela Palomo-Muñoz.

References

- Balme, G. A., Slotow, R., & Hunter, L. T. B. (2009). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation*, 142(11), 2681–2690. <https://doi.org/10.1016/J.BIOCON.2009.06.020>
- Bateman, P. W., & Fleming, P. A. (2017). Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biological Conservation*, 211, 10–19. <https://doi.org/10.1016/j.biocon.2017.05.003>
- Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64(2), 377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>
- Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long term conservation. *PLoS ONE*, 11(5), 1–14. <https://doi.org/10.1371/journal.pone.0153973>
- Broekhuis, F. (2018). Natural and anthropogenic drivers of cub recruitment in a large carnivore. *Ecology and Evolution*, 8(13), 6748–6755. <https://doi.org/10.1002/ECE3.4180>
- Buckley, R. C., Morrison, C., & Castley, J. G. (2016). Net Effects of Ecotourism on Threatened Species Survival. *PLOS ONE*, 11(2), e0147988. <https://doi.org/10.1371/JOURNAL.PONE.0147988>
- Burnham, Kenneth. P., & Anderson, David. R. (2002). *Model Selection and Multimodel Inference*. In *Model Selection and Multimodel Inference - A Practical Information-Theoretic Approach* (2nd ed.). Springer Science. <http://www.springer.com/gb/book/9780387953649>
- Clerici, N., Salazar, C., Pardo-Díaz, C., Jiggins, C. D., Richardson, J. E., & Linares, M. (2019). Peace in Colombia is a critical moment for Neotropical connectivity and conservation: Save the northern Andes-Amazon biodiversity bridge. *Conservation Letters*, 12(1), e12594. <https://doi.org/10.1111/conl.12594>
- Conde, D. A., Colchero, F., Zarza, H., Christensen, N. L., Sexton, J. O., Manterola, C., Chávez, C., Rivera, A., Azuara, D., & Ceballos, G. (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, 143(9), 1980–1988. <https://doi.org/10.1016/J.BIOCON.2010.04.049>
- Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1578), 2642–2651. <https://doi.org/10.1098/rstb.2011.0120>
- Devlin, A. L., Frair, J. L., Crawshaw, P. G., Hunter, L. T. B., Tortato, F. R., Hoogesteijn, R., Robinson, N., Robinson, H. S., & Quigley, H. B. (2023). Drivers of large carnivore density in non-hunted, multi-use landscapes. *Conservation Science and Practice*, 5(1). <https://doi.org/10.1111/csp2.12745>
- di Minin, E., Slotow, R., Hunter, L. T. B., Montesino Pouzols, F., Toivonen, T., Verburg, P. H., Leader-Williams, N., Petracca, L., & Moilanen, A. (2016). Global priorities for national carnivore

- conservation under land use change. *Scientific Reports* 2016 6:1, 6(1), 1–9. <https://doi.org/10.1038/srep23814>
- Dickman, A. J., Macdonald, E. A., & Macdonald, D. W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 108(34), 13937–13944. <https://doi.org/10.1073/PNAS.1012972108/>
- Doherty, P. F., White, G. C., & Burnham, K. P. (2012). Comparison of model building and selection strategies. *Journal of Ornithology*, 152(SUPPL. 2), 317–323. <https://doi.org/10.1007/s10336-010-0598-5>
- Efford, M. G. (2004). Density estimation in live-trapping studies. *Oikos*, 106(3), 598–610. <https://doi.org/10.1111/j.0030-1299.2004.13043.x>
- Efford, M. G. (2020). *secr: Spatially Explicit Capture-Recapture models*. R package version 4.3.0.
- Efford, M. G., Dawson, D. K., & Borchers, D. L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, 90(10), 2676–2682. <https://doi.org/10.1890/08-1735.1>
- Eshoo, P. F., Johnson, A., Duangdala, S., & Hansel, T. (2018). Design, monitoring and evaluation of a direct payments approach for an ecotourism strategy to reduce illegal hunting and trade of wildlife in Lao PDR. *PLoS ONE*, 13(2). <https://doi.org/10.1371/journal.pone.0186133>
- Fragoso, C. E., Rampim, L. E., Quigley, H., Buhrke Haberfeld, M., Ayala Espíndola, W., Cabral Araújo, V., Rodrigues Sartorello, L., & May Júnior, J. A. (2023). Unveiling demographic and mating strategies of *Panthera onca* in the Pantanal, Brazil. *Journal of Mammalogy*. <https://doi.org/10.1093/jmammal/gyac123>
- Gerber, B. D., Ivan, J. S., & Burnham, K. P. (2014). Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small. *Population Ecology*, 56(3), 463–470. <https://doi.org/10.1007/s10144-014-0431-8>
- Grünewald, C., Schleuning, M., & Böhning-Gaese, K. (2016). Biodiversity, scenery and infrastructure: Factors driving wildlife tourism in an African savannah national park. *Biological Conservation*, 201, 60–68. <https://doi.org/10.1016/J.BIOCON.2016.05.036>
- Gutiérrez-González, C. E., Gómez-Ramírez, M. A., López-González, C. A., & Doherty, P. F. (2015). Are Private Reserves Effective for Jaguar Conservation? *PLOS ONE*, 10(9), e0137541. <https://doi.org/10.1371/journal.pone.0137541>
- Harmsen, B. J., Foster, R. J., Sanchez, E., Gutierrez-González, C. E., Silver, S. C., Ostro, L. E. T., Kelly, M. J., Kay, E., & Quigley, H. (2017). Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of carnivores. *PLOS ONE*, 12(6), e0179505. <https://doi.org/10.1371/journal.pone.0179505>
- Hazzah, L., Bath, A., Dolrenry, S., Dickman, A., & Frank, L. (2017). From Attitudes to Actions: Predictors of Lion Killing by Maasai Warriors. *PLoS ONE*, 12(1). <https://doi.org/10.1371/JOURNAL.PONE.0170796>

- Huertas-Ramirez, H., & Huertas-Herrera, A. (2015). Historiografía de la ganadería en la Orinoquía. AICA, 6, 300–307. <https://www.researchgate.net/publication/286053933>
- Huggins, R. M. (1991). Some Practical Aspects of a Conditional Likelihood Approach to Capture Experiments. *Biometrics*, 47(2), 725. <https://doi.org/10.2307/2532158>
- Hyde, M., Boron, V., Rincón, S., Viana, D. F. P., Larcher, L., Reginato, G. A., & Payán, E. (2022). Refining carbon credits to contribute to large carnivore conservation: The jaguar as a case study. *Conservation Letters*, 15(3). <https://doi.org/10.1111/conl.12880>
- IDEAM. (2014). Distribución de la temperatura media anual (C) Promedio Multianual 1981-2010. . http://atlas.ideam.gov.co/basefiles/Temp_Med_Anual.pdf
- Jędrzejewski, W., Puerto, M. F., Goldberg, J. F., Hebblewhite, M., Abarca, M., Gamarra, G., Calderón, L. E., Romero, J. F., Viloría, Á. L., Carreño, R., Robinson, H. S., Lampo, M., Boede, E. O., Biganzoli, A., Stachowicz, I., Velásquez, G., & Schmidt, K. (2017). Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring. *Mammal Research*, 62(1), 9–19. <https://doi.org/10.1007/s13364-016-0300-2>
- Jędrzejewski, W., Robinson, H. S., Abarca, M., Zeller, K. A., Velasquez, G., Paemelaere, E. A. D., Goldberg, J. F., Payan, E., Hoogesteijn, R., Boede, E. O., Schmidt, K., Lampo, M., Viloría, Á. L., Carreño, R., Robinson, N., Lukacs, P. M., Nowak, J. J., Salom-Pérez, R., Castañeda, F., ... Quigley, H. (2018). Estimating large carnivore populations at global scale based on spatial predictions of density and distribution – Application to the jaguar (*Panthera onca*). *PLOS ONE*, 13(3), e0194719. <https://doi.org/10.1371/journal.pone.0194719>
- Kantek, D. L. Z., Trinca, C. S., Tortato, F., Devlin, A. L., de Azevedo, F. C. C., Cavalcanti, S., Silveira, L., Miyazaki, S. S., Junior, P. G. C., May-Junior, J. A., Fragoso, C. E., Sartorello, L. R., Rampim, L. E., Haberfeld, M. B., de Araujo, G. R., Morato, R. G., & Eizirik, E. (2021). Jaguars from the Brazilian Pantanal: Low genetic structure, male-biased dispersal, and implications for long-term conservation. *Biological Conservation*, 259, 109153. <https://doi.org/10.1016/J.BIOCON.2021.109153>
- Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, 87(11), 2925–2937.
- Kendall, W. L., Barker, R. J., White, G. C., Lindberg, M. S., Langtimm, C. A., & Peñaloza, C. L. (2013). Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods in Ecology and Evolution*, 4(9), 828–835. <https://doi.org/10.1111/2041-210X.12077>
- Knight, J. (2009). Making Wildlife Viewable: Habituation and Attraction. *Society & Animals*, 17(2), 167–184. <https://doi.org/https://doi.org/10.1163/156853009X418091>
- Lute, M. L., Carter, N. H., López-Bao, J. V., & Linnell, J. D. C. (2018). Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biological Conservation*, 218, 223–232. <https://doi.org/10.1016/J.BIOCON.2017.12.035>
- Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., & Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biological Conservation*, 215(1), 132–141. <https://doi.org/10.1016/j.biocon.2017.07.013>

- Macdonald, D. W., Johnson, P. J., Burnham, D., Dickman, A., Hinks, A., Sillero-Zubiri, C., & Macdonald, E. A. (2022). Understanding nuanced preferences for carnivore conservation: To know them is not always to love them. *Global Ecology and Conservation*, 37, e02150. <https://doi.org/10.1016/j.gecco.2022.e02150>
- Marchini, S., & Macdonald, D. W. (2012). Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. *Biological Conservation*, 147(1), 213–221. <https://doi.org/10.1016/j.biocon.2012.01.002>
- Miller, J. R. B., Stoner, K. J., Cejtin, M. R., Meyer, T. K., Middleton, A. D., & Schmitz, O. J. (2016). Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin*, 40(4), 806–815. <https://doi.org/10.1002/wsb.720>
- Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., de Paula, R. C., Ferraz, K. M. P. M., Kantek, D. L. Z., Miyazaki, S. S., Pereira, T. D. C., Araujo, G. R., Paviolo, A., de Angelo, C., di Bitetti, M. S., Cruz, P., Lima, F., Cullen, L., Sana, D. A., Ramalho, E. E., Carvalho, M. M., ... Leimgruber, P. (2016). Space use and movement of a neotropical top predator: The endangered jaguar. *PLoS ONE*, 11(12). <https://doi.org/10.1371/journal.pone.0168176>
- Mossaz, A., Buckley, R. C., & Castley, J. G. (2015). Ecotourism contributions to conservation of African big cats. *Journal for Nature Conservation*, 28, 112–118. <https://doi.org/10.1016/J.JNC.2015.09.009>
- M'soka, J., Creel, S., Becker, M. S., & Droge, E. (2016). Spotted hyaena survival and density in a lion depleted ecosystem: The effects of prey availability, humans and competition between large carnivores in African savannahs. *Biological Conservation*, 201, 348–355. <https://doi.org/https://doi.org/10.1016/j.biocon.2016.07.011>
- Noss, A. J., Polisar, J., Maffei, L., Garcia, R., & Silver, S. (2013). Evaluating jaguar densities with camera traps (Issue 2004).
- Nyhus, P. J. (2016). Human-Wildlife Conflict and Coexistence. *Annual Review of Environment and Resources*, 41, 143–171. <https://doi.org/10.1146/annurev-environ-110615-085634>
- Ohrens, O., Tortato, F. R., Hoogesteijn, R., Sarno, R. J., Quigley, H., Goic, D., & Elbroch, L. M. (2021). Predator tourism improves tolerance for pumas, but may increase future conflict among ranchers in Chile. *Biological Conservation*, 258, 109150. <https://doi.org/10.1016/J.BIOCON.2021.109150>
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs*, 3–135. <https://doi.org/10.2307/3830650>
- Payan, E., & Trujillo, L. A. (2006). The Tigrilladas in Colombia. *CAT News*, 44.
- Pereira, K. S., Gibson, L., Biggs, D., Samarasinghe, D., & Braczkowski, A. R. (2022). Individual Identification of Large Felids in Field Studies: Common Methods, Challenges, and Implications for Conservation Science. *Frontiers in Ecology and Evolution*, 10, 350. <https://doi.org/10.3389/fevo.2022.866403>
- Petracca, L. S., Hernández-Potosme, S., Obando-Sampson, L., Salom-Pérez, R., Quigley, H., & Robinson, H. S. (2014). Agricultural encroachment and lack of enforcement threaten connectivity of range-wide

- jaguar (*Panthera onca*) corridor. *Journal for Nature Conservation*, 22(5), 436–444. <https://doi.org/10.1016/j.jnc.2014.04.002>
- Pledger, S. (2000). Unified Maximum Likelihood Estimates for Closed Capture-Recapture Models Using Mixtures. *Biometrics*, 56, 434–442.
- Quigley, H. Foster, R. Petracca, L. Payan, E. Salom, R. Harmsen, B. (2017). *Panthera onca*, Jaguar. IUCN Red List, 8235, 1–29. <http://www.iucnredlist.org/details/15953/0>
- Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143(4), 939–945. <https://doi.org/10.1016/j.biocon.2010.01.002>
- Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., Wich, S. A., McNutt, J. W., & Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, 29(14), R681–R682. <https://doi.org/10.1016/j.cub.2019.05.056>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World’s Largest Carnivores. *Science*, 343(6167). <https://doi.org/10.1126/science.1241484>
- Robinson, H. S., Goodrich, J. M., Miquelle, D. G., Miller, C. S., & Seryodkin, I. V. (2015). Mortality of Amur tigers: The more things change, the more they stay the same. *Integrative Zoology*, 10(4), 344–353. <https://doi.org/10.1111/1749-4877.12147>
- Romero-Ruiz, M. H., Flantua, S. G. A., Tansey, K., & Berrio, J. C. (2012). Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. *Applied Geography*, 32(2), 766–776. <https://doi.org/10.1016/j.apgeog.2011.08.010>
- Royle, J. A., Nichols, J. D., Karanth, K. U., & Gopalaswamy, A. M. (2009). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, 46(1), 118–127. <https://doi.org/10.1111/j.1365-2664.2008.01578.x>
- Royle, J. A., & Young, K. v. (2008). A hierarchical model for spatial capture recapture data. *Ecology*, 89(8), 2281–2289. <https://doi.org/10.1890/07-0601.1>
- Salerno, J., Borgerhoff Mulder, M., Grote, M. N., Ghiselli, M., & Packer, C. (2016). Household livelihoods and conflict with wildlife in community-based conservation areas across northern Tanzania. *Oryx*, 50(4), 702–712. <https://doi.org/10.1017/S0030605315000393>
- Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T. A., Tôrres, N. M., & Silveira, L. (2011). Improving density estimates for elusive carnivores: Accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation*, 144(3), 1017–1024. <https://doi.org/10.1016/j.biocon.2010.12.011>
- Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Egli, L., Jafari, A., Ahmadpour, M., Qashqaei, A., Ghadirian, T., Filla, M., Kiabi, B., Balkenhol, N., Waltert, M., & Khorozyan, I. (2019). Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock

- depredation rate by large carnivores. *Journal of Applied Ecology*, 56(2), 365–374. <https://doi.org/https://doi.org/10.1111/1365-2664.13266>
- Srbek-Araujo, A. C., & Chiarello, A. G. (2017). Population status of the jaguar *Panthera onca* in one of its last strongholds in the Atlantic Forest. *Oryx*, 51(2), 246–253. <https://doi.org/10.1017/S0030605315001222>
- Suárez-Castro, A. F., Ramírez-Chaves, H. E., Noguera-Urbano, E. A., Velásquez-Tibatá, J., González-Maya, J. F., & Lizcano, D. J. (2021). Vacíos de información espacial sobre la riqueza de mamíferos terrestres continentales de Colombia. *Caldasia*, 43(2), 247–260. <https://doi.org/10.15446/caldasia.v43n2.85443>
- Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Rabinowitz, A., & Quigley, H. (2016). Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). *Ecological Applications*, 26(4), 1112–1124. <https://doi.org/10.1890/15-0602>
- Tobler, M. W., & Powell, G. V. N. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, 159, 109–118. <https://doi.org/10.1016/j.biocon.2012.12.009>
- Tortato, F., Izzo, T., Hoogesteijn, R., & Peres, C. (2017). The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation*, 11, 106–114. <https://doi.org/10.1016/j.gecco.2017.05.003>
- Van Der Meer, E., & Dullemont, H. (2021). Human-carnivore coexistence: factors influencing stakeholder attitudes towards large carnivores and conservation in Zimbabwe. *Environmental Conservation*, 48(1), 48–57. <https://doi.org/10.1017/S0376892920000491>
- Vélez, D., Tamayo, E., Ayerbe-Quiñones, F., Torres, J., Rey, J., Castro-Moreno, C., Ramírez, B., & Ochoa-Quintero, J. M. (2021). Distribution of birds in Colombia. <https://doi.org/10.3897/BDJ.9.e59202>
- Venumière-Lefebvre, C. C., Breck, S. W., & Crooks, K. R. (2022). A systematic map of human-carnivore coexistence. *Biological Conservation*, 268, 109515. <https://doi.org/10.1016/j.biocon.2022.109515>
- White, G. C. (1982). Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory.
- White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46(sup1), S120–S139. <https://doi.org/10.1080/00063659909477239>

Chapter 2 : Food subsidies reduce livestock depredations by a recovering carnivore

Introduction

Anthropogenic activities have led to species extinction globally (Ceballos et al., 2017; McCallum, 2015). Large terrestrial carnivores are particularly vulnerable to extinction due to their large home ranges, low reproduction rate, and systematic persecution due to conflict with humans (Nyhus, 2016; Ripple et al., 2014). Shifting societal values and attitudes towards carnivores away from extirpation to conservation have led to new policies aimed at protecting remaining populations and, in some cases, reintroducing locally extirpated species (Carver et al., 2021; Manfredo et al., 2021; Seddon et al., 2014). Charismatic carnivores that were extirpated from significant portions of their historical range are often the focus of reintroduction efforts (Corlett, 2016; Evans et al., 2022).

Once reintroduced, a primary hurdle for carnivore recovery can be conflict with human livelihoods resulting from livestock depredations (Breck et al., 2012; Muhly & Musiani, 2009). Consequently, an important management and conservation goal is to implement preventative strategies to reduce livestock depredations, thereby minimizing livelihood impacts and lethal removal of carnivores (Lute et al., 2018). Significant barriers exist, however, in the creation and adoption of new conflict reduction strategies due to disparate desired outcomes between conservationists and livestock producers (Lute & Carter, 2020) and limited practicality of many tools designed without input from the agricultural community (Hyde, Breck, et al., 2022; Miller et al., 2016). The development and evaluation of new techniques to reduce losses (van Eeden et al., 2018), coupled with studies of underlying factors that influence depredation, are needed to reduce human-carnivore conflict (Gervasi et al., 2021).

Quantifying the temporal, spatial, and ecological dynamics that underpin livestock depredation is critical to understand and mitigate such conflict. Many depredations, however, are not encountered, especially on extensive rangelands that are remote and have limited human oversight (Breck et al., 2011; Oakleaf et al., 2003). Furthermore, if detected, some conflict incidents are not reported by producers to management agencies, even if compensation is available for livestock losses (Bhushal et al., 2024; Marino et al., 2016; Nickerson, 2021). It is therefore necessary to account for imperfect detection of depredation events in models to accurately represent the frequency and distribution of conflict incidents. Failure to accurately estimate conflicts may constrain efforts to reduce depredation rates and to mitigate illegal killings of carnivores (Liberg et al., 2012) and livelihood impacts (Goswami et al., 2015).

The endangered Mexican wolf (*Canis lupus baileyi*) was extirpated from its range in the Southwestern United States by the 1970s following decades of an extensive eradication program. In 1998, 11 wolves were first reintroduced in Arizona (US Fish and Wildlife Service, 1999) and recovery efforts are ongoing in Arizona, New Mexico, and Mexico. Restoring a viable population of Mexican wolves is challenging because of extensive rangelands in the recovery area where monitoring wolf-livestock conflict is difficult. Thus, there is a need to find effective methods for reducing livestock depredations on large, rugged, open landscapes where some conflict reduction tools, such as electric fencing, fladry and scare devices, are often impractical or ineffective. The Interagency Field Team (IFT) conducts management of Mexican wolves in the field and is composed of personnel from the Arizona Game and Fish Department, New Mexico Department of Game and Fish, US Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (herein Wildlife Services), US Department of Agriculture-Forest Service, United

States Fish and Wildlife Service, and the White Mountain Apache Tribe. The IFT coordinates with ranchers and conducts work to reduce conflict while promoting wolf recovery.

One method hypothesized to reduce conflict with Mexican wolves is diversionary feeding, whereby managers provide food caches of carnivore logs (<https://www.nebraskabrand.com/>) or ungulate roadkill to reduce the likelihood of livestock depredation (U.S. Fish and Wildlife Service, 2017). Diversionary feeding to divert animals from potential conflict has been attempted in other systems with large carnivores (e.g., bears; Garshelis et al., 2017). Such anthropogenic subsidies are known to alter carnivore diet, movement, and activities (Ciucci et al., 2020; Fritts et al., 2003; Lischka et al., 2019; Newsome et al., 2015; Northrup & Boyce, 2012), maximizing energetic returns while reducing costs, and in some cases, risks (Petroelje et al., 2019). The IFT began using diversionary feeding in 2008, but despite the method's 16-year history, its effectiveness at reducing livestock depredation has not been evaluated.

In this study we tested the hypothesis that diversionary feeding reduces livestock depredations by Mexican wolves. We developed a Bayesian hierarchical model to evaluate its efficacy by estimating what biotic factors correlate with depredations and estimating the probability of detection of livestock depredations within a wolf pack territory. In doing so, we were able to estimate depredations as a factor of observed (i.e., reported and verified) depredations. Our model can be used to estimate unobserved variables (i.e., those that cannot be directly measured) for other cases of human-carnivore conflict, and we discuss the importance of estimating depredations and probability of detections of depredation to promote shared landscapes with carnivores.

Materials and methods

Study area

The Mexican Wolf Experimental Population Area (MWEPA) includes parts of the US states of Arizona and New Mexico, including the Fort Apache Indian Reservation, within historical range, south to the US-Mexico border (Figure 2.1). The MWEPA consists of three zones with differential management. All wolf packs in this study resided in zone 1 of the MWEPA (inclusive of what was designated Blue Range Wolf Recovery Area), consisting of the Gila, Apache-Sitgreaves, Tonto, and Cibola National Forests. The area consists of ~32,400 km² (8 million acres) with primarily evergreen forest (57%), shrubland (36%), and grassland (6%) vegetation. Details of the study area can be found in (Martínez-Meyer et al., 2021; U.S. Fish and Wildlife Service, 2014). Cattle ranching, and in particular cow-calf operations, is the principal land use activity across the Mexican wolf recovery zone. Cattle are typically grazed on public land allotments during the summer months (June-October) in Arizona and year-round in New Mexico. Compensation for livestock losses is available in both states for confirmed wolf depredations (U.S. Fish and Wildlife Service, 2022).

Data collection and processing

We collected data on pack size, diversionary feeding date, depredations, and locations for wolf packs that received diversionary feeding between 2014-2021. Data prior to 2014 were not used because GPS collars were not yet common in the program. Our unit of evaluation was the pack-year, the calendar year for which pack data were obtained and analyzed by the program. Minimum pack sizes were determined by IFT staff through annual counts which culminated with helicopter operations (USFWS permit number: TE091551). GPS collars were placed on at least one individual in each wolf pack each year. We selected one non-dispersing wolf per pack to

represent the pack's annual home range, with preference given to the breeding female. We thinned points to have 2 or less points per day. We used the resulting GPS locations to calculate kernel density estimators for each pack's annual home range using a 95% extrapolated isopleth as the home range contour and a smoothing factor of the reference bandwidth (Silverman, 1986) in the terra package (Hijmans et al., 2023) in R version 4.1.1 (R Core Team, 2022). Two packs were removed due to insufficient GPS locations to calculate annual home ranges. Single wolves, depredations attributed to them, and unidentified wolves were excluded from the analysis (Figure 2.2A).

Diversionsary feeding via food caches was applied by the IFT to packs that previously had a series of depredations or that were suspected of depredations. The IFT collected dates, locations, and target pack of all food caches. We excluded packs that received supplementary feeding, which was implemented for packs with fostered pups to increase survival probability. Food caches were in areas frequently used by wolves traveling to/from dens or rendezvous sites, where a wolf pack rears pups after abandoning dens in late summer or fall (Mech & Boitani, 2003). One cache would be placed at a time, and if a cache was not used or was intercepted by other species, an additional cache would be placed. Most (76%) food caches were placed from 1 April to 31 October when wolf movements are more predictable because of the utilization of dens and rendezvous sites (Figure 2.2B).

Livestock depredations were located by producers or members of the IFT and reported to Wildlife Services. A trained Wildlife Services employee inspected the carcass and surrounding area and determined whether the depredation was by a wolf. We only used confirmed depredations that were attributed to a specific pack by the USFWS. For the before-after comparison of depredations, we used depredations that occurred three months before the food cache was placed

and depredations that occurred three months after. When multiple caches were placed, we considered the date of the first deployment to be the starting date for the three-month period.

We used a set of covariates from the literature that potentially affect depredation risk. Annual livestock density is an important factor for assessing depredation risk (DeCesare et al., 2018), but exact numbers of livestock are not available for the region. We used the linear regression analysis of Animal Unit Month (AUM) data from lands managed by the US Forest Service and Bureau of Land Management with a set of biologically relevant variables, such as land cover and productivity. We extracted AUM data for each pack-year's home range and divided by the 95% KDE home range area to obtain density. Complete methods for the regression can be found in supplementary information S2.1 and Goljani Amirkhiz et al. (2018). We predicted that higher densities of cattle would be correlated with higher depredations before and after diversionary feeding.

Elk (*Cervus canadensis*), mule (*Odocoileus hemionus*) and white-tailed (*O. virginianus*) deer comprise the majority of Mexican wolves' native prey biomass (Smith et al., 2023). Prey data at the wolf home range scale were unavailable. We therefore used available occurrence data from state management agencies and the Global Biodiversity Information Facility (gbif.org) to create species distribution models for elk and both species of deer. The species distribution models were created using machine learning methods in Maxent (Phillips et al., 2006). Species distribution models are correlated with local abundances, and Maxent's raw output can be directly interpreted as a model of relative abundance (Phillips et al., 2017). Complete methods can be found in supplementary information S2.2 and Goljani Amirkhiz et al. (2018). Though earlier studies demonstrate that native prey density can be positively correlated with depredations (Bradley & Pletscher, 2005; Treves et al., 2004), a recent systematic review of wolf diets found that

depredations were negatively correlated with prey density (Janeiro-Otero et al., 2020). We therefore predicted relative abundance of ungulates within a wolf pack's home (herein prey density) to be negatively correlated with depredations before and after diversionary feeding.

Pack size may be positively correlated with depredations, presumably because larger packs have larger energy requirements and higher encounter rates with livestock when pack members are dispersed (Bradley et al., 2015). We used a quadratic term for minimum pack size as a covariate on depredations because pack size has a non-linear relationship with predation due to an increased proportion of individuals in larger packs that utilize resources but contribute less to capturing prey (MacNulty et al., 2012; Mech et al., 2015). We predicted that pack size would have a positive relationship with depredations before the start of diversionary feeding because of larger energy requirements for the pack. We did not expect pack size to be positively or negatively correlated with depredations after diversionary feeding because diversionary feeding would presumably satisfy the energetic needs of all pack members.

We used a zero-inflated model to assess the impact of the variables on observed depredations and reduce incorrect findings caused by excessive zeros in the data (Martin et al., 2005). Zeros can arise in a depredation dataset from missing detections, non-reporting of depredation events and the absence of depredations (Soh et al., 2014). We used whether depredations were discovered in the home range before and after diversionary feeding for zero-inflation. We employed a logistic regression that models covariates associated with the human accessibility of grazing allotments to estimate probability of detection as an unobserved variable. We used each wolf pack's annual home range to define the area where detections occurred. From each home range we calculated percent road coverage, median slope, and forest cover and used these variables as covariates to model detection of livestock carcasses. We predicted that

increasing slope and forest cover would be negatively correlated with probability of detection and that increasing road density would be positively correlated with probability of detection.

We extracted percent forest cover for each year using the most recent National Land Cover Dataset (2013, 2016, 2019) for forests (Homer et al., 2012). We calculated median slope for each pack's yearly home range using U.S. Geological Survey elevation data 30-meter resolution from the `elevatr` package (Earth Resources Observation and Science Center/U.S. Geological Survey/U.S. Department of the Interior, 1997). We calculated road density (Boeing, 2017) as a percent of each pack's home range in the `terra` package (Hijmans et al., 2023). We tested covariates for correlation, and no covariates had a correlation higher than 0.6.

A challenge in our study system was disentangling changes in depredations from seasonal variation in native prey vulnerability, particularly if post-treatment reductions in depredation could be attributable to increased predation on elk neonates in May and June. We therefore ran our model with a subset of pack-years whose post-diversionary feeding period did not include elk calving season to determine if depredation reduction rates were consistent between groups.

Deterministic & process model

We created a Bayesian hierarchical model to estimate depredations by Mexican wolf packs before and after the treatment, given that not all are found or reported. We modeled our response variable of observed depredations as the product of the latent variable estimated depredations and the detection process. We modeled estimated depredations as a Poisson regression, where λ_{ij} is a function of minimum pack size, prey density, and annual livestock density. We modeled probability of detection p_{ij} in a logistic regression as the product of slope, forest cover, and road coverage. We modeled the intercept as a fixed effect for each state in both the depredation and detection process. Our dataset had a state-structure in the frequency and location of depredation

events (Figure 2.2C and Figure 2.2D). This state-structure is due to year-round grazing of cattle on public lands in New Mexico being more common, and wolves in areas with year-around grazing consumed 21% more livestock in a study of summer diets (Merkle et al., 2009).

We specified flat priors for all intercepts and covariates and used normally distributed priors for the Poisson regression of depredation. We considered covariates to be strongly meaningful if the 95% credible intervals did not overlap zero and moderately meaningful if their 75% credible intervals did not overlap zero.

The posterior distribution of the model is expressed as follows:

$$[\lambda_{ij}, p_{ij}, z_{ij}, \boldsymbol{\beta}, \boldsymbol{\alpha} \mid y_{ij}, \lambda_{ij}, p_{ij}, z_{ij}] \propto \prod_{i=1}^{73} \prod_{j=1}^2 [y_{ij} \mid \lambda_{ij}, p_{ij}, z_{ij}, \boldsymbol{\beta}, \boldsymbol{\alpha}] [z_{ij} \mid p_{ij}, \boldsymbol{\alpha}] [p_{ij} \mid \boldsymbol{\alpha}] [\lambda_{ij} \mid \boldsymbol{\beta}] [\boldsymbol{\beta}] [\boldsymbol{\alpha}] \quad (1)$$

Where:

$$y_{ij} \begin{cases} 0 & \text{if } z_{ij} = 0 \\ \text{Poisson}(\lambda_{ij}) & \text{if } z_{ij} = 1 \end{cases} \quad (2)$$

The distributions for the likelihoods and priors are modeled by:

$$y_{ij} \sim \text{Poisson}(y_{ij} \mid \lambda_{ij} \times z_{ij}) \quad (3) \\ \text{Bernoulli}(z_{ij} \mid p_{ij})$$

The detection process (p_{ij}) is modeled by:

$$p_{ij} = \text{logit}^{-1}(\alpha_{0j} + \alpha_1 r_i + \alpha_2 s_i + \alpha_3 f_i) \quad (4) \\ \boldsymbol{\alpha} \sim \text{logistic}(0, 1)$$

Parameters for the Poisson regression of the depredation process are:

$$\text{Poisson}(\lambda_{ij} \times z_{ij}) \quad (5) \\ \lambda_{ij} = e^{(\beta_{0,j} + \beta_1 w_{1,i}^2 + \beta_2 w_{2,i} + \beta_3 w_{3,i} + \beta_4 w_{4,i})} \\ \boldsymbol{\beta} \sim \text{normal}(0, 1000)$$

We then estimated the percent reduction and mean reduction in depredations before and after diversionary feeding within the model.

Estimation

We estimated the marginal posterior distribution of the parameters using Markov chain Monte Carlo (MCMC) methods in JAGS 4.3.1 (Plummer, 2022a) in R (R Core Team, 2022) through the rjags package (Plummer, 2022b). We ran each of four chains for 250,000 iterations, used a 100,000-iteration burn-in, and thinned samples by 5. We inspected trace plots and Gelman-Rubin diagnostics for convergence (Gelman et al., 1995), ensuring that all R-hat values were < 1.01.

Model evaluation

We conducted posterior predictive checks to evaluate the fit of the data. We simulated data based on our dataset, where observed data, T^{obs} , and simulated data, T^{sim} , are:

$$T^{obs} = \sum_{i=1}^I (y_{ij}^{obs} - \lambda_{ij})^2 \quad T^{sim} = \sum_{i=1}^I (y_{ij}^{sim} - \lambda_{ij})^2 \quad (6)$$

and y_{ij} is the mean of draw from the posterior distribution of the simulated data and λ_{ij} is the model prediction for mean depredeations of each pack per year. We then calculated a Bayesian p-value using the following equation, where lack of fit occurs when P_b is close to 0 or 1 (Gelman et al., 2014):

$$P_b = Pr[T^{sim}(y_{ij}^{sim}, \theta) \geq T^{obs}(y_{ij}^{obs}, \theta) | y_{ij}] \quad (7)$$

Results

We evaluated the use of diversionary feeding for 73 pack-years from 2014 -2021 in the full model. Bayesian p-values were 0.50 for depredeations before, 0.50 for depredeations after, and 0.54 for detection, indicating adequate model fit. The R-hat values of the Gelman-Rubin diagnostics for all parameters were ≤ 1.01 .

Depredation

From 2014-2021 the IFT verified 79 confirmed depredations in the three months before diversionary feeding began and 44 in the three months after for the pack-years included in this study. Model estimates for the total number of depredations from 2014-2021 were 127 (SE: 1.71; 95% CI: 100.06 – 157.16) depredations before and 70 (SE: 1.31; 95% CIs: 50.29 – 94.16) depredations after diversionary feeding. Of the 127 estimated depredations before diversionary feeding, 36 (SE: 4.51; 95% CI: 17.46 – 63.65) were in Arizona and 91 (SE: 7.58; 95% CI: 57.46 – 135.55) were in New Mexico. After diversionary feeding, 21 (SE: 3.30; 95% CI: 8.59 – 42.10) depredations were in Arizona and 49 (SE: 6.12; 95% CI: 24.51 – 87.04) were in New Mexico.

The mean of estimated depredations per pack-year before diversionary feeding was 1.74 (SE: 0.02, 95% CI: 1.37 – 2.15), and the mean of estimated depredations per pack-year after diversionary feeding was 0.96 (SE: 0.02, 95% CI: 0.68 – 1.29; Figure 2.3). Of the 73 pack-years evaluated, 62 (85%) had fewer depredations after diversionary feeding. Eleven pack-years (15%) had more depredations after diversionary feeding than before. The overall reduction in depredations after diversionary feeding was $43.9 \pm 0.01\%$ or 0.78 ± 0.03 depredations per pack-year.

The model of the subset of pack-years ($n = 47$) whose post-diversionary period did not include elk calving season had a higher overall reduction in depredations of $53.6 \pm 0.02\%$ or 1.14 ± 0.05 depredations per pack-year. The comparable estimate indicates that elk calving season did not account for the depredation reduction in the full model.

Before diversionary feeding, prey density was negatively correlated with depredations and moderately meaningful ($\beta = -0.23$, 75% CI: $-0.44 - -0.03$; Figure 2.4A). Minimum pack size ($\beta = 0.00$, 95% CI: $-0.26 - 0.23$) was not correlated to depredations, nor was annual livestock density

($\beta = -0.06$, 95% CI: $-0.32 - 0.20$). The intercept for New Mexico was $\beta = 0.61$ (95% CI: $0.23 - 0.97$) with a back-transformed value of 1.84. The intercept for Arizona was $\beta = 0.23$ (95% CI: $0.29 - 0.71$) with a back-transformed value of 1.26.

After diversionary feeding, minimum pack size ($\beta = -0.53$, 95% CI: $-1.10 - -0.06$; Figure 2.5B) was negatively correlated with depredations and strongly meaningful. Prey density ($\beta = 0.43$, 75% CI: $0.16 - 0.69$) was positively correlated and moderately meaningful, and annual livestock density ($\beta = -0.23$, 75% CI: $-0.43 - -0.04$) was negatively correlated and moderately meaningful. The intercept for New Mexico was $\beta = 0.53$ (95% CI: $0.03 - 1.00$) with a back-transformed value of 1.70. The intercept for Arizona was $\beta = -3.1$ (95% CI: $-1.02 - 0.34$) with a back-transformed value of 0.73.

Detection

The detection of livestock depredations varied by year (Figure 2.5A). The mean probability of detection before diversionary feeding over the eight-year period was 0.63 (SE 0.04, 95% CI: $0.39 - 0.84$). The highest recorded annual probability of detection of 0.67 (SE 0.04, 95% CI: $0.42 - 0.86$) was in 2019. The lowest probability of detection of 0.57 (SE 0.05, 95% CI: $0.31 - 0.82$) was in 2021. Detection of depredation events also varied by pack.

No covariate of detection of depredations events was meaningful (Figure 2.5B). Median slope had a β coefficient of -0.13 (95% CI: $-0.72 - 0.47$), forest had a β coefficient of 0.16 (95% CI: $-0.36 - 0.69$), and road coverage had a β coefficient of 0.29 (95% CI: $-0.58 - 1.18$).

Discussion

We evaluated the effectiveness of diversionary feeding to reduce livestock depredations by Mexican wolves. We found that depredations were reduced by 43.9% after diversionary feeding

began, a mean decrease of 0.78 depredations per pack-year. This reduction is important for meeting Mexican wolf recovery goals of conflict prevention to support population growth (Breck et al., 2023). Our results suggest that the practice is effective across a range of ecological conditions. Eighty-five percent of pack-years had fewer depredations after diversionary feeding, despite differences in pack size, prey density, and annual livestock density within their range.

Our model elucidated the predictors of depredations before and after diversionary feeding. Contrary to our prediction, pack size was negatively correlated with depredations and strongly meaningful after diversionary feeding and had no correlation before diversionary feeding. The factors that influence wolf pack size have received much attention in the literature (Barber-Meyer et al., 2016; Cassidy et al., 2015; Fuller et al., 2003; MacNulty et al., 2014; Sells et al., 2022), though the relationship between pack size and depredations is yet to be established. We put forward two hypotheses for the negative correlation between pack size and depredations. First, smaller packs of Mexican wolves having longer handling times and losing more kills to scavengers (Peterson & Ciucci, 2003), which in turn leads small packs to have higher kill rates (Smith et al., 2023). Alternatively, larger packs may locate diversionary caches more quickly, while smaller packs may have more difficulty locating the cache and their cache may be more likely to be consumed by scavengers. Future research could evaluate wolves' ability to find the cache and interspecific competition with the local scavenging community to disentangle the relationship between pack size and diversionary feeding effectiveness.

Our prediction that prey density would be negatively correlated to depredations was only supported before diversionary feeding. We found moderate support that prey density was negatively correlated before but positively correlated after diversionary feeding. The positive correlation between prey density and depredations after diversionary feeding may be spurious, as

prey vulnerability was generally higher in the period following diversionary feeding. Alternatively, cattle may occupy flatter grasslands that prey vacate to avoid predation by wolves (Goljani Amirkhiz et al., 2018). Similarly, we found moderate support for a negative correlation for annual livestock density and depredations. The negative relationship between annual livestock density and depredations may be driven in part because unattended and freely grazing livestock, which are potentially more vulnerable to depredation, tend to occur at low densities (Janeiro-Otero et al., 2020). In our study, annual livestock density was modeled through regression methods and prey density through machine learning due to the unavailability of free-ranging livestock and prey data at the desired spatial scale. Finer scale data may be necessary to distinguish the relative influence of cattle and prey density and vulnerability on depredation rates by wolves.

A novel contribution of our assessment of this conflict prevention tool is the estimation of probability of detection, based on our collective experience and supporting literature that not all depredations are found or reported (Oakleaf, Mack & Murray 2003, Breck et al., 2011; Nickerson, 2021). The inclusion of detection probability of conflict events is an important step to address the livelihood impacts of human-wildlife conflict (Goswami et al., 2015). The probability of detection in our model is intended to represent an interaction between accessibility and human behavior in the process of finding and reporting a depredation. We chose three factors—slope, road coverage, and forest cover—that we hypothesized to be related to human behaviors of accessibility to pastures.

Over the eight years of our study, we estimated that 63% of depredations were reported and verified. Our model estimated more than triple the detection probability that is officially recognized by the Mexican Wolf Recovery Program, that estimates that one in five depredations will be found, reported, and verified (U.S. Fish and Wildlife Service 2014). In a study that

compared depredations on two ranches in the Mexican Wolf recovery area, Breck et al. (2011) found that the detection probability was 77.5% on one ranch and 33.0% on a second, concluding that search time was the primary driver behind the difference. This may explain some of the variation of detection probability between packs in our study, though we were unable to model search time or labor inputs because of the large number of operations and limited data availability.

While diversionary feeding was impactful for reducing depredations by Mexican wolves, the success of diversionary feeding as a conflict reduction tool depends on management goals and the target species' ecology. Species that are dietary generalists are more likely to accept diversionary feeding, but managers should have an effective distribution method and target individuals most likely to cause conflict rather than the population as a whole (Kubasiewicz et al., 2016). A consequence of diversionary feeding is that it may lead to increased survival and abundance of the target species (Miller, 2017), possibly exacerbating interactions between carnivores and livestock (Conover & Conover, 2021; Morehouse & Boyce, 2017). While increasing wolf abundance is an explicit goal for Mexican wolf population recovery (U.S. Fish and Wildlife Service, 2017), it may not be for other carnivore populations and should thus be monitored in conjunction with diversionary feeding.

Findings from other studies provide additional insight on when and where diversionary feeding is effective. Quasi-experimental studies in 1987-1991 in Alaska revealed that diversionary feeding of wolves and brown bears (*Ursus arctos*) enhanced survival of moose calves (Boertje et al., 1995). Similarly, diversionary feeding of red foxes (*Vulpes vulpes*) using moose remains decreased nest predation and increased breeding success by 43% and 57% in two locations in Norway (Finne et al., 2019). In contrast, Lewis et al. (2017) found that diversionary feeding of coyotes (*Canis latrans*) and black bears using beaver (*Castor canadensis*) carcasses and bakery

waste provided nearly no improvement of calf survival of caribou (*Rangifer tarandus*) in Newfoundland, Canada. This may have been due to effectively treating only black bears, since coyotes did not use bait stations. Similarly, studies from Europe and North America on diversionary feeding of brown and black bears found mixed results. Where unsuccessful, the quality of provided foods and the ease of access were similar to other anthropogenic sources where conflict occurred (Garshelis et al., 2017). Intraspecific competition may also be a factor hindering effectiveness of diversionary feeding for bears (Garshelis et al., 2017; Morehouse & Boyce, 2017).

Diversionary feeding as a depredation prevention strategy presents two main benefits to wildlife managers. First, it does not initially depend on producer adoption like other practices since it is implemented directly by the management agency. Second, many other nonlethal tools for wolves focus on fear conditioning in small areas to repel animals from a particular operation, as is the case with electric fences (Bruns, Waltert, & Khorozyan, 2020), fladry (Iliopoulos et al., 2019), and in some instances range riding (Parks & Messmer, 2016). The perceived risk-benefit tradeoff of the deterrent for the carnivore, frequency of its application, and long-term maintenance of the fear stimulus is necessary for these practices to be effective (Mumby & Plotnik, 2018). Unlike other conflict mitigation tools, diversionary feeding alters predators' feeding ecology voluntarily by offering low-risk and high reward food sources (Conover & Conover, 2021) during periods of higher caloric requirements and localized movements (i.e., denning and rendezvous season). This practice may be especially useful for small, highly monitored populations such as reintroduced or recovering populations. We suggest using diversionary feeding as a stop-gap method when vulnerable domestic calves and lambs are on the ground at the beginning of wolf denning season. It is likely best served to alleviate depredation problems of an individual pack rather than a widespread population management tool.

Diversionsary feeding has limitations and requires careful assessment of management goals and resources prior to implementation. In the Mexican Wolf recovery program, continued funding and stable human resources facilitate intensive monitoring of wolf movements and behavior. Managers are therefore able to quickly and effectively deploy and maintain food caches. Diversionsary feeding may be challenging for programs with limited human resources and monitoring capabilities. Additionally, caution is needed when moving ungulate carcasses between areas. In the study area, for example, ungulate roadkill is not moved between New Mexico and Arizona to prevent the transmission of chronic wasting disease. Like all conflict prevention tools, diversionsary feeding should be implemented in conjunction with a suite of tools. In New Mexico and Arizona, diversionsary feeding is used alongside range riding, turbo-fladry, and hazing. Ultimately, successful implementation of diversionsary feeding and other conflict mitigation tools hinges on collaborative efforts between producers, wildlife managers, and other interest groups.

Tables and Figures

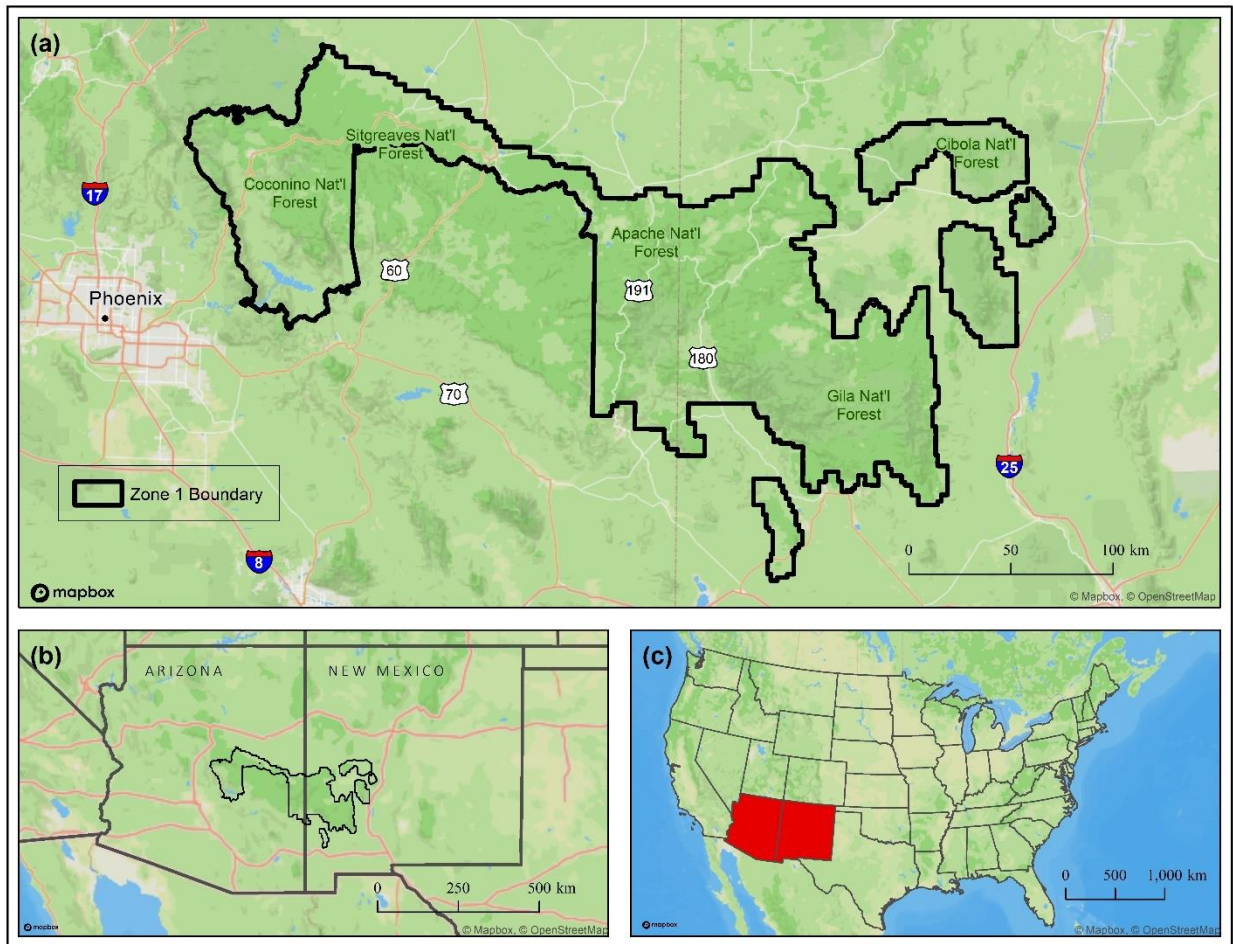


Figure 2.1. Study area of the Mexican Wolf Recovery Area Zone 1 in the US states of Arizona and New Mexico. Sources: US Fish and Wildlife Service, Mapbox.

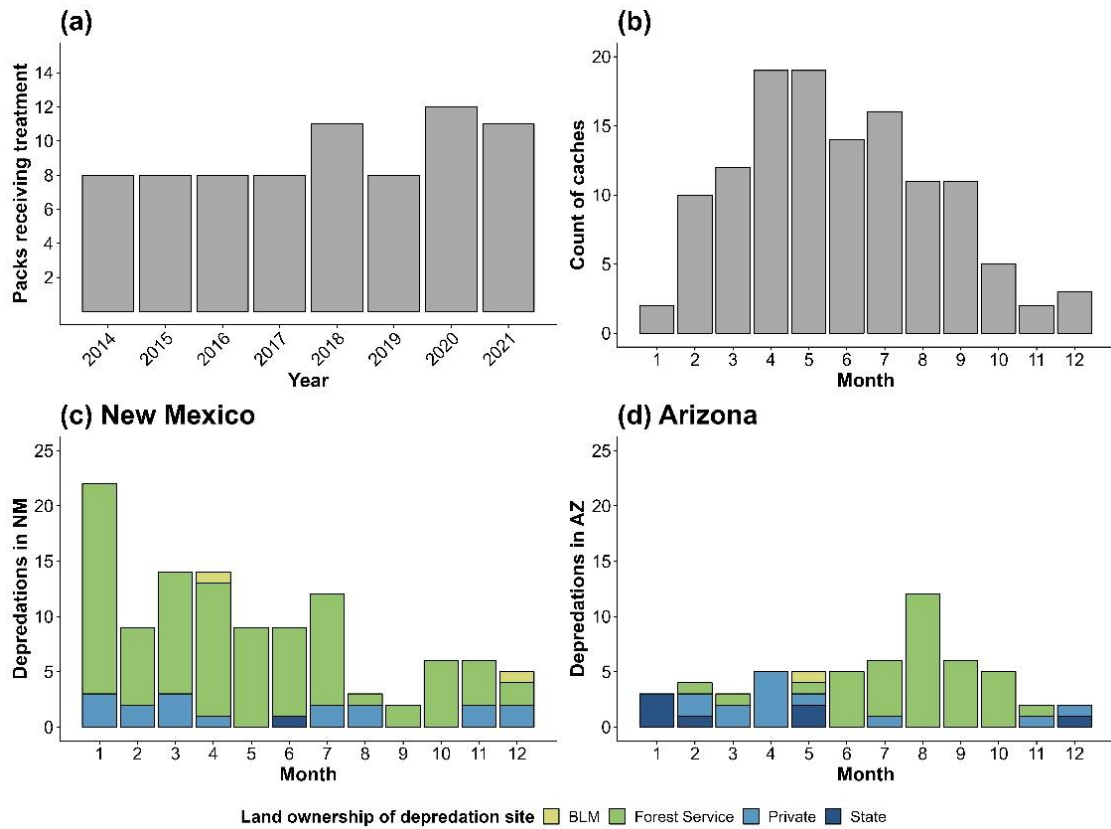


Figure 2.2. a) Mexican wolf packs receiving diversionary feeding by year. b) Month of food cache deployment between 2014-2021. c) The number of depredations from 2014-2014 in New Mexico by month by packs included in this study and land ownership. d) The number of depredations from 2014-2021 in Arizona by month by packs included in this study and land ownership. BLM = Bureau of Land Management, Forest Service = US Forest Service.

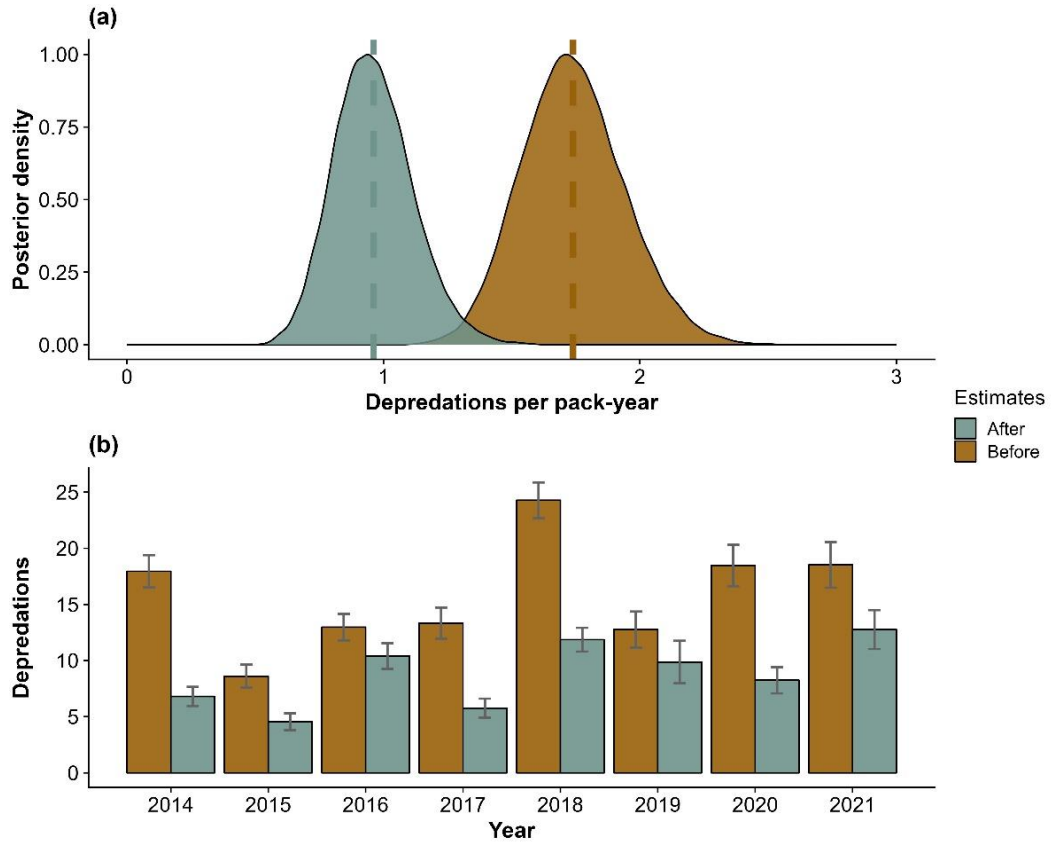


Figure 2.3. a) Posterior density of model estimated mean depredations per pack-year before (brown) and after (blue/green) diversionary feeding. b) Yearly distribution of model estimated depredations before and after diversionary feeding was applied with standard error depicted by the gray bars.

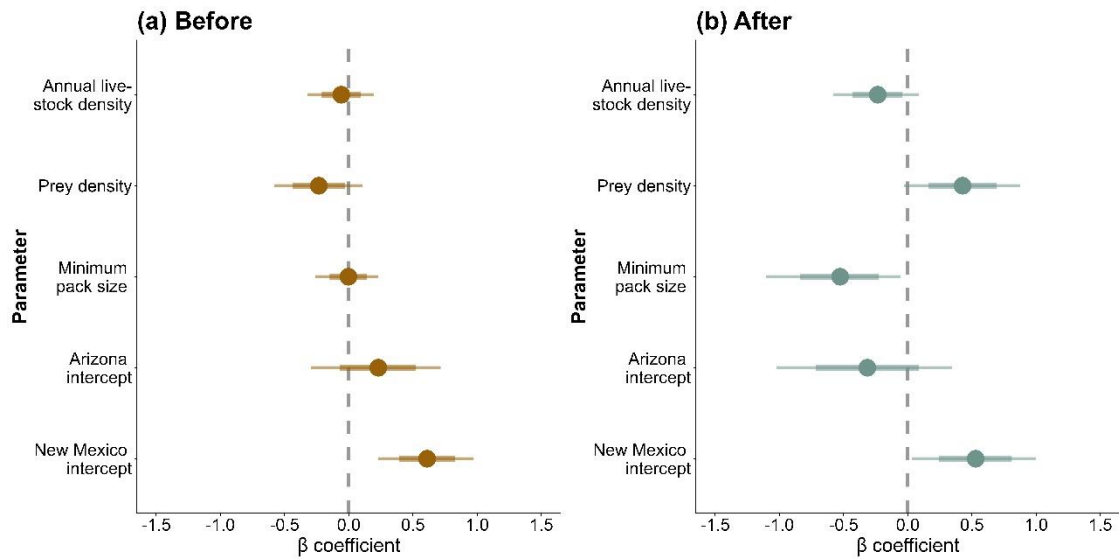


Figure 2.5. β coefficients for depredation before and after diversionary feeding. Points represent mean estimates, thick lines represent 75% credible intervals and thin lines represent 95% credible intervals. State differences of Arizona and New Mexico are modeled due to differences in grazing regimes.

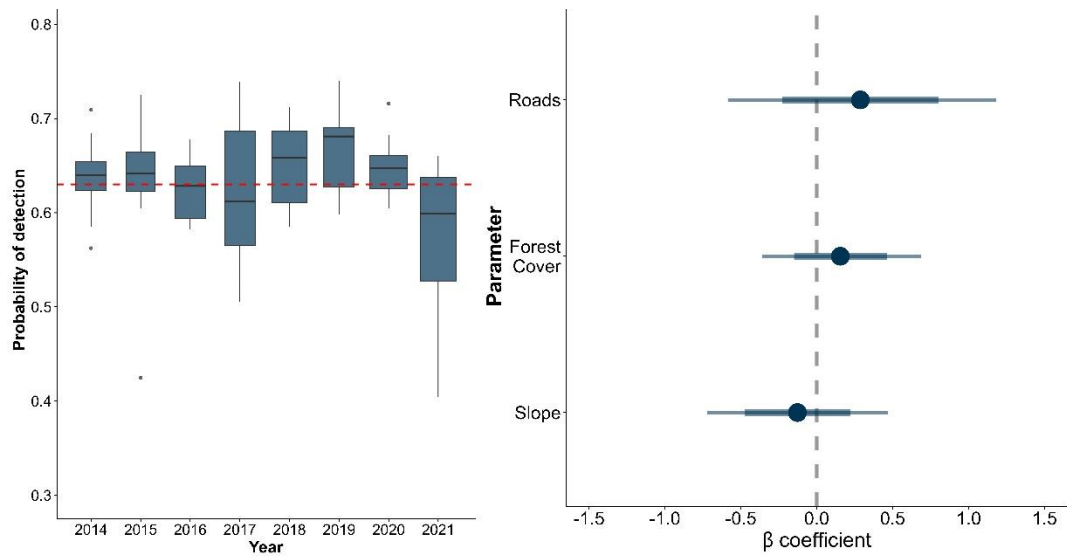


Figure 2.4. a) Probability of detections of livestock depredations from 2014-2021. The dashed red line represents the 2014-2021 mean probability of detection. b) Beta coefficients of detection covariates in the model. Thick lines represent 75% CIs and thin lines represent 95% CIs.

References

- Barber-Meyer, S. M., Mech, L. D., Newton, W. E., & Borg, B. L. (2016). Differential wolf-pack-size persistence and the role of risk when hunting dangerous prey. *Behaviour*, 153(12), 1473–1487. <https://doi.org/https://doi.org/10.1163/1568539X-00003391>
- Bhushal, G., Wolde, B., & Lal, P. (2024). Human-Wildlife Conflict and the Likelihood of Reporting Losses in Nepal. *Trees, Forests and People*, 100512. <https://doi.org/https://doi.org/10.1016/j.tfp.2024.100512>
- Boeing, G. (2017). U.S. Street Network Shapefiles, Node/Edge Lists, and GraphML Files (V2 ed.). Harvard Dataverse. <https://doi.org/doi/10.7910/DVN/CUWWYJ>
- Boertje, R. D., Kelleyhouse, D. G., & Hayes, R. D. (1995). Methods for Reducing Natural Predation on Moose in Alaska and Yukon: An Evaluation. In *Ecology and Conservation of Wolves in a Changing World* (pp. 505–515).
- Bradley, E. H., & Pletscher, D. H. (2005). Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. *Wildlife Society Bulletin*, 33(4), 1256–1265. [https://doi.org/10.2193/0091-7648\(2005\)33\[1256:afirtwd\]2.0.co;2](https://doi.org/10.2193/0091-7648(2005)33[1256:afirtwd]2.0.co;2)
- Bradley, E. H., Robinson, H. S., Bangs, E. E., Kunkel, K., Jimenez, M. D., Gude, J. A., & Grimm, T. (2015). Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. *The Journal of Wildlife Management*, 79(8), 1337–1346. <https://doi.org/10.1002/JWVG.948>
- Breck, S., Clark, P., Howery, L., Johnson, D., Kluever, B., Smallidge, S., & Cibils, A. (2012). A Perspective on Livestock–Wolf Interactions on Western Rangelands. *Rangelands*, 34(5), 6–11. <https://doi.org/10.2111/rangelands-d-11-00069.1>
- Breck, S. W., Davis, A. J., Oakleaf, J. K., Bergman, D. L., deVos, J., Greer, J. P., & Pepin, K. (2023). Factors affecting the recovery of Mexican wolves in the Southwest United States. *Journal of Applied Ecology*, n/a(n/a). <https://doi.org/https://doi.org/10.1111/1365-2664.14483>
- Breck, S. W., Kluever, B. M., Panasci, M., Oakleaf, J., Johnson, T., Ballard, W., Howery, L., & Bergman, D. L. (2011). Domestic calf mortality and producer detection rates in the Mexican wolf recovery area: Implications for livestock management and carnivore compensation schemes. *Biological Conservation*, 144(2), 930–936. <https://doi.org/10.1016/j.biocon.2010.12.014>
- Bruns, A., Waltert, M., & Khorozyan, I. (2020). The effectiveness of livestock protection measures against wolves (*Canis lupus*) and implications for their co-existence with humans. *Global Ecology and Conservation*, 21. <https://doi.org/10.1016/j.gecco.2019.e00868>
- Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S. R., Nelson, C., Gann, G. D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W. J., Davis, J., Sinclair, A., Bekoff, M., ... Soulé, M. (2021). Guiding principles for rewilding. *Conservation Biology*, 35(6), 1882–1893. <https://doi.org/https://doi.org/10.1111/cobi.13730>

- Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behavioral Ecology*, 26(5), 1352–1360. <https://doi.org/10.1093/beheco/arv081>
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114(30), E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., & Grottoli, L. (2020). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. *Global Ecology and Conservation*, 21, e00841. <https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00841>
- Conover, M. R., & Conover, D. O. (2021). *Human–Wildlife Interactions*. CRC Press. <https://doi.org/10.1201/9780429401404>
- Corlett, R. T. (2016). Restoration, Reintroduction, and Rewilding in a Changing World. *Trends in Ecology & Evolution*, 31(6), 453–462. <https://doi.org/https://doi.org/10.1016/j.tree.2016.02.017>
- DeCesare, Nicholas. J., Wilson, S. M., Bradley, E. H., Gude, J. A., Inman, R. M., Lance, N. J., Laudon, K., Nelson, A. A., Ross, M. S., & Smucker, T. D. (2018). Wolf-livestock conflict and the effects of wolf management. *The Journal of Wildlife Management*, 82(4), 711–722. <https://doi.org/10.1002/jwmg.21419>
- Earth Resources Observation and Science Center/U.S. Geological Survey/U.S. Department of the Interior. (1997). USGS 30 ARC-second Global Elevation Data, GTOPO30 (1997). In Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory.
- Evans, M. J., Gordon, I. J., Pierson, J. C., Neaves, L. E., Wilson, B. A., Brockett, B., Ross, C. E., Smith, K. J., Rapley, S., Andrewartha, T. A., Humphries, N., & Manning, A. D. (2022). Reintroduction biology and the IUCN Red List: The dominance of species of Least Concern in the peer-reviewed literature. *Global Ecology and Conservation*, 38, e02242. <https://doi.org/https://doi.org/10.1016/j.gecco.2022.e02242>
- Finne, M. H., Kristiansen, P., Rolstad, J., & Wegge, P. (2019). Diversionary feeding of red fox in spring increased productivity of forest grouse in southeast Norway. *Wildlife Biology*, 2019(1), 1–12. <https://doi.org/10.2981/wlb.00492>
- Fritts, S. H., Stephenson, R. O., Hayes, R. D., & Boitani, L. (2003). Wolves and humans. In *Wolves: Behavior, Ecology, and Conservation* (Issue 2, pp. 1–317). <https://doi.org/10.14430/arctic540>
- Fuller, T. K., Mech, L. D., Cochrane, J. F., Mech, L. D., & Boitani, L. (2003). *Wolf population dynamics*. University of Chicago Press.
- Garshelis, D. L., Baruch-Mordo, S., Bryan, A., Gunther, K. A., & Jerina, K. (2017). Is diversionary feeding an effective tool for reducing human–bear conflicts? Case studies from North America and Europe. *Ursus*, 28(1), 31–55.

- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (1995). Bayesian Data Analysis. Bayesian Data Analysis. <https://doi.org/10.1201/9780429258411>
- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2014). Bayesian data analysis (Vol. 2). Taylor & Francis Boca Raton.
- Gervasi, V., Linnell, J. D. C., Berce, T., Boitani, L., Cerne, R., Ciucci, P., Cretois, B., Derron-Hilfiker, D., Duchamp, C., Gastineau, A., Grente, O., Huber, D., Iliopoulos, Y., Karamanlidis, A. A., Kojola, I., Marucco, F., Mertzanis, Y., Männil, P., Norberg, H., ... Gimenez, O. (2021). Ecological correlates of large carnivore depredation on sheep in Europe. *Global Ecology and Conservation*, 30, e01798. <https://doi.org/https://doi.org/10.1016/j.gecco.2021.e01798>
- Goljani Amirkhiz, R., Frey, J. K., Cain, J. W., Breck, S. W., & Bergman, D. L. (2018). Predicting spatial factors associated with cattle depredations by the Mexican wolf (*Canis lupus baileyi*) with recommendations for depredation risk modeling. *Biological Conservation*, 224, 327–335. <https://doi.org/10.1016/J.BIOCON.2018.06.013>
- Goswami, V. R., Medhi, K., Nichols, J. D., & Oli, M. K. (2015). Mechanistic understanding of human-wildlife conflict through a novel application of dynamic occupancy models. *Conservation Biology*, 29(4), 1100–1110. <https://doi.org/10.1111/cobi.12475>
- Hijmans, R. J., Bivand, R., Pebesma, E., & Sumer, M. D. (2023). terra (pp. 1–319).
- Homer, C. G., Fry, J. A., Barnes, C. A., & Survey, U. S. G. (2012). The National Land Cover Database. In Fact Sheet. <https://doi.org/10.3133/fs20123020>
- Hyde, M., Breck, S. W., Few, A., Beaver, J., Schrecengost, J., Stone, J., Krebs, C., Talmo, R., Eneas, K., Nickerson, R., Kunkel, K. E., & Young, J. K. (2022). Multidisciplinary engagement for fencing research informs efficacy and rancher-to-researcher knowledge exchange. *Frontiers in Conservation Science*, 3, 88. <https://doi.org/10.3389/fcosc.2022.938054>
- Iliopoulos, Y., Astaras, C., Lazarou, Y., Petridou, M., Kazantzidis, S., & Waltert, M. (2019). Tools for co-existence: Fladry corrals efficiently repel wild wolves (*Canis lupus*) from experimental baiting sites. *Wildlife Research*, 46(6), 484–498. <https://doi.org/10.1071/WR18146>
- Janeiro-Otero, A., Newsome, T. M., Van Eeden, L. M., Ripple, W. J., & Dormann, C. F. (2020). Grey wolf (*Canis lupus*) predation on livestock in relation to prey availability. *Biological Conservation*, 243, 108433. <https://doi.org/https://doi.org/10.1016/j.biocon.2020.108433>
- Kubasiewicz, L. M., Bunnefeld, N., Tulloch, A. I. T., Quine, C. P., & Park, K. J. (2016). Diversionary feeding: an effective management strategy for conservation conflict? *Biodiversity and Conservation*, 25(1), 1–22. <https://doi.org/10.1007/S10531-015-1026-1/FIGURES/2>
- Lewis, K. P., Gullage, S. E., Fifield, D. A., Jennings, D. H., & Mahoney, S. P. (2017). Manipulations of black bear and coyote affect caribou calf survival. *The Journal of Wildlife Management*, 81(1), 122–132. <https://doi.org/https://doi.org/10.1002/jwmg.21174>
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Thompson Hobbs, N., & Sand, H. (2012). Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings*

- of the Royal Society B: Biological Sciences, 279(1730), 910–915.
<https://doi.org/10.1098/rspb.2011.1275>
- Lischka, S. A., Teel, T. L., Johnson, H. E., & Crooks, K. R. (2019). Understanding and managing human tolerance for a large carnivore in a residential system. *Biological Conservation*, 238. <https://doi.org/10.1016/j.biocon.2019.07.034>
- Lute, M. L., & Carter, N. H. (2020). Are We Coexisting With Carnivores in the American West? *Frontiers in Ecology and Evolution*, 8, 48. <https://doi.org/10.3389/FEVO.2020.00048/BIBTEX>
- Lute, M. L., Carter, N. H., López-Bao, J. V., & Linnell, J. D. C. (2018). Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biological Conservation*, 218, 223–232. <https://doi.org/10.1016/J.BIOCON.2017.12.035>
- MacNulty, D. R., Smith, D. W., Mech, L. D., Vucetich, J. A., & Packer, C. (2012). Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, 23(1), 75–82. <https://doi.org/10.1093/BEHECO/ARR159>
- MacNulty, D. R., Tallian, A., Stahler, D. R., & Smith, D. W. (2014). Influence of group size on the success of wolves hunting bison. *PloS One*, 9.
- Manfredo, M. J., Berl, R. E. W., Teel, T. L., & Bruskotter, J. T. (2021). Bringing social values to wildlife conservation decisions. *Frontiers in Ecology and the Environment*, 19(6), 355–362. <https://doi.org/10.1002/fee.2356>
- Marino, A., Braschi, C., Ricci, S., Salvatori, V., & Ciucci, P. (2016). Ex post and insurance-based compensation fail to increase tolerance for wolves in semi-agricultural landscapes of central Italy. *European Journal of Wildlife Research*, 62(2), 227–240. <https://doi.org/10.1007/s10344-016-1001-5>
- Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A. J., & Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters*, 8(11), 1235–1246. <https://doi.org/10.1111/j.1461-0248.2005.00826.x>
- Martínez-Meyer, E., González-Bernal, A., Velasco, J. A., Swetnam, T. L., González-Saucedo, Z. Y., Servín, J., López-González, C. A., Oakleaf, J. K., Liley, S., & Heffelfinger, J. R. (2021). Rangeswide habitat suitability analysis for the Mexican wolf (*Canis lupus baileyi*) to identify recovery areas in its historical distribution. *Diversity and Distributions*, 27(4), 642–654. <https://doi.org/https://doi.org/10.1111/ddi.13222>
- McCallum, M. L. (2015). Vertebrate biodiversity losses point to a sixth mass extinction. *Biodiversity and Conservation*, 24(10), 2497–2519. <https://doi.org/10.1007/s10531-015-0940-6>
- Mech, L. D., & Boitani, L. (2003). Wolf social ecology. In *Wolves: Ecology, Behavior, and Conservation*. University of Chicago Press.
- Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. University of Chicago Press. <http://ebookcentral.proquest.com/lib/csu/detail.action?docID=3570563>

- Merkle, J. A., Krausman, P. R., Stark, D. W., Oakleaf, J. K., & Ballard, W. B. (2009). Summer diet of the Mexican Gray Wolf (*Canis lupus baileyi*). *Southwestern Naturalist*, 54(4), 480–485. <https://doi.org/10.1894/CLG-26.1>
- Miller, J. R. B., Stoner, K. J., Cejtin, M. R., Meyer, T. K., Middleton, A. D., & Schmitz, O. J. (2016). Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin*, 40(4), 806–815. <https://doi.org/10.1002/wsb.720>
- Miller, P. S. (2017). Mexican Wolf PVA Draft Report.
- Morehouse, A. T., & Boyce, M. S. (2017). Evaluation of intercept feeding to reduce livestock depredation by grizzly bears. *Ursus*, 28(1), 66–80. <https://doi.org/10.2192/URSU-D-16-00026.1>
- Muhly, T. B., & Musiani, M. (2009). Livestock depredation by wolves and the ranching economy in the Northwestern U.S. *Ecological Economics*, 68(8–9), 2439–2450. <https://doi.org/10.1016/J.ECOLECON.2009.04.008>
- Mumby, H. S., & Plotnik, J. M. (2018). Taking the Elephants' Perspective: Remembering Elephant Behavior, Cognition and Ecology in Human-Elephant Conflict Mitigation. *Frontiers in Ecology and Evolution*, 6. <https://www.frontiersin.org/articles/10.3389/fevo.2018.00122>
- Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24(1), 1–11. <https://doi.org/10.1111/GEB.12236/SUPPINFO>
- Nickerson, R. (2021). Exploring compensation programs and depredation reporting for wolf-livestock conflict across the North American West [Thesis]. Colorado State University.
- Northrup, J. M., & Boyce, M. S. (2012). Mad cow policy and management of grizzly bear incidents. *Wildlife Society Bulletin*, 36(3), 499–505. <https://doi.org/10.1002/wsb.167>
- Nyhus, P. J. (2016). Human-Wildlife Conflict and Coexistence. *Annual Review of Environment and Resources*, 41, 143–171. <https://doi.org/10.1146/annurev-environ-110615-085634>
- Oakleaf, J. K., Mack, C., & Murray, D. L. (2003). Effects of Wolves on Livestock Calf Survival and Movements in Central Idaho. *The Journal of Wildlife Management*, 67(2), 299. <https://doi.org/10.2307/3802771>
- Parks, M., & Messmer, T. (2016). Participant perceptions of Range Rider Programs operating to mitigate wolf–livestock conflicts in the western United States. *Wildlife Society Bulletin*, 40(3), 514–524. <https://doi.org/https://doi.org/10.1002/wsb.671>
- Peterson, R. O., & Ciucci, P. (2003). Wolves: behavior, ecology, and conservation. In *Wolves: behavior, ecology, and conservation*. Chicago: University of Chicago Press.
- Petroelje, T. R., Belant, J. L., Beyer, D. E., & Svoboda, N. J. (2019). Subsidies from anthropogenic resources alter diet, activity, and ranging behavior of an apex predator (*Canis lupus*). *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-49879-3>

- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: an open-source release of Maxent. *Ecography*, 40(7), 887–893. <https://doi.org/https://doi.org/10.1111/ecog.03049>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3), 231–259. <https://doi.org/https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Plummer, M. (2022a). JAGS: a Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling v 4.3.1.
- Plummer, M. (2022b). rjags: Bayesian Graphical Models using MCMC. <https://CRAN.R-project.org/package=rjags>
- R Core Team. (2022). R: A Language and Environment for Statistical Computing.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World’s Largest Carnivores. *Science*, 343(6167). <https://doi.org/10.1126/science.1241484>
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, 345(6195), 406–412. <https://doi.org/10.1126/science.1251818>
- Sells, S. N., Mitchell, M. S., Podruzny, K. M., Ausband, D. E., Emlen, D. J., Gude, J. A., Smucker, T. D., Boyd, D. K., & Loonam, K. E. (2022). Competition, prey, and mortalities influence gray wolf group size. *The Journal of Wildlife Management*, 86(3), e22193. <https://doi.org/https://doi.org/10.1002/jwmg.22193>
- Silverman, B. W. (1986). Density estimation for statistics and data analysis (Vol. 26). CRC press.
- Smith, J. B., Greenleaf, A. R., & Oakleaf, J. K. (2023). Kill rates on native ungulates by Mexican gray wolves in Arizona and New Mexico. *The Journal of Wildlife Management*, 87(8), e22491. <https://doi.org/10.1002/jwmg.22491>
- Soh, Y. H., Carrasco, L. R., Miquelle, D. G., Jiang, J., Yang, J., Stokes, E. J., Tang, J., Kang, A., Liu, P., & Rao, M. (2014). Spatial correlates of livestock depredation by Amur tigers in Hunchun, China: Relevance of prey density and implications for protected area management. *Biological Conservation*, 169, 117–127. <https://doi.org/10.1016/J.BIOCON.2013.10.011>
- Treves, A., Naughton-Treves, L., Harper, E. K., Mladenoff, D. J., Rose, R. A., Sickley, T. A., & Wydeven, A. P. (2004). Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock. *Conservation Biology*, 18(1), 114–125. <https://doi.org/https://doi.org/10.1111/j.1523-1739.2004.00189.x>
- US Fish and Wildlife Service. (1999). Mexican Wolf Reintroduction Annual Report 1.
- U.S. Fish and Wildlife Service. (2014). Endangered and Threatened Wildlife and Plants; Proposed Revision to the Nonessential Experimental Population of the Mexican Wolf. www.regulations.gov

U.S. Fish and Wildlife Service. (2017). Mexican Wolf Recovery Plan, First Version.

U.S. Fish and Wildlife Service. (2022). Mexican Wolf Recovery Plan, Second Revision.

U.S. Fish and Wildlife Service Southwest Regional Office. (2014). Environmental Impact Statement for the Proposed Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf (*Canis lupus baileyi*) Final Mexican Wolf Recovery Program.

van Eeden, L. M., Crowther, M. S., Dickman, C. R., Macdonald, D. W., Ripple, W. J., Ritchie, E. G., & Newsome, T. M. (2018). Managing conflict between large carnivores and livestock. *Conservation Biology*, 32(1), 26–34. <https://doi.org/10.1111/cobi.12959>

Chapter 3 Tolerance for and retaliation against jaguars in the Colombian Llanos

Introduction

The persistence of large carnivores in ever-expanding shared landscapes largely depends on human willingness to coexist with them (Carter & Linnell, 2016). This willingness, termed tolerance, is often described as one's acceptance of wildlife behaviors that one dislikes (Brenner & Metcalf, 2020; Kansky et al., 2016; Lischka et al., 2019), whereas intolerance is described as attitudes or behaviors that negatively affect wildlife (Bruskotter & Wilson, 2014; Jordan et al., 2020). Although tolerance is widely recognized as essential for large carnivore conservation, the definition and measurement of tolerance remain variable across the literature (Brenner & Metcalf, 2020; Bruskotter et al., 2015; Frank, 2016; Knox et al., 2021). The variability of terminology and inconsistent measurement create challenges for practitioners who implement strategies to increase tolerance for large carnivores.

Conservation practitioners often attempt to increase tolerance for large carnivores to change illicit human behaviors (e.g., killing of carnivores) that drive population declines. Measuring such behaviors is difficult because of its sensitive and often illegal nature (Solomon et al., 2015; St. John et al., 2011). Many tolerance studies therefore measure psychological constructs, such as attitudes, as proxies for behavior or behavioral intention (Brenner & Metcalf, 2020). Attitudes are positive or negative evaluations of an object (Manfredo, 2008), and often are situational and incorporate an action (e.g., is it justified to kill a carnivore following a livestock depredation). While some studies demonstrate a high correlation between attitudes and behavioral intention (Bruskotter et al., 2015) or behavior (Hazzah et al., 2017), few demonstrate consistency between attitudes and behaviors (St. John et al., 2011). For practitioners, providing guidance to

measure behavioral underpinnings of tolerance will improve measurement of management actions to improve social support for large carnivores (Lischka et al., 2019).

The theory of planned behavior (TPB) is a common method in conservation psychology literature (Wallen & Landon, 2020) to predict behavioral intentions and behavior (Ajzen, 1991; Fishbein & Ajzen, 2010). TPB posits that attitudes, subjective norms, and perceived behavioral control are important predictors of behavior. Subjective norms are informal rules that define acceptable actions for a person (Cialdini & Trost, 1998), and perceived behavioral control is one's belief of their ability and resources to carry out an action (Ajzen, 1991). In the context of retaliatory killing of carnivores, TPB supposes that people who have positive attitudes toward lethal removal believe there is normative support for it and perceive that they or someone paid by them could kill a carnivore, and thus have an intention to do so (Marchini & Macdonald, 2012).

One strategy hypothesized to increase tolerance is the prevention of livestock losses under the premise that ranchers will accept large carnivore presence and be less likely to kill them if livestock loss is reduced or eliminated (Dickman, 2010; Pooley et al., 2017; Treves & Bruskotter, 2014). The prevention or reduction of livestock losses is critical to mitigating impacts to ranching livelihoods such as lost income (Jordan et al., 2020), food insecurity (Brackowski et al., 2023), labor requirements, and emotional suffering (Barua et al., 2013). However, deep-rooted psychological and cultural factors can be equally, if not more, important for predicting tolerance (Dickman, 2010; Inskip & Zimmermann, 2009; Kansky & Knight, 2014).

Quantifying the psychological and cultural factors that predict tolerance has far-reaching implications for interventions, given that such efforts can have variable impacts. In Sweden, subsidies for tools to reduce depredations led to more positive attitudes toward wolves (*Canis lupus*) (Karlsson & Sjöström, 2011). Similarly, farmers in Northern Zimbabwe had more positive

attitudes towards lions (*Panthera leo*) after participating in a community program to reduce livestock depredation (Sibanda et al., 2021). On the contrary, in the Western United States, using livestock guardian dogs did not lead to more positive attitudes towards wolves and grizzly bears (*Ursus arctos*) (Kinka & Young, 2019). In China's Sanjiangyuan Region, conservation interventions to increase tolerance for snow leopards (*Panthera uncia*) were overshadowed by the strong disapproval by community and religious leaders of retaliatory killings (Piaopiao et al., 2023). Importantly, identifying trends of psychological and cultural factors broadly across a species' range is unlikely because of strong variation in intra- and intercommunity perspectives, necessitating local studies to understand the context-specific drivers of tolerance for carnivores (Zimmermann et al., 2021).

In this study, we sought to quantify conflict between humans and jaguars (*Panthera onca*) and identify drivers of tolerance—specifically attitudes and behavioral intentions for retaliatory killing—of jaguars on rangelands in Colombia. We conducted interview-assisted surveys before and after the implementation of mitigation strategies (i.e., electric fencing) to reduce livestock loss. We sought to answer three questions: 1) What are the characteristics of human-jaguar conflict (i.e., livestock losses and perception of mitigation tools)? 2) What are the drivers of intolerance of jaguars in the system, specifically behavioral intention to kill jaguars? 3) Did implementing the conflict reduction strategy affect tolerance? We hypothesized that social psychological variables from TPB better predicted retaliation than livestock losses and that the intervention would improve tolerance for the treatment group of those who implemented electric fencing. Our study provides insight into human-jaguar conflict mitigation and predictors of retaliatory killings in the Colombian Llanos and a roadmap for measuring tolerance related to management interventions to reduce retaliatory killings.

Methods

Theoretical background

In this study, we seek to explicitly link human-carnivore conflict interventions to theories and developments in conservation psychology and tolerance literature. Human-wildlife interactions are the result of the juxtaposition of wildlife and human activities where humans, wildlife, or both are affected (Lischka et al. 2018). Human and animal behaviors, the proximate drivers of human-wildlife interactions, are shaped by nested levels of external factors within ecological and human social systems (Jochum et al., 2014; Lischka et al., 2018) (Figure 3.1). In addition to societal, institutional, and in-group dynamics, an individual's unique attributes also shape their behavior (Lischka et al., 2018). For humans, these individual attributes include socio-demographic characteristics such as livelihood and income, as well as psychological factors such as values, attitudes, norms, and emotions. Similarly, animal behavior, including that of predation on livestock, is nested within a larger context of ecosystem, community, and population-level processes. Examples of such processes include land use change due to the introduction of livestock (ecosystems), prey depletion from over-hunting (communities), and density-dependent use of resources (populations) (Wilkinson et al., 2020).

The nexus of behavioral responses of humans and animals leads to conflict, namely negative impacts to human lives and livelihoods from wildlife behaviors and the killing of large carnivores by humans. We therefore employ the definition of tolerance as “accepting wildlife and/or wildlife behaviors that one dislikes (Brenner & Metcalf, 2020, pg. 262).” The human behavior of interest in this study is retaliatory killing, given that it is the behavior that most directly affects large carnivore survival.

We derive our understanding of illegal killings from rational actor models. The cognitive hierarchy (Manfredo, 2008), also known as the value-attitude-behavior framework (Homer & Kahle, 1988), emerged from this theoretical tradition. In this theory, behaviors are related by hierarchical and interrelated cognitions that begin with values, then proceed to value orientations, attitudes, norms, and behavioral intentions (Table 3.1: The cognitive hierarchy and contextualization in human-carnivore conflict). TPB is derived from the same tradition of rational actor models, and posits that attitudes, subjective norms, and perceived behavioral control predict behavioral intentions, and that behavioral intentions with perceived behavioral control predict behavior (Ajzen, 1991; Fishbein & Ajzen, 2010).

Study area

The Colombian Llanos are a tropical savannah landscape in the Orinoquia region (Figure 3.2) in Eastern Colombia. The principal land use in the Llanos region is extensive cattle ranching, though rice monocultures and oil palm are increasing. Ranching there consists of privately managed herds of predominantly zebu cattle grazed on private land with limited human supervision. Approximately 29% of the region is protected under National Natural Parks, regional integrated management districts, and private reserves where productive activities such as cattle ranching are permitted (*reservas naturales de la sociedad civil*; Parques Nacionales Naturales de Colombia, 2024).

Jaguars are protected in Colombia under Decree 1076 of 2015 and are listed nationally as vulnerable (Ministerio de Ambiente y Desarrollo Sostenible, 2024). The Llanos is a critical corridor within the country (Machado-Aguilera et al., 2024), though population estimates are sparse regionally and nationally (Hyde et al., 2023). Conflict between ranchers and carnivores is known to occur and has been documented throughout the Llanos region (Garrote, 2012; Garrote et al., 2018; Payan & Diaz-Pulido, 2016). Retaliatory killings of large felids are thought to be

common and a major cause of mortality (Boron et al., 2016; Garrote, 2012; Payan et al., 2009) but remain unstudied in the country. At the time of data collection, there was no official reporting system of conflict events. Local conservation organizations implement conflict prevention strategies (e.g., electric fences, integrating criollo cattle to defend livestock herds, night penning) to reduce livestock loss on farms (i.e., Botero-Cruz et al., 2018; Valderrama-Vásquez et al., 2016). There is no compensation for livestock losses and no legal lethal removal of large carnivores.

A nonprofit conservation organization implements livestock protection strategies in priority areas for jaguar conservation. The purpose of the strategies is three-fold: reducing livestock losses for ranches in the area; demonstrating to the community that non-lethal tools are effective to reduce losses; and building tolerance for the presence of large carnivores. The organization was interested in evaluating the effectiveness of strategies to prioritize conservation strategies. Funding is limited; thus, ranches are prioritized based on livestock losses and willingness to implement tools. In 2022, select ranches received electric fencing to protect calving pastures in four communities in the Llanos region. Electric fences, consisting of four hot wires and one barbed wire at the bottom, were installed and monitored continuously through the end of the study in December 2023.

Data collection methods

We developed a 27-question interview-assisted survey to answer our research questions. The survey was pre-tested with conservation practitioners who worked in the region. The Institutional Review Board for the protection of human participants at Colorado State University approved the survey for distribution (Protocol #2787). Surveys consisted of six sections: self-reported losses and wildlife acceptance capacity; past and future harm to oneself and neighbors from felids; attitudes towards nonlethal tools; attitudes towards hunting of jaguars; personal and

subjective norms of nonlethal tools and retaliatory killing; and perceived behavioral control of nonlethal tools and hunting (S3 for English and Spanish interview questions). Questions were Likert scale responses consisting of 1-5 and 1-7-point scales.

We conducted in-person interviews in the four communities before and after the implementation of electric fences. First year interviews (pre-treatment) were conducted in May 2022, while second year interviews (post-treatment) were conducted in May and June of 2023. We sought to have a complete census of ranches in the four communities. We visited all ranches in the communities (n = 91). Community names are kept confidential given the nature of the behavior analyzed. At each ranch, we interviewed the most senior person involved in livestock husbandry, starting with ranch owners. When owners were unavailable, we interviewed ranch administrators. Informed verbal consent was solicited from all participants. In the case that no one was home, researchers made one attempt to return on a different day at a different time. All interviews were conducted in Spanish, the native language of all participants.

Measure of human-jaguar conflict

There was no centralized reporting of depredations at the time of our study. We therefore quantified conflict through self-reported losses to jaguars. We asked respondents how much damage jaguars had caused them in the past 12 months, how much they caused neighbors, and how likely it would be that they and their neighbors would have damage from jaguars in the following 12 months. We asked respondents about the effectiveness of the three most common mitigation tools proposed used in the region (electric fence, night penning, and criollo cattle), and whether they planned to implement those in the next 12 months. We additionally asked whether they believed lethal management or electric fence was more effective to prevent damage.

Measurement of tolerance and predictor models

The tolerance definition that we adapted requires both attitudinal and behavioral measurement (Brenner & Metcalf, 2020). We selected two attitudinal measures: 1) desired future population size (Bruskotter et al., 2015; Carpenter et al., 2000; Lischka et al., 2019) as an attitudinal measure of accepting wildlife, and 2) attitudes towards retaliatory killings to understand acceptability of a management action (Brenner & Metcalf, 2020; Bruskotter & Wilson, 2014). For desired future population size, we assessed whether respondents wanted jaguar populations to increase, stay the same, or decrease. For attitudes towards retaliatory killings, we assessed whether respondents believed that killing a jaguar after one depredation was justified through a Likert-scale question where 1-very unjustified and 7-very justified.

Human behavior has direct implications on wildlife survival, thus we sought to identify behavioral intention as a proxy for behavior, given that actual behavior may be underreported because of its illegality. We therefore assessed behavioral intention to retaliate against a jaguar for the next depredation through a Likert-scale question of 1-very unlikely to 7-very likely.

Retaliation predictor models

We constructed a model set to test which model best predicts intention to kill a jaguar following the next depredation. We generated five hypotheses to test empirical approaches (hypotheses 1, 2, and 5) and social psychological approaches (3 and 4) for predicting intent to kill a jaguar (Table 3.2): 1) past and expected losses to jaguars, number of cattle, and gender; 2) past and expected losses to jaguar, attitudes towards retaliation, number of cattle, and gender; 3) attitudes towards retaliation, subjective norms of killing jaguars, behavioral control of killing a jaguar (variables from theory of planned behavior), number of cattle, and gender; 4) past and expected losses to jaguars, attitudes towards retaliation, subjective norms of killing jaguars, and

behavioral control of killing a jaguar. (losses + variables from theory of planned behavior) and 5) perceived effectiveness of electric fences and behavioral control to implement them, number of cattle, and gender. The number of cattle was classified in groups (0, 1-50, 51-150, 151-300, 301-1000, 1000+) due to the sensitivity of reporting exact numbers in the region.

Data analysis for predictors of tolerance

We analyzed interview data through a Bayesian ordinal regression using the cumulative approach described by Burkner & Vuorre (2019). This methodology accounts for the unequal mental distance between neighboring Likert responses. For example, if asking a rancher how much harm a jaguar has caused them, the mental distance between severe damage, moderate damage, and little damage is unlikely to be equivalent for the respondent. The Bayesian ordinal approach reduces Type I (false-positive) error and yields more accurate effect size estimates (Bürkner & Vuorre, 2019; Liddell & Kruschke, 2018).

In this model, observed Likert response for a given response variable Y is the result of a continuous, unobserved variable \tilde{Y} , which is predicted by $n + \varepsilon$, where n is the predictor term for $n = b_1x_1 + b_2x_2 + \varepsilon$ and ε is the unexplained variation (Bürkner & Vuorre, 2019). For example, the reported intention to kill a jaguar, rated from 1-7, with 7 very likely to kill a jaguar and 1 very unlikely, is a categorization of a continuous, unobservable intention to kill a jaguar. Predictors, in the form of multiple Likert items such as perceived severity of harm from jaguars to cattle or personal norms around wildlife protection, are then incorporated into the model (i.e., $x_1, x_2 \dots$). Many of these predictors were monotonic in that they have a unidirectional nature (e.g., reported damages from jaguars) and thus were incorporated as such in the model. We modeled a random effect for each community to account for differing levels of exposure to jaguars.

We fit all models in the brms package (Bürkner, 2017) in program R (R Core Team, 2022). We used four Markov chain Monte Carlo chains with 10,000 iterations each and a 5,000-iteration burn-in thinned by 5 for a total of 1,000 samples per chain. We used weakly informative priors for all parameters (prior \sim normal(0,5)). We inspected traceplots for convergence (Gelman et al., 2014) and ensured that all parameters had an effective number of samples $> 1,000$ and an R-hat < 1.01 . We conducted posterior predictive checks for all models in the bayesplot package (Gabry & Mahr, 2017) by inspecting bar plots and rootograms with 1,000 simulated draws. We used Pareto-smoothed importance sampling leave-one-out (PSIS-LOO) cross validation in the loo package (Vehtari et al., 2021) to ensure that all Pareto-K estimates were under 0.7 (Vehtari et al., 2017). We estimated goodness of fit via McKelvey-Zavoina R^2 (McKelvey & Zavoina, 1975) to describe how much variance was explained by each model.

We used Leave-one-out cross-validation (loo-cv) model selection to identify which model best predicted our data. Loo-cv can perform better than other Bayesian information criterion when priors are weak or certain observations (i.e., polarized responses towards jaguars) are influential (Vehtari et al., 2017). We identified the most parsimonious model by selecting the model with the lowest looic (Leave one-out information criteria) value and expected log predictive density difference (elpd_diff) in the loo package (Vehtari et al., 2021). We considered a predictor to be meaningful if the 90% BCI of the posterior density estimates did not cross zero and moderately meaningful if the 75% BCI of the posterior density estimates did not cross zero.

Data analysis for changes in tolerance

We sought to evaluate the intervention's impact on our three measures of tolerance—desired future population size, attitudes towards retaliatory killings, and behavioral intention to retaliate—in a quasi-experimental study design. We interviewed participants in the treatment and

control groups before and after implementation of electric fencing. We had unequal group sizes because of limited funds to implement fences (i.e., a pretest-posttest nonequivalent group design). The conservation organization selected ranches by prioritizing higher reported losses and willingness to implement an electric fence and were therefore self-selected to the treatment group through willingness to implement. We were unable to compare desired future population size across years because no respondent desired a larger jaguar population in the second year of the study. Therefore, we had three response categories for year 1 and only two categories for year 2, thus data were no longer comparable through an ordinal regression. Consequently, to allow comparisons across years, our analyses included only two tolerance variables—attitudes towards retaliatory killings and behavioral intention to retaliate.

We evaluated whether the implementation of electric fencing was successful through a cumulative probit model for each of the two tolerance variables (attitudes and behavioral intentions) with year, group, an interaction between year and group, and a random effect for respondent. We interpreted the interaction term as whether the intervention changed the tolerance variable in year 2, while the treatment variable indicated the effect of the treatment group at year 1. We again treated the response variables as latent outcomes because we assume that the variable of interest is a continuous quantity represented by the observation in our dataset (Bürkner & Vuorre, 2019). All models were fit in the brms packages (Bürkner, 2017) in R (R Core Team, 2022) and posterior predictive checks were carried out as described above. We considered there to be a meaningful change if the 90% BCI of the posterior density estimates did not cross zero and moderately meaningful if the 75% BCI of the posterior density estimates did not cross zero.

Results

Year 1 summary of human-jaguar conflict

We interviewed 70 ranchers in the four communities in year 1. Seventy-seven percent of respondents were male and 23% were female. All but two respondents owned cattle (97%, n = 68), and all respondents owned small livestock. Of the 70 respondents, 65% of respondents (n = 46) reported that they would like to see the population of jaguars reduced, 29% (n = 20) would like the population to stay the same, and 6% (n = 4) wanted the population to increase (median (M) = be reduced; Figure 3.3A). Seventy-one percent of respondents (n = 50) reported having livestock losses to jaguars in the past year (Figure 3.3B; categories 2-5 of 5), and 60% (n = 42) had suffered moderate to very significant losses (M = moderate loss). Importantly, losses varied by community. All respondents in community 1 (n = 13) experienced losses, and all but one respondent had losses in community 4 (n = 12). In community 2, 62% of respondents (n = 18) had experienced losses in the past year, and 50% (n = 8) had experienced losses in community 3 in the past year. When asked about how likely it was that they would have losses over the next 12 months, 67% of respondents (n = 47) stated that it was more likely than not that they would lose livestock to jaguars, while 23% stated it was unlikely (M = moderately likely; Figure 3.3C).

When surveyed in year 1 about the most effective intervention proposed by conservation organizations (Figure 3.4A), 64% of respondents (n = 45) thought night penning to be somewhat to very effective in reducing livestock loss (M = somewhat effective). Similarly, 62% of respondents (n = 43) believed electric fencing to be somewhat to very effective in reducing livestock losses (M = moderately effective). The use of criollo cattle breeds to defend livestock was perceived to be somewhat to very effective by 51% of respondents (n = 36, M = somewhat effective).

In year 1, reported intent to use any of the three mitigation tools in the future was low (Figure 3.4B). Electric fencing and night penning were the most likely to be implemented, with 34% stating they were somewhat to very likely to implement these in the future (electric fence M = moderately unlikely; night penning M = very unlikely). Ranchers were unlikely to purchase and integrate criollo cattle into their herd (M = very unlikely); only 14% of ranchers said they are more likely than not to integrate criollo cattle into their operation.

Year 2 summary of human-jaguar conflict

We interviewed 63 ranchers in the four communities in year 2, 56 of whom had been interviewed in year 1. Three of the ranches interviewed in year 1 were abandoned. Four other participants were unreachable or did not consent to a second interview. All respondents in year 2 owned cattle. Eighty-one percent of respondents were male (n = 51) and 19% were female (n = 12). Of the 63 respondents, 63% (n = 40) reported that they would like to see the population of jaguars reduced, 37% would like the population to stay the same, and no respondents wanted the population to increase (M = be reduced; Figure 3.3D). Sixty-six percent of respondents (n = 42) reported having livestock losses to jaguars in the past year (Figure 3.3E; categories 2-5 of 5), and 54% (n = 34) had suffered moderate to very significant losses (M = moderate loss). As in year 1, losses varied by community. All respondents in community 1 (n = 11) experienced some losses, and all but one respondent (n = 13) had losses in community 4. In community 2, 54% of respondents (n = 13) reported losses to jaguars, and 36% (n = 5) reported losses to jaguars in community 3. When asked about how likely it was that they would have losses over the next 12 months, 65% of respondents (n = 41) stated that it was more likely than not that they would lose livestock to jaguars, while 32% stated it was unlikely (M = moderately likely; Figure 3.3F).

The perceived effectiveness of mitigation tools was similar in year 2 compared to year 1. Night penning was perceived to be the most effective conflict mitigation strategy (Figure 3.4A). Seventy-eight percent of respondents (n = 49) thought it to be somewhat to very effective in reducing livestock loss (M = somewhat effective). Sixty percent of respondents (n = 38) believed electric fencing to be somewhat to very effective in reducing livestock losses (M = moderately effective). The use of criollo cattle breeds to defend livestock was perceived to be somewhat to very effective by 52% of respondents (n = 32, M = neither effective nor ineffective).

Reported intent to use any of the three mitigation tools in the future was higher in year 2 than year 1 (Figure 3.4B). Electric fencing was the tool that ranchers most reported intention to implement (M = moderately likely); 81% of respondents (n = 50) said they are somewhat likely to very likely to implement an electric fence in the future. Respondents were similarly likely to implement night penning in the future, with 78% of respondents (n = 49) stating they are more likely than not to implement it in the future (M = moderately likely). Ranchers were more likely to purchase and integrate criollo cattle into their herd (M = somewhat likely) in year 2, with 52% (n = 33) more likely than not to use criollo cattle.

Predictors of tolerance for jaguars

The top predictor model of behavioral intentions of retaliatory killing of jaguars was that of the social psychological variables of theory of planned behavior (Table 3.3). Attitudes towards retaliatory killings ($\beta = 0.62$, 90% BCIs: 0.34, 0.94), subjective norms of retaliatory killings ($\beta = 0.48$, 90% BCIs: 0.28, 0.68), and behavioral control of killing jaguars ($\beta = 0.34$, 90% BCIs: 0.07, 0.61) were meaningful and positive predictors of retaliation (Figure 3.5B). Number of cattle ($\beta = -0.07$, 90% BCIs: -0.26, 0.12) and gender ($\beta = 0.05$, 90% BCIs: -0.55, 0.65) were not meaningful predictors of tolerance. The top model had an R^2 value of 0.79 ± 0.06 . The model of social

psychological variables from theory of planned behavior and losses (hypothesis 4) had slightly more predictive power ($R^2 = 0.83 \pm 0.05$) than the top model, and a Δ looiic of 1.51. In the model of theory of planned behavior and losses, past losses were a moderately meaningful and positive predictor of intent to retaliate ($\beta = 0.26$, 75% BCIs 0.07, 0.45). The models of past and expected damages from jaguars (hypothesis 1) and the perceived effectiveness of reducing depredations via electric fences (hypothesis 5) explained little variation in intention to retaliate and had high Δ looiic values. All model results are available in Table S5.

Seventy-four percent of respondents ($n = 50$) believed retaliatory killings of jaguars to be justified ($M =$ moderately justified; Figure 3.5A). Moreover, 41.1% ($n = 29$) of participants believed retaliatory killings of jaguars were highly justified. Most respondents (53%, $n = 37$) thought the people important to them would admire them if they killed a jaguar ($M =$ somewhat agree). Behavioral control of killing jaguars was low, with 93% of respondents ($n = 65$) stating that it was somewhat to very difficult to kill a jaguar. Reported intention to retaliate against jaguars after the next depredation was low. Only 17.1% ($n=12$) were more likely than not to retaliate against a jaguar. Notably, all respondents that said they were very likely ($n = 4$) to retaliate were in community 1.

Impact of fencing on tolerance

We interviewed 56 respondents both years, eight of whom implemented fences (treatment) and 48 who did not implement fences (control). Empirical data and model results indicate that before the intervention, the treatment group was less likely to retaliate against jaguars following the next depredation and more likely to have negative attitudes towards retaliatory killing than the control group. In year 1, 75% of respondents in the control group believed retaliatory killings were justified, while 50% of the treatment group believed they were justified (Figure 3.6). For

behavioral intention, 17% of the control group in year 1 intended to kill a jaguar following the next depredation, while 12% of the treatment group intended to kill a jaguar after the next depredation. In year 2, 69% of respondents in the control group believed retaliatory killings were justified, while 50% of the treatment group believed they were justified (Figure 3.6). For behavioral intention, 12% of the control group in year 2 intended to kill a jaguar following the next depredation, while 25% of the treatment group intended to kill a jaguar after the next depredation.

In year 1, there was a meaningful negative correlation between the treatment group and behavioral intentions to retaliate ($\beta = -2.43$, 90% BCIs: -4.72, -0.31); thus, the treatment group was less likely to have intentions to kill a jaguar than the control group. The moderately meaningful negative correlation between the treatment group and attitudes towards retaliatory killing ($\beta = -1.15$, 75% BCIs: -2.27, -0.03) indicates that the treatment group was less likely to believe that retaliatory killings were justified than the control group in year 1.

The fence intervention was unsuccessful at increasing tolerance for jaguars in the treatment group. Attitudes ($\beta = 0.15$, 90% BCIs: -0.83, 1.11) did not change as a result of the intervention. Moreover, behavioral intention to retaliate meaningfully increased after the intervention for the treatment group ($\beta = 1.50$, 90% BCIs: 0.26, 2.76), indicating that the treatment group had higher intentions of killing a jaguar after receiving electric fencing.

Discussion

We assessed human-jaguar conflict, predictors of tolerance for jaguars, and the effectiveness of an intervention to increase tolerance in the Colombian Llanos. We found that an approach focused only on reducing depredations is unlikely to improve tolerance of jaguars, as losses are not the only driver of intentions to retaliate against jaguars and treatment participants were already largely tolerant before the intervention. The ubiquity of depredations, high social

acceptance of retaliatory killings, and number of intolerant community members suggest the need for alternative conflict approaches—such as community-wide tolerance surveys and focus groups to understand community needs—to prioritize interventions that reduce livelihood impacts and conserve sustainable jaguar populations in the region.

Robust evaluations of carnivore conflict interventions are essential to prioritize scarce resources (van Eeden et al., 2018), and interdisciplinary approaches are necessary to mitigate conflicts (Baynham-Herd et al., 2018). In this study we demonstrate how psychological factors can improve our understanding of a human-carnivore conflict intervention's effectiveness. We found that the intervention of electric fencing did not increase tolerance in the treatment group — behavioral intention to retaliate was higher for the treatment group after the installation of fencing and attitudes were unchanged. However, our statistical analysis identified the treatment group as unlikely to kill jaguars before the intervention of electric fencing. Self-selection bias led to a treatment group of ranchers who were predisposed to tolerant attitudes and behaviors before conflict mitigation was implemented. This is corroborated by meaningful negative correlations between attitudes towards retaliatory killings of jaguars and behavioral intentions to retaliate against jaguars in the treatment group in year 1. Though our sample size of fence implementers was small due to funding limitations, our study provides insight for practitioners to understand how group selection may affect the outcome of interventions. Community members' engagement with conservation organizations is likely influenced by a combination of their tolerance for jaguars and their disposition to work with the conservation organization (i.e., the liking principle; Abrahamse & Steg, 2013; Cialdini & Goldstein, 2004). It is therefore crucial to assess community engagement strategies to understand how to reach intolerant community members. We recommend that future initiatives collect baseline information on individual ranchers' and the community's

tolerance for carnivores prior to interventions. This will enable organizations to understand the scale of attitudes and behavioral intentions that can affect carnivore populations, ensure that interventions are adequately addressing target individuals, and provide a reference point to evaluate effectiveness.

Social psychological variables from the theory of planned behavior are a better predictor of retaliation against jaguars than past or expected depredations. This finding contributes to a growing body of literature that demonstrates that the level of livestock losses and lethal removal of carnivores are seldom proportional (Dickman, 2010; Inskip & Zimmermann, 2009; Kansky & Knight, 2014; Pooley et al., 2017; Redpath et al., 2013). In the Brazilian Pantanal, for example, intention to kill jaguars was predicted by personal and social motivations along with perceived impact on livestock (Marchini & Macdonald, 2012). Similarly, jaguar persecution in the Bolivian Amazon is common and socially accepted where cattle depredation is not a concern (Knox et al., 2019). Attitudes, which are a strong predictor of behavioral intention (Manfredo, 2008; St. John et al., 2010), were not correlated with livestock losses in a series of range-wide case studies of jaguars (Zimmermann et al., 2021). We recommend that future conflict mitigation approaches that seek to increase tolerance go beyond livestock losses and measure attitudes and behavioral intentions to design interventions that target the desired behavioral outcome (Nilsson et al., 2020).

Positive attitudes towards retaliation, held by nearly three-quarters of respondents, were the strongest predictor of retaliation. The pervasiveness of attitudes and normative support in favor of retaliation are a concern for the persistence of jaguars. Coupled with the number of respondents with intent to retaliate, these results demonstrate that actions are needed to reduce intent to retaliate against jaguars if the goal is to sustain or increase jaguar populations. We did, however, find that behavioral control to kill a jaguar was low; only 7% of respondents believed it to be easier than

difficult. We attribute this to the nocturnality and elusive nature of jaguars, as well as many respondents' admission that they did not have proper firearms or hunting dogs to pursue jaguars. Because of the illegal nature of killing jaguars and owning firearms in Colombia, both actions are likely underreported. In addition to technical fixes like fences, organizations could implement financial incentives that dissuade hunting jaguars (Baynham-Herd et al., 2018), such as carbon credits for habitat conservation (Hyde, Boron, et al., 2022) and alternative livelihood training. Increasing tolerance, however, to maximize carnivore populations should not be the sole purpose of conservation initiatives, as it perpetuates the disproportionate burden of living with carnivores felt by rural and Global South communities (Harris et al., 2023; Jordan et al., 2020). Conservation programs could mitigate lost income and food insecurity from livestock depredations to foster equity and justice for rural communities (Barua et al., 2013; Harris et al., 2023; Jordan et al., 2020).

The prevalence of livestock losses to jaguars underscores the urgent need for a systematic response to address the disproportionate impacts of carnivores in these communities. Seventy-one percent of respondents reported losses in the past year, with 60% experiencing moderate to severe losses. Current human-jaguar conflict approaches in Colombia are limited in scale and lack evaluation (Pineda, 2023). Electric fences are the most common solution but only reduce depredations in a small area (0.7 - 7%) of each ranch in the Llanos region (Valderrama-Vasquez et al., 2023), indicating that this strategy is impractical for extensive rangelands with low forage quality. At the regional scale, environmental authorities lack personnel, training, and financial resources to address livestock losses and illegal killings. Authorities commission descriptive reports of human-carnivore conflict in their jurisdiction. These reports are often unavailable to the scientific community, focus on ecological and basic economic impacts (Aconcha-Abril et al., 2016), and present one-size-fits-all solutions to a complex issue. It is therefore important that

national authorities implement a nationwide assessment of human-jaguar conflict, put forth stronger reporting systems for jaguar conflicts, and convene experts to develop and evaluate a suite of conflict mitigation tools that are adapted to local conditions. National authorities could then fortify local governance structures of regional authorities to respond to human-jaguar conflicts within their jurisdictions.

Facilitating community-based approaches to designing and evaluating depredation mitigation programs would benefit Colombian carnivore management by creating locally grounded solutions. Government agencies and non-governmental organizations should first work with communities to co-identify the drivers of human-carnivore conflict and social and biodiversity outcomes (Mishra et al., 2017). A bottom-up approach may garner local ownership, encourage participation, and balance power dynamics between outsiders and community members (Bijoor et al., 2021; Redpath et al., 2017; Young et al., 2021). Interventions could then be designed in conjunction with local stakeholders, who can provide practical knowledge about local ecological and production systems that can improve the suitability of strategies (Hyde, Breck, et al., 2022; Mishra et al., 2017). Regional authorities, private donors, and international development programs could foster on-the-ground partnerships through flexible funding that allows organizations to ensure continued presence in the area and operate according to the community's timeline. Ideally, future conflict mitigation initiatives should integrate social science research methods from the onset and facilitate community-driven approaches to mediate livelihood impacts and the unequal burden endured by rural communities in the Global South that live with carnivores.

Tables and Figures

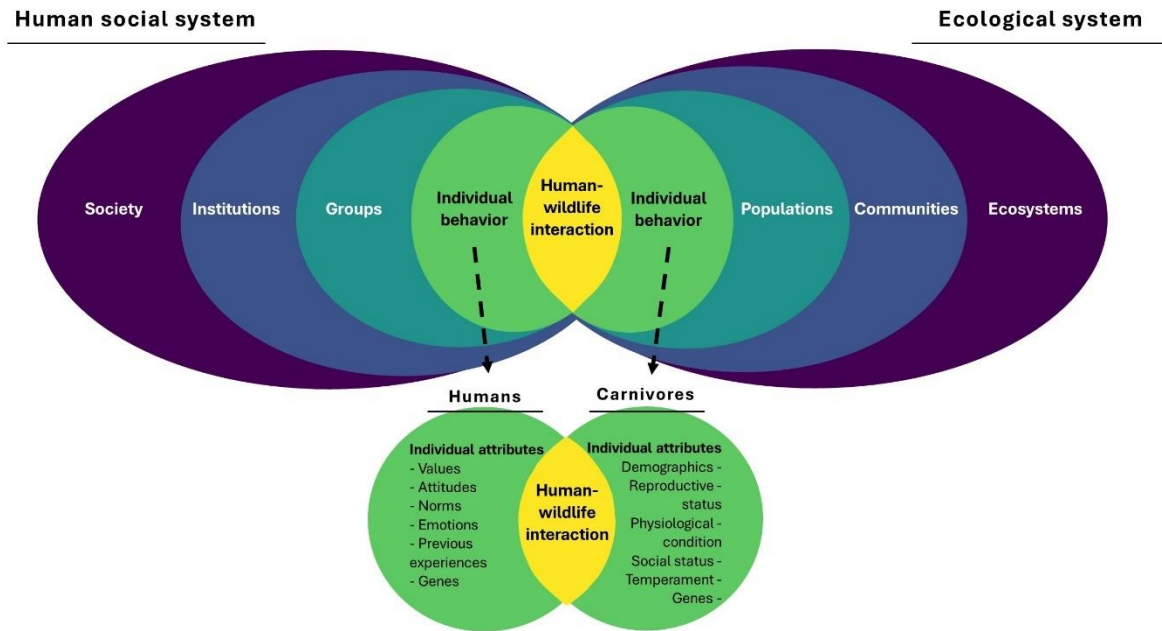


Figure 3.1. The socio-ecological system of human-wildlife interactions, adapted from Lischka et al. 2018.

Table 3.1. The cognitive hierarchy, definitions of its concepts, and examples in human-carnivore conflict.

The cognitive hierarchy and contextualization in human-carnivore conflict		
Concept	Definition	Example in Human-carnivore conflict
Values	Motivational goals that influence thought and ultimately behavior (Schwartz, 1992). These are ordered according to importance for oneself. Values are typically few in number and are unlikely to change after childhood (Manfredo et al., 2017).	<p>Example of the 10 broad values that could be relevant to conflict:</p> <p>Power: Control over people or resources, such as control of wildlife.</p> <p>Tradition: Commitment to acceptance of customs of one’s culture, like historic killing of jaguars or maintaining ranching customs.</p> <p>Universalism: Appreciation for the welfare of all people and nature.</p>
Value orientations	Basic beliefs that give contextual meaning to values in relation to a certain domain (Manfredo et al., 2009; Teel & Manfredo, 2010).	<p>Examples of the four orientations:</p> <p>Mutualism: Jaguars are worthy of care and compassion—i.e., we invaded their territory, and we should safeguard them.</p> <p>Domination: Human endeavors should be prioritized over jaguar wellbeing, and jaguars should be managed for human benefit.</p> <p>Pluralism: We should find a balance between human endeavors and jaguar welfare.</p> <p>Distanced: Little interest or value in jaguars or the value of wildlife.</p>
Attitudes	Positive or negative evaluation of an object which are formed based on values (Manfredo, 2008). Attitudes can change are commonly a target of conservation initiatives (Wallen & Landon, 2020).	Whether retaliatory killing of a jaguar following a livestock depredation is justified.
Norms	Informal rules that define acceptable actions for a person or group (Cialdini & Trost, 1998). Personal and descriptive norms may be of particular importance for intention (Niemiec et al., 2020).	Whether one’s family or social circle would approve of them killing a jaguar.
Behavioral intentions		Intention to retaliate against a jaguar for livestock loss

	Intention to carry out an action, informed by one's belief of their ability and resources (Ajzen, 1985).	
Behavior	One's action or conduct	Retaliation against a jaguar for livestock loss

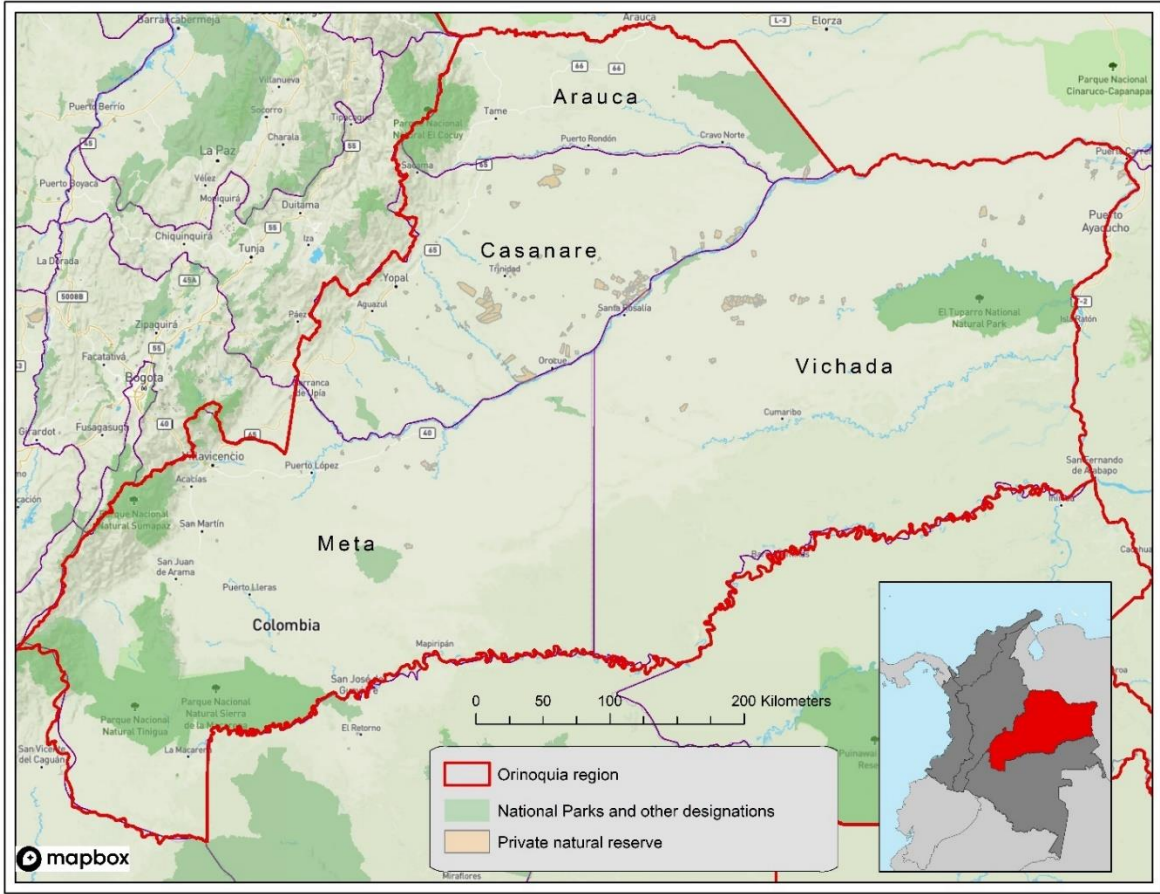


Figure 3.2. Map of the Colombian Orinoquia Region where the study was conducted.

Table 3.2. Hypotheses of predictor models for tolerance (intent to kill a jaguar).

Predictor models for tolerance	
#	Hypothesis
1	Past and expected losses to jaguars, number of cattle, and gender.
2	Past and expected losses to jaguars, attitudes towards retaliation, number of cattle, and gender.
3	Attitudes towards retaliation, subjective norms of killing jaguars, behavioral control of killing a jaguar (variables from theory of planned behavior), number of cattle, and gender.
4	Past and expected losses to jaguars, attitudes towards retaliation, subjective norms of killing jaguars, and behavioral control of killing a jaguar. (losses + variables from theory of planned behavior + losses).
5	Perceived effectiveness of electric fences and behavioral control of implementing them, number of cattle, and gender.

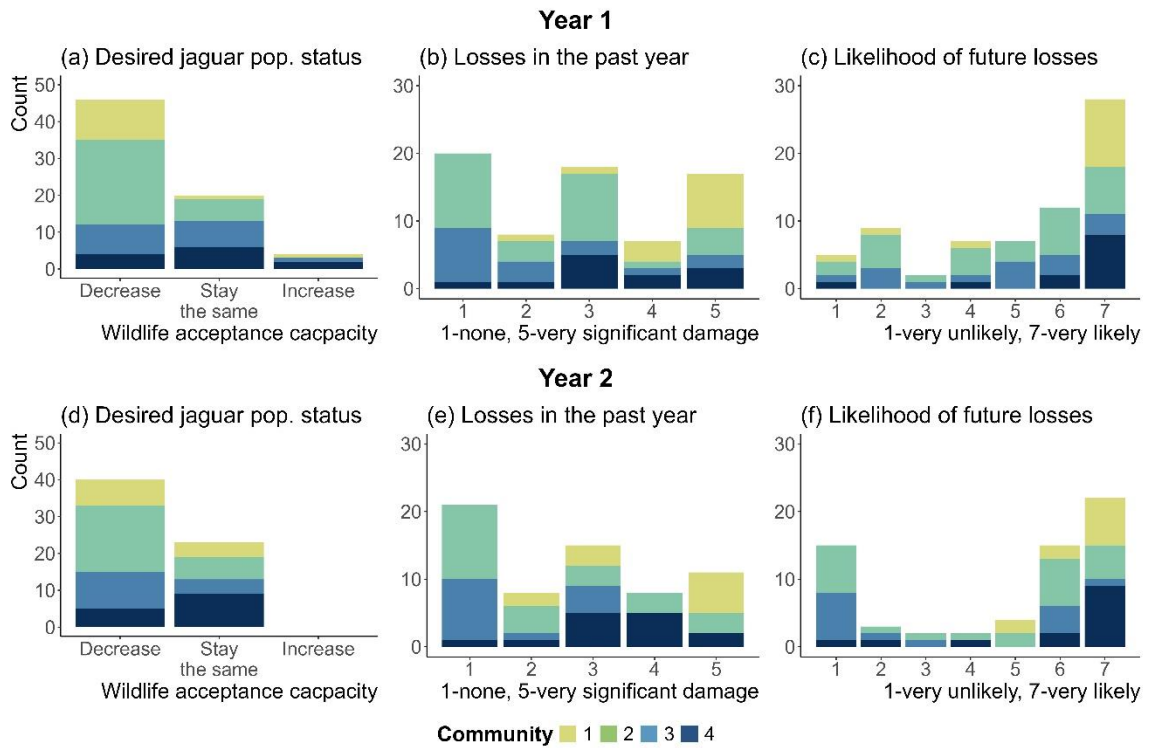


Figure 3.3. Summaries of interview results on losses and wildlife acceptance capacity. a & d) wildlife acceptance capacity; b & e) Self-reported losses in the past 12 months; c & f) reported likelihood of losses in the next 12 months.

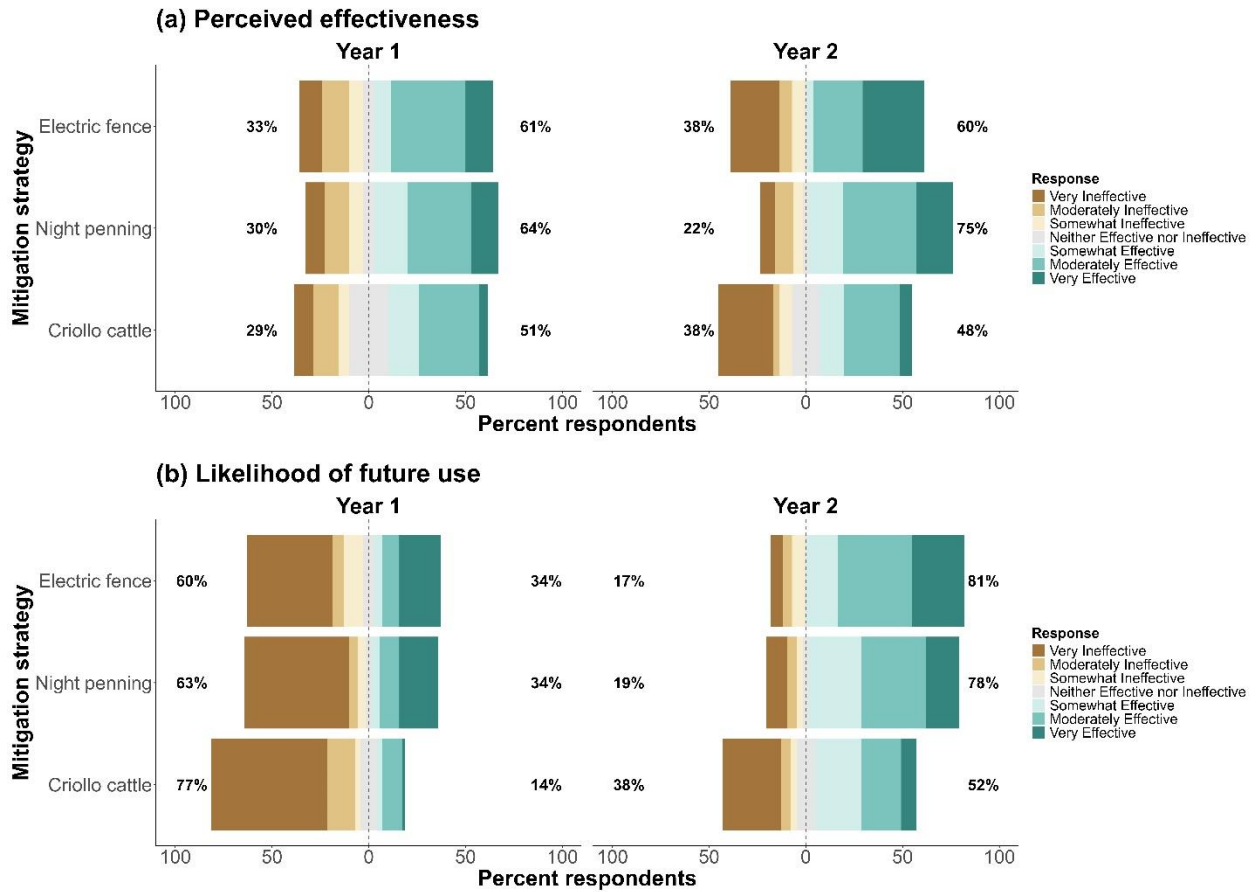


Figure 3.4. A) Perceived effectiveness of conflict mitigation strategies in the Colombian Llanos. b) reported intention to implement conflict mitigation strategies in the future.

Table 3.3. Tolerance model selection in year 1.

Tolerance model selection results					
Model	Hypothesis	$\Delta loaic$	elpd_diff	p_loo	R ²
Attitudes towards retaliation, subjective norms of killing jaguars, behavioral control of killing a jaguar (variables from theory of planned behavior), number of cattle, and gender predict intention to kill a jaguar.	3	0	0	14.36	0.79 ±0.06
Past and expected losses to jaguars, attitudes towards retaliation, subjective norms of killing jaguars, and behavioral control of killing a jaguar. (losses + variables from theory of planned behavior + losses) predict intention to kill a jaguar.	4	1.45	-0.73	17.53	0.83 ±0.05
Past and expected losses to jaguars, attitudes towards retaliation, number of cattle, and gender predict intention to kill a jaguar.	2	13.09	-6.55	15.17	0.76 ±0.07
Past and expected losses to jaguars, number of cattle, and gender predict intention to kill a jaguar.	1	39.57	-19.79	13.10	0.33 ±0.09
Perceived effectiveness of electric fences and behavioral control of implementing them, number of cattle, and gender predict intention to kill a jaguar.	5	48.53	-24.26	14.59711	0.28 ±0.09

$\Delta loaic$ = Leave-one-out cross-validation information criterion, elpd_diff = expected log predictive density difference. p_loo = effective number of parameters. The variables of number of cattle and gender were included on all models but were not meaningful predictors.

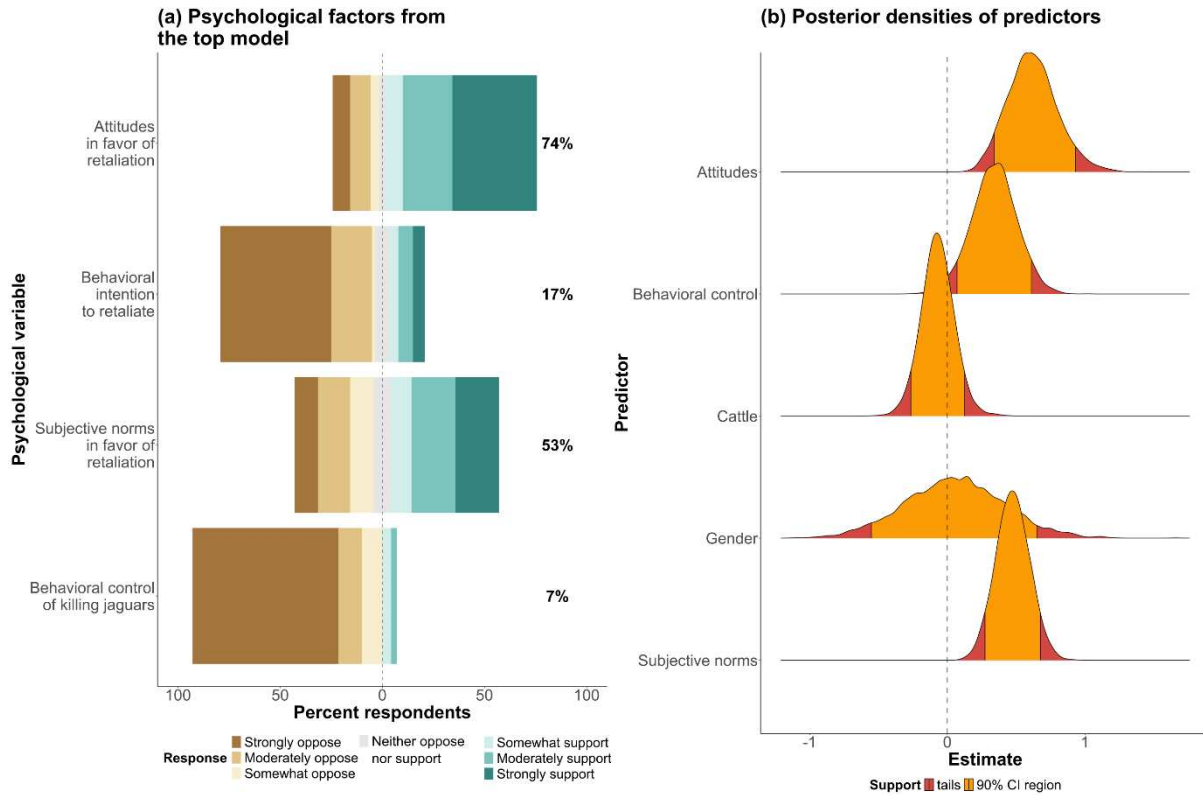


Figure 3.5. a) Reported intent to kill a jaguar following the next depredation in year 1. The scale is modified to show support and opposition for each psychological variable due to differing original scales. b) Predictors and posterior density estimates from the top retaliation model. Orange represents the 90% Bayesian credible intervals, and red is the tails of the posterior densities (5%, 95%). Predictors were considered meaningful if the 90% BCI did not cross zero.

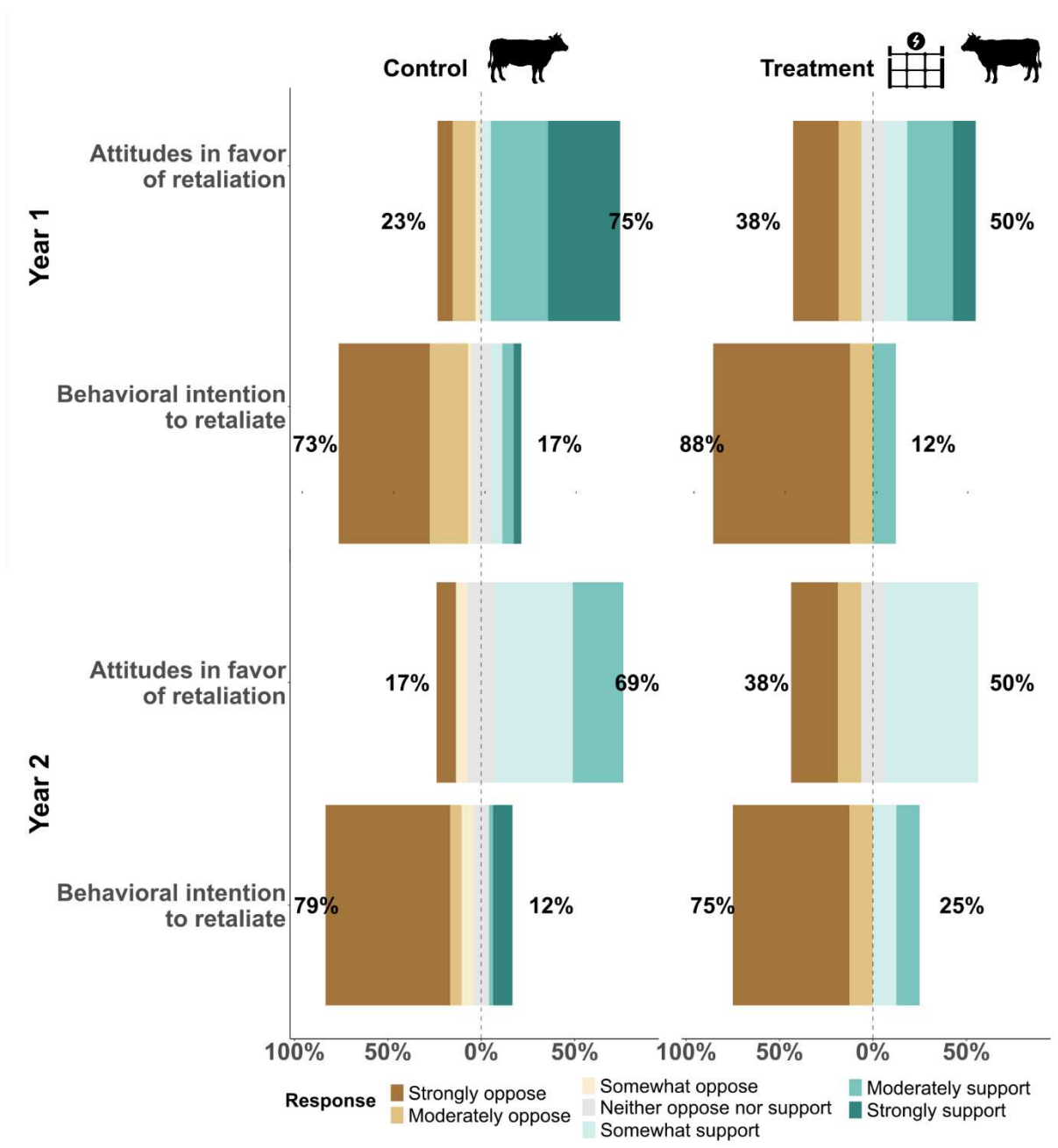


Figure 3.6. Comparison of the control group (n = 48 ranches) and treatment group (n = 8 ranches) in year 1. The scale is modified to show support and opposition for each psychological variable due to differing original scales. The treatment group disapproved of retaliatory killings and had lower intention to kill a jaguar than the control group. Icon credit: Andi Nur Abdillah (fence) and Mozillian (cattle).

References

- Abrahamse, W., & Steg, L. (2013). Social influence approaches to encourage resource conservation: A meta-analysis. *Global Environmental Change*, 23(6), 1773–1785. <https://doi.org/10.1016/j.gloenvcha.2013.07.029>
- Aconcha-Abril, I., Jiménez-Alvarado, J. S., C, C. M.-D., Zárrate-Charry, D. A., & González-Maya, J. F. (2016). Estado del conocimiento del conflicto por grandes felinos y comunidades rurales en Colombia: avances y vacíos de información. *Mammalogy Notes*, 3(1–2). <https://doi.org/10.47603/manovol3n1.46-51>
- Ajzen, I. (1985). From Intentions to Actions: A Theory of Planned Behavior. In J. Kuhl & J. Beckmann (Eds.), *Action Control: From Cognition to Behavior* (pp. 11–39). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-69746-3_2
- Ajzen, I. (1991). The Theory of Planned Behavior. *Organizational Behavior and Human Decision Processes*, 50, 179–211.
- Barua, M., Bhagwat, S. A., & Jadhav, S. (2013). The hidden dimensions of human–wildlife conflict: Health impacts, opportunity and transaction costs. *Biological Conservation*, 157, 309–316. <https://doi.org/10.1016/j.biocon.2012.07.014>
- Baynham-Herd, Z., Redpath, S., Bunnefeld, N., Molony, T., & Keane, A. (2018). Conservation conflicts: Behavioural threats, frames, and intervention recommendations. *Biological Conservation*, 222, 180–188. <https://doi.org/https://doi.org/10.1016/j.biocon.2018.04.012>
- Bijoor, A., Khanyari, M., Dorjay, R., Lobzang, S., & Suryawanshi, K. (2021). A Need for Context-Based Conservation: Incorporating Local Knowledge to Mitigate Livestock Predation by Large Carnivores. *Frontiers in Conservation Science*, 0, 107. <https://doi.org/10.3389/FCOSC.2021.766086>
- Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., & Payán, E. (2016). Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long term conservation. *PLoS ONE*, 11(5), 1–14. <https://doi.org/10.1371/journal.pone.0153973>
- Botero-Cruz, A. M., Bohórquez-Galindo, D. C., Mosquera-Guerra, F., Parra-Sandoval, C. A., & Trujillo, F. (2018). Protocolo para la atención y el manejo del conflicto con felinos por depredación de animales domésticos en el departamento del Meta Editores.
- Braczkowski, A. R., O’Bryan, C. J., Lessmann, C., Rondinini, C., Crysell, A. P., Gilbert, S., Stringer, M., Gibson, L., & Biggs, D. (2023). The unequal burden of human-wildlife conflict. *Communications Biology* 2023 6:1, 6(1), 1–9. <https://doi.org/10.1038/s42003-023-04493-y>
- Brenner, L. J., & Metcalf, E. C. (2020). Beyond the tolerance/intolerance dichotomy: incorporating attitudes and acceptability into a robust definition of social tolerance of wildlife. *Human Dimensions of Wildlife*, 25(3), 259–267. <https://doi.org/10.1080/10871209.2019.1702741>

- Bruskotter, J. T., Singh, A., Fulton, D. C., & Slagle, K. (2015). Assessing Tolerance for Wildlife: Clarifying Relations Between Concepts and Measures. *Human Dimensions of Wildlife*, 20(3), 255–270. <https://doi.org/10.1080/10871209.2015.1016387>
- Bruskotter, J. T., & Wilson, R. S. (2014). Determining Where the Wild Things will be: Using Psychological Theory to Find Tolerance for Large Carnivores. *Conservation Letters*, 7(3), 158–165. <https://doi.org/10.1111/CONL.12072>
- Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Bürkner, P.-C., & Vuorre, M. (2019). Ordinal Regression Models in Psychology: A Tutorial. *Advances in Methods and Practices in Psychological Science*, 2(1), 77–101. <https://doi.org/10.1177/2515245918823199>
- Carter, N. H., & Linnell, J. D. C. (2016). Co-Adaptation Is Key to Coexisting with Large Carnivores. *Trends in Ecology & Evolution*, 31(8), 575–578. <https://doi.org/10.1016/j.tree.2016.05.006>
- Cialdini, R. B., & Goldstein, N. J. (2004). Social influence: Compliance and conformity. *Annu. Rev. Psychol.*, 55(1), 591–621.
- Cialdini, R. B., & Trost, M. R. (1998). Social influence: Social norms, conformity and compliance. In *The handbook of social psychology*, Vols. 1-2, 4th ed. (pp. 151–192). McGraw-Hill.
- Decker, D. J., & Purdy, K. G. (1988). Toward A Concept of Wildlife Acceptance Capacity in Wildlife Management. *Wildlife Society Bulletin (1973-2006)*, 16(1), 53–57. <http://www.jstor.org/stable/3782353>
- Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation*, 13(5), 458–466. <https://doi.org/10.1111/J.1469-1795.2010.00368.X>
- Fishbein, M., & Ajzen, I. (2010). Predicting and changing behavior: The reasoned action approach. Psychology Press. <https://psycnet.apa.org/record/2009-17267-000>
- Frank, B. (2016). Human–Wildlife Conflicts and the Need to Include Tolerance and Coexistence: An Introductory Comment. *Society & Natural Resources*, 29(6), 738–743. <https://doi.org/10.1080/08941920.2015.1103388>
- Gabry, J., & Mahr, T. (2017). bayesplot: Plotting for Bayesian models. R Package Version, 1(0).
- Garrote, G. (2012). Depredación del jaguar (*Panthera onca*) sobre el ganado en los llanos orientales de Colombia. *Mastozoología Neotropical*, 19(1), 139–145.
- Garrote, G., Castellanos, P., Trujillo, F., & Mosquera Guerra, F. (2018). Características de los ataques de jaguar (*Panthera onca*) sobre el ganado y evaluación económica de las pérdidas en fincas ganaderas de los Llanos Orientales (Vichada, Colombia). <https://doi.org/10.13140/RG.2.2.15453.87526>
- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2014). *Bayesian data analysis* (Vol. 2). Taylor & Francis Boca Raton.

- Harris, N. C., Wilkinson, C. E., Fleury, G., & Nhleko, Z. N. (2023). Responsibility, equity, justice, and inclusion in dynamic human–wildlife interactions. *Frontiers in Ecology and the Environment*, 21(8), 380–387. <https://doi.org/10.1002/fee.2603>
- Homer, P. M., & Kahle, L. R. (1988). A structural equation test of the value-attitude-behavior hierarchy. *Journal of Personality and Social Psychology*, 54(4), 638–646. <https://doi.org/10.1037/0022-3514.54.4.638>
- Hyde, M., Boron, V., Rincón, S., Viana, D. F. P., Larcher, L., Reginato, G. A., & Payán, E. (2022). Refining carbon credits to contribute to large carnivore conservation: The jaguar as a case study. *Conservation Letters*, 15(3). <https://doi.org/10.1111/conl.12880>
- Hyde, M., Breck, S. W., Few, A., Beaver, J., Schrecengost, J., Stone, J., Krebs, C., Talmo, R., Eneas, K., Nickerson, R., Kunkel, K. E., & Young, J. K. (2022). Multidisciplinary engagement for fencing research informs efficacy and rancher-to-researcher knowledge exchange. *Frontiers in Conservation Science*, 3, 88. <https://doi.org/10.3389/fcosc.2022.938054>
- Hyde, M., Payán, E., Barragan, J., Stasiukynas, D., Rincón, S., Kendall, W. L., Rodríguez, J., Crooks, K. R., Breck, S. W., & Boron, V. (2023). Tourism-supported working lands sustain a growing jaguar population in the Colombian Llanos. *Scientific Reports*, 13(1), 10408. <https://doi.org/10.1038/s41598-023-36935-2>
- Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: A review of patterns and priorities worldwide. *Oryx*, 43(1), 18–34. <https://doi.org/10.1017/S003060530899030X>
- Jochum, K. A., Kliskey, A. A., Hundertmark, K. J., & Alessa, L. (2014). Integrating complexity in the management of human-wildlife encounters. *Global Environmental Change*, 26, 73–86. <https://doi.org/https://doi.org/10.1016/j.gloenvcha.2014.03.011>
- Jordan, N. R., Smith, B. P., Appleby, R. G., van Eeden, L. M., & Webster, H. S. (2020). Addressing inequality and intolerance in human–wildlife coexistence. *Conservation Biology*, 34(4), 803–810. <https://doi.org/10.1111/COBI.13471>
- Kansky, R., Kidd, M., & Knight, A. T. (2016). A wildlife tolerance model and case study for understanding human wildlife conflicts. *Biological Conservation*, 201, 137–145. <https://doi.org/https://doi.org/10.1016/j.biocon.2016.07.002>
- Kansky, R., & Knight, A. T. (2014). Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation*, 179, 93–105. <https://doi.org/https://doi.org/10.1016/j.biocon.2014.09.008>
- Karlsson, J., & Sjöström, M. (2011). Subsidized fencing of livestock as a means of increasing tolerance for wolves. *Ecology and Society*, 16(1).
- Kinka, D., & Young, J. K. (2019). The tail wagging the dog: positive attitude towards livestock guarding dogs do not mitigate pastoralists’ opinions of wolves or grizzly bears. *Palgrave Communications*, 5(1), 117. <https://doi.org/10.1057/s41599-019-0325-7>
- Knox, J., Negrões, N., Marchini, S., Barboza, K., Guanacoma, G., Balhau, P., Tobler, M. W., & Glikman, J. A. (2019). Jaguar Persecution Without “Cowflict”: Insights From Protected Territories in the Bolivian Amazon. *Frontiers in Ecology and Evolution*, 7. <https://www.frontiersin.org/articles/10.3389/fevo.2019.00494>

- Knox, J., Ruppert, K., Frank, B., Sponarski, C. C., & Glikman, J. A. (2021). Usage, definition, and measurement of coexistence, tolerance and acceptance in wildlife conservation research in Africa. *Ambio*, 50(2), 301–313. <https://doi.org/10.1007/s13280-020-01352-6>
- Liddell, T. M., & Kruschke, J. K. (2018). Analyzing ordinal data with metric models: What could possibly go wrong? *Journal of Experimental Social Psychology*, 79, 328–348.
- Lischka, S. A., Teel, T. L., Johnson, H. E., & Crooks, K. R. (2019). Understanding and managing human tolerance for a large carnivore in a residential system. *Biological Conservation*, 238. <https://doi.org/10.1016/j.biocon.2019.07.034>
- Lischka, S. A., Teel, T. L., Johnson, H. E., Reed, S. E., Breck, S., Don Carlos, A., & Crooks, K. R. (2018). A conceptual model for the integration of social and ecological information to understand human-wildlife interactions. *Biological Conservation*, 225, 80–87. <https://doi.org/10.1016/j.biocon.2018.06.020>
- Machado-Aguilera, M. C., Lemus-Mejía, L., Pérez-Torres, J., Zárrate-Charry, D. A., Arias-Alzate, A., & González-Maya, J. F. (2024). Preserving the spots: Jaguar (*Panthera onca*) distribution and priority conservation areas in Colombia. *PLOS ONE*, 19(3), e0300375-. <https://doi.org/10.1371/journal.pone.0300375>
- Manfredo, M. J. (2008). Who Cares About Wildlife? In *Who Cares About Wildlife? Social Science Concepts for Exploring Human-Wildlife Relationships and Conservation Issues* (Vol. 1). Springer US. <https://doi.org/10.1007/978-0-387-77040-6>
- Manfredo, M. J., Bruskotter, J. T., Teel, T. L., Fulton, D., Schwartz, S. H., Arlinghaus, R., Oishi, S., Uskul, A. K., Redford, K., Kitayama, S., & Sullivan, L. (2017). Why social values cannot be changed for the sake of conservation. *Conservation Biology*, 31(4), 772–780. <https://doi.org/10.1111/cobi.12855>
- Marchini, S., & Macdonald, D. W. (2012). Predicting ranchers' intention to kill jaguars: Case studies in Amazonia and Pantanal. *Biological Conservation*, 147(1), 213–221. <https://doi.org/10.1016/j.biocon.2012.01.002>
- McKelvey, R. D., & Zavoina, W. (1975). A statistical model for the analysis of ordinal level dependent variables. *The Journal of Mathematical Sociology*, 4(1), 103–120. <https://doi.org/10.1080/0022250X.1975.9989847>
- Mishra, C., Young, J. C., Fiechter, M., Rutherford, B., & Redpath, S. M. (2017). Building partnerships with communities for biodiversity conservation: lessons from Asian mountains. *Journal of Applied Ecology*, 54(6), 1583–1591.
- Niemiec, R. M., Champine, V., Vaske, J. J., & Mertens, A. (2020). Does the Impact of Norms Vary by Type of Norm and Type of Conservation Behavior? A Meta-Analysis. In *Society and Natural Resources* (Vol. 33, Issue 8, pp. 1024–1040). Routledge. <https://doi.org/10.1080/08941920.2020.1729912>
- Nilsson, D., Fielding, K., & Dean, A. J. (2020). Achieving conservation impact by shifting focus from human attitudes to behaviors. *Conservation Biology*, 34(1), 93–102. <https://doi.org/https://doi.org/10.1111/cobi.13363>

- Parques Nacionales Naturales de Colombia. (2024). Registro Único Nacional de Áreas Protegidas . RUNAP - Registro Unico Nacional AP.
- Payan, E., & Diaz-Pulido, A. (2016). Estado crítico del jaguar en la cuenca del río Meta. In F. Trujillo, R. Antelo, & S. Usma (Eds.), *Biodiversidad de las cuencas media y baja de los ríos Meta* (pp. 313–325). Fundación Omacha, Fundación Palmarito & WWF.
- Payan, E., Ruiz-García, M., & Franco, C. (2009). Distribución de jaguares en Colombia y el conflicto por depredación como amenaza para su conservación en la Orinoquia colombiana. In M. Romero (Ed.), *Informe sobre el estado de biodiversidad en Colombia 2007-2008: piedemonte orinoquense, sabanas y bosques asociados al norte del río Guaviare* (pp. 103–109). Instituto Alexander von Humboldt.
- Piaopiao, T., Suryawanshi, K. R., Lingyun, X., Mishra, C., Zhi, L., & Alexander, J. S. (2023). Factors shaping the tolerance of local Tibetan herders toward snow leopards. *Journal for Nature Conservation*, 71, 126305. <https://doi.org/https://doi.org/10.1016/j.jnc.2022.126305>
- Pineda, A. A. (2023). *Human-Carnivore Coexistence: The Functional and Perceived Effectiveness of Solar Lights, and Attitudes Toward Jaguars and Pumas in Colombia* [Dissertation]. University of Wisconsin-Madison.
- Pooley, S., Barua, M., Beinart, W., Dickman, A., Holmes, G., Lorimer, J., Loveridge, A. J., Macdonald, D. W., Marvin, G., Redpath, S., Sillero-Zubiri, C., Zimmermann, A., & Milner-Gulland, E. J. (2017). An interdisciplinary review of current and future approaches to improving human–predator relations. *Conservation Biology*, 31(3), 513–523. <https://doi.org/10.1111/cobi.12859>
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing*.
- Redpath, S. M., Linnell, J. D. C., Festa-Bianchet, M., Boitani, L., Bunnefeld, N., Dickman, A., Gutiérrez, R. J., Irvine, R. J., Johansson, M., Majić, A., McMahon, B. J., Pooley, S., Sandström, C., Sjölander-Lindqvist, A., Skogen, K., Swenson, J. E., Trouwborst, A., Young, J., & Milner-Gulland, E. J. (2017). Don't forget to look down – collaborative approaches to predator conservation. *Biological Reviews*, 92(4), 2157–2163. <https://doi.org/https://doi.org/10.1111/brv.12326>
- Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., Amar, A., Lambert, R. A., Linnell, J. D. C., Watt, A., & Gutiérrez, R. J. (2013). Understanding and managing conservation conflicts. *Trends in Ecology and Evolution*, 28(2), 100–109.
- Resolución 0126 de 2024, 1 (2024). Ministerio de Ambiente de Colombia.
- Solomon, J. N., Gavin, M. C., & Gore, M. L. (2015). Detecting and understanding non-compliance with conservation rules. *Biological Conservation*, 189, 1–4. <https://doi.org/https://doi.org/10.1016/j.biocon.2015.04.028>
- Schwartz, S. H. (1992). Universals in the Content and Structure of Values: Theoretical Advances and Empirical Tests in 20 Countries. In M. P. Zanna (Ed.), *Advances in Experimental Social Psychology* (Vol. 25, pp. 1–65). Academic Press. [https://doi.org/https://doi.org/10.1016/S0065-2601\(08\)60281-6](https://doi.org/https://doi.org/10.1016/S0065-2601(08)60281-6)
- Sibanda, L., van der Meer, E., Johnson, P. J., Hughes, C., Dlodlo, B., Parry, R. H., Mathe, L. J., Hunt, J. E., Macdonald, D. W., & Loveridge, A. J. (2021). Evaluating the effects of a conservation intervention

- on rural farmers' attitudes toward lions. *Human Dimensions of Wildlife*, 26(5), 445–460. <https://doi.org/10.1080/10871209.2020.1850933>
- St. John, F. A. V., Edwards-Jones, G., & Jones, J. P. G. (2010). Conservation and human behaviour: Lessons from social psychology. *Wildlife Research*, 37(8), 658–667.
- St. John, F., Keane, A., Edwards-Jones, G., Jones, L., Yarnell, R., & Jones, J. (2011). Identifying indicators of illegal behaviour: Carnivore killing in human-managed landscapes. *Proceedings. Biological Sciences / The Royal Society*, 279, 804–812.
- Teel, T. L., & Manfredo, M. J. (2010). Understanding the diversity of public interests in wildlife conservation. *Conservation Biology*, 24(1), 128–139.
- Treves, A., & Bruskotter, J. (2014). Tolerance for predatory wildlife. *Science*, 344(6183), 476–477. https://doi.org/10.1126/SCIENCE.1252690/ASSET/2263AB02-DA89-41CB-8CC8-A0A73085E69F/ASSETS/GRAPHIC/344_476_F1.JPEG
- Valderrama-Vásquez, C. A., Hoogesteijn, R., & Payán, E. (2016). GRECO: Manual de campo para el manejo del conflicto entre humanos y felinos. (Fernando Peña Editores, Ed.). Panthera y USFWS.
- Valderrama-Vasquez, C., Hoogesteijn, R., Payán, E., Quigley, H., & Hoogesteijn, A. (2023). Predator-friendly ranching, use of electric fences, and creole cattle in the Colombian savannas. *European Journal of Wildlife Research*, 70(1), 1. <https://doi.org/10.1007/s10344-023-01754-3>
- van Eeden, L. M., Eklund, A., Miller, J. R. B., López-Bao, J. V., Chapron, G., Cejtin, M. R., Crowther, M. S., Dickman, C. R., Frank, J., Krofel, M., Macdonald, D. W., McManus, J., Meyer, T. K., Middleton, A. D., Newsome, T. M., Ripple, W. J., Ritchie, E. G., Schmitz, O. J., Stoner, K. J., ... Treves, A. (2018). Carnivore conservation needs evidence-based livestock protection. *PLoS Biology*, 16(9). <https://doi.org/10.1371/journal.pbio.2005577>
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Vehtari, A., Gelman, A., Gabry, J., & Yao, Y. (2021). Package ‘loo.’ Efficient Leave-One-Out Cross-Validation and WAIC for Bayesian Models.
- Wallen, K. E., & Landon, A. C. (2020). Systematic map of conservation psychology. *Conservation Biology*, 34(6), 1339–1352. <https://doi.org/10.1111/COBI.13623>
- Wilkinson, C. E., McInturff, A., Miller, J. R. B., Yovovich, V., Gaynor, K. M., Calhoun, K., Karandikar, H., Martin, J. V., Parker-Shames, P., Shawler, A., Van Scoyoc, A., & Brashares, J. S. (2020). An ecological framework for contextualizing carnivore–livestock conflict. *Conservation Biology*, 34(4), 854–867. <https://doi.org/https://doi.org/10.1111/cobi.13469>
- Young, J. C., Alexander, J. S., Bijoor, A., Sharma, D., Dutta, A., Agvaantseren, B., Mijiddorj, T. N., Jumabay, K., Amankul, V., Kabaeva, B., Nawaz, A., Khan, S., Ali, H., Rullman, J. S., Sharma, K., Murali, R., & Mishra, C. (2021). Community-Based Conservation for the Sustainable Management of Conservation Conflicts: Learning from Practitioners. *Sustainability*, 13(14), 7557. <https://doi.org/10.3390/su13147557>

Zimmermann, A., Johnson, P., de Barros, A. E., Inskip, C., Amit, R., Soto, E. C., Lopez-Gonzalez, C. A., Sillero-Zubiri, C., de Paula, R., Marchini, S., Soto-Shoender, J., Perovic, P. G., Earle, S., Quiroga-Pacheco, C. J., & Macdonald, D. W. (2021). Every case is different: Cautionary insights about generalisations in human-wildlife conflict from a range-wide study of people and jaguars. *Biological Conservation*, 260, 109185. <https://doi.org/10.1016/J.BIOCON.2021.109185>

Supplementary information

Chapter 1

Table S1. Hypotheses are parameters of the application of the Barker Robust Design methodology for jaguars in Hato La Aurora, Colombia.

Parameter	Parameter description	Variable in models	Model description
S^*	Probability that individual i in primary sampling period t survives to period $t + 1$.	S(.)	Constant apparent survival
		S(sex)	Apparent survival based on sex
		S(sex*time)	Apparent survival depends on sex and time interactions
		S(time)	Survival depends on time
p^*	Probability that an individual i is detected in primary period t , given that it is alive, in the population, and available for detection.	p(.)	Constant detection probability
		p (year)	Detection probability changes with session
		p (sex)	Sex specific detection
		p (year*sex)	Time and sex differences in detection
π^1	Heterogeneity in recapture probabilities based on individual characteristics	Mixture 1	Group of individuals whose home range mostly occurs outside of the reserve
		Mixture 2	Group of individuals whose home range mostly falls within the core of the reserve
R^*	Probability that an individual i is detected alive and reported between primary periods t and $t + 1$, given it survives to period $t + 1$.	R(.)	Constant resighting probability
		R(time)	Resighting probability changes over time
		R(sex)	Resighting probability is different based on sex
		R(sex*time)	Resighting probability depends on sex and time interactions
		R(T)	Resighting probability fitted with a linear trend
R'^*	Probability that individual i is detected alive and reported between primary periods	R'(.)	Constant probability of being seen though dead and not reported
		R'(time)	Time dependent probability

	t and $t + I$, given that it dies in that interval but is not recovered and reported.	$R'(\text{sex})$	Sex dependent probability
		$R'(\text{sex}*\text{time})$	Sex and time interaction for the probability
a'^*	Probability individual i is available for detection in primary period $t + I$, given it was unavailable in period t , and survived and remained faithful to the population from t to $t + I$.	$a'(\cdot)$	Random movement
		$a'(\text{time})$	Markovian movement
		$a'(\text{sex}*t)$	Markovian movement based on sex and time interactions
		$a'(\text{sex})$	Markovian movement based on sex
a''^*	Probability individual i is available for detection in primary period $t + I$, given it was available in period t , and survived and remained faithful to the population from period t to $t + I$.	$a''(=1)$	No movement
		$a''(\text{time})$	Time varying movement (Markovian)
		$a''(\text{sex})$	Movement varying by sex
		$a''(\text{sex}*time)$	Movement varying by sex and time interactions
N^*	The size of the subset of the population that is available in the study area during primary period t .	Derived parameter	

¹ All models included heterogeneity in detection probably because of the selected data type (Huggins with heterogeneity and p).

* Parameter descriptions from Kendall et al. 2013

Table S2. Model averaged estimates for the Barker Robust Design model for jaguars in Hato La Aurora.

	Sex	Year	Estimate	SE	LCI	UCI		
	Abundance (N)	Males	2014	3.0003	0.01726	2.96647	3.03412	
2015			6.64823	0.88181	4.91987	8.37658		
2016			3.40103	0.68572	2.05702	4.74504		
2017			6.80206	0.98567	4.87016	8.73397		
2018			3.14794	0.41412	2.33626	3.95962		
2019			5.47555	0.75336	3.99896	6.95213		
2020			6.54166	0.80274	4.9683	8.11503		
2021			10.5697	0.83708	8.92906	12.2104		
2022			14.5394	1.3924	11.8103	17.2685		
Females			2014	2.26735	0.55679	1.17604	3.35866	
		2015	3.40103	0.68572	2.05702	4.74504		
		2016	1.00011	0.01056	0.97942	1.0208		
		2017	6.80206	0.98567	4.87016	8.73397		
		2018	8.85966	1.02311	6.85437	10.8649		
		2019	6.80206	0.98567	4.87016	8.73397		
		2020	6.6945	0.91365	4.90374	8.48526		
		2021	9.60783	0.85582	7.93044	11.2852		
		2022	14.3691	1.30716	11.8071	16.9312		
		Apparent survival (S)	Males	2014	0.78075	0.09547	0.54411	0.91398
				2015	0.78387	0.07321	0.60858	0.89429
				2016	0.78372	0.07267	0.60997	0.89357
2017				0.78362	0.07309	0.60874	0.89395	
2018	0.78383			0.07253	0.61044	0.8935		
2019	0.78386			0.07244	0.6107	0.89343		
2020	0.78376			0.07246	0.61057	0.89338		
2021	0.78386			0.0723	0.61109	0.89328		
2022	0.78396			0.07239	0.61092	0.89347		
Females	2014			0.79519	0.0908	0.56557	0.9205	
	2015		0.79831	0.06547	0.6408	0.89777		
	2016		0.79825	0.06541	0.6409	0.89766		
	2017		0.79818	0.06543	0.6408	0.89762		
	2018		0.79829	0.06541	0.64095	0.89769		
	2019		0.7983	0.06542	0.64092	0.89772		
	2020		0.79827	0.06538	0.64102	0.89763		

		2021	0.7983	0.0654	0.64097	0.89769
		2022	0.79833	0.06546	0.64083	0.89778
Resighting (R)	Sex	Year	Estimate	SE	LCI	UCI
	Males	2014	0.07789	0.11029	0.00415	0.63149
		2015	0.07789	0.11029	0.00415	0.63149
		2016	0.07789	0.11029	0.00415	0.63149
		2017	0.07789	0.11029	0.00415	0.63149
		2018	0.34233	0.15846	0.11584	0.67406
		2019	0.32112	0.14718	0.11186	0.63983
		2020	0.40318	0.18169	0.1333	0.74795
		2021	0.18585	0.08291	0.07234	0.40054
		2022	0.27305	0.11419	0.10844	0.53702
	Females	2014	0.08048	0.1138	0.00428	0.64064
		2015	0.08048	0.1138	0.00428	0.64064
		2016	0.08048	0.1138	0.00428	0.64064
		2017	0.08048	0.1138	0.00428	0.64064
		2018	0.34764	0.15704	0.12062	0.67432
		2019	0.32632	0.14575	0.11667	0.63982
		2020	0.40862	0.18083	0.13748	0.74971
		2021	0.19	0.08444	0.0741	0.40742
		2022	0.27816	0.11515	0.11129	0.54251
Seen given dead and not recovered (R')	Sex	Year	Estimate	SE	LCI	UCI
	Males	2014	0.02091	0.05608	9.9E-05	0.82097
		2015	0.02091	0.05608	9.9E-05	0.82097
		2016	0.02091	0.05608	9.9E-05	0.82097
		2017	0.02091	0.05608	9.9E-05	0.82097
		2018	0.03832	0.13127	3.7E-05	0.97723
		2019	0.02091	0.05608	9.9E-05	0.82097
		2020	0.16459	0.29501	0.00293	0.92961
		2021	0.02091	0.05608	9.9E-05	0.82097
		2022	0.17236	0.3663	0.00136	0.96964
	Females	2014	0.26681	0.35745	0.01003	0.92894
		2015	0.26681	0.28807	0.0199	0.86709
		2016	0.26681	0.28379	0.02075	0.86206
		2017	0.26681	0.28361	0.02079	0.86185
		2018	0.40193	0.32797	0.0443	0.90693
		2019	0.26681	0.28361	0.02079	0.86185
		2020	0.53903	0.35789	0.06497	0.95164

		2021	0.26681	0.28361	0.02079	0.86185
		2022	0.52979	0.36082	0.06183	0.95065
Available given previously in the reserve (a'')	Sex	Year	Estimate	SE	LCI	UCI
	Males	2015	0.99998	0.00179	0.99647	1.00349
		2016	0.44208	0.20665	0.13298	0.80367
		2017	0.99305	0.16537	0.66893	1.31718
		2018	0.97367	0.20234	7.1E-06	1
		2019	0.95994	0.11625	0.06017	0.99989
		2020	0.75397	0.16543	0.34795	0.94623
		2021	0.95055	0.10091	0.22242	0.99923
		2022	0.99998	0.0018	0.99645	1.00351
	Females	2015	0.99999	0.00147	0.9971	1.00287
		2016	0.43978	0.20474	0.13345	0.80007
		2017	0.99306	0.16527	0.66913	1.31698
		2018	0.9758	0.19814	2.9E-06	1
		2019	0.95952	0.11675	0.06147	0.99988
		2020	0.75508	0.16452	0.35031	0.94632
		2021	0.95055	0.10083	0.22296	0.99922
2022		0.99998	0.00149	0.99707	1.0029	
Available given previously outside the reserve (a')	Sex	Year	Estimate	SE	LCI	UCI
	Males	2015	0.38845	0.21003	0.00158	0.99608
		2016	0.38846	0.21005	0.00158	0.99608
		2017	0.38845	0.21003	0.00158	0.99608
		2018	0.38845	0.21003	0.00158	0.99608
		2019	0.38845	0.21003	0.00158	0.99608
		2020	0.38846	0.21005	0.00158	0.99608
		2021	0.38846	0.21005	0.00158	0.99608
	Females	2015	0.38844	0.21003	0.00158	0.99608
		2016	0.38845	0.21004	0.00158	0.99608
		2017	0.38844	0.21003	0.00158	0.99608
		2018	0.38844	0.21003	0.00158	0.99608
		2019	0.38844	0.21003	0.00158	0.99608
		2020	0.38845	0.21004	0.00158	0.99608
2021		0.38845	0.21005	0.00158	0.99608	

SE = standard error, LCI = lower 95% confidence interval, UCI = upper 95% confidence interval.

Chapter 2

Description of livestock data

Spatial data on the abundance of livestock is unavailable for the study area. We therefore used the annual livestock density data developed by Goljani Amirkhiz et al. (2018). The authors obtained Animal Unit Month (AUM) data from 3876 allotments of the US Forest Service and Bureau of Land Management in the study area. AUM is the restriction placed on public grazing allotments for the number of livestock that can be grazed on the allotment, which is based on an estimate for the amount of available forage (Holechek, 1988; Sprinkle & Bailey, 2004). Therefore, annual AUM density is based on the carrying capacity for livestock based on spatial variables such as precipitation, elevation, and others. The authors summed across the year to get an annual abundance for each allotment. They then used a generalized linear model to model annual AUM density. Using a set of 37 ecological, bioclimatic, and topographic covariates, the authors compared 108 models and ranked models using Akaike Information Criterion adjusted for small sample sizes (AICc). The top model consisted of the following variables:

Table S3. Variables included in the annual livestock density top model.

Variable name	Description
Land cover	Arc GIS 10.3 Zonal Statistics tool to identify the major land cover category within each allotment. We reduced the number of land cover categories from 50 to 19 by combining similar land cover types (e.g., Madrean Pine-Oak Forest and Woodland and Southern Rocky Mountain Ponderosa Pine Woodland were considered pine woodland). Southwest Regional Gap Analysis land cover map (USGS 2007, http://swregap.nmsu.edu/)
Canopy cover	Considering the middle range of tree cover categories to obtain a continuous raster LANDFIRE canopy cover (USGS 2013, http://www.landfire.gov/)
Canopy cover squared	Quadratic term of canopy cover
Terrain ruggedness index	Arc GIS 10.3 Raster Calculator tool to calculate the average absolute difference between each pixel elevation value and each of its eight neighbors
CV of vertical distance to water resources	ArcGIS 10.3 Cost Path tool by using the variation of

	slope as a cost layer.
Precipitation in the warmest quarter	Sum of mean precipitation for three consecutive months with highest mean precipitation
Precipitation in the warmest quarter squared	Quadratic term of precipitation in the warmest quarter
Temperature seasonality	Standard deviation of the 12 mean monthly temperature values multiplied by 100
Temperature seasonality squared	Quadratic term of temperature seasonality
Precipitation seasonality	Standard deviation of the means of monthly precipitation
Precipitation seasonality squared	Quadratic term of precipitation seasonality
Precipitation seasonality CV	Coefficient of variation (CV) of precipitation seasonality
Precipitation of driest quarter	Sum of mean precipitation for three consecutive months with lowest mean precipitation
Precipitation of driest quarter squared	Quadratic term of precipitation of driest quarter
Precipitation of driest quarter CV	Coefficient of variation (CV) of precipitation of the driest month

Full details of the methodology are available in Goljani Amirkhiz et al. (2018).

References

- Goljani Amirkhiz, R., Frey, J. K., Cain, J. W., Breck, S. W., & Bergman, D. L. (2018). Predicting spatial factors associated with cattle depredations by the Mexican wolf (*Canis lupus baileyi*) with recommendations for depredation risk modeling. *Biological Conservation*, 224, 327–335. <https://doi.org/10.1016/J.BIOCON.2018.06.013>
- Holechek, J. L. (1988). An approach for setting the stocking rate. *Rangelands*, 10(1), 10–14.
- Sprinkle, J., & Bailey, D. (2004). How Many animals can I graze on my Pasture? Retrieved from <https://extension.arizona.edu/pubs>

Description of native ungulate data

Again, spatial data on the abundance or density of native ungulates (elk, *Cervus canadensis*, mule deer *Odocoileus hemionus*, and white-tailed deer *Odocoileus virginiana*) were unavailable for the study area at the resolution of the analysis. We therefore used relative abundance estimates from Goljani Amirkhiz et al. (2018). The authors obtained presence points for each of the three prey species (elk n = 1775, mule deer n = 1120, white-tailed deer n = 367) from the Global Biodiversity Information Facility, Arizona Game and Fish Department, and New Mexico Department of Game and Fish. These data were then used in a Maxent model with 19 bioclimatic, 7 biotic, and 8 landscape and human variables. Models were evaluated with k-fold cross validation, then the authors evaluated model prediction's accuracy based on expert knowledge of the species distribution across the study area and prey occurrence in Arizona and New Mexico's game management units. When experts selected more than one model, model estimates were averaged for the prediction map to enhance accuracy. When the model predicted the presence of a species, but it was known to not inhabit that area, the values of those areas were changed to zero. The models selected by experts for each species are as follows:

Table S4. Top models for native ungulate density data. Table adapted from Goljani Amirkhiz et al. (2018).

Species	Background extent ^a	Presence points filter scale ^b	Uncorrelated variables w/ contribution > 5%
Elk	No	MHRS (14 km)	Mean temperature of warmest quarter (59%), Precipitation of coldest quarter (24%), Isothermality (17%)
Mule deer	No	MHRS (6.6 km)	Temperature annual range (34%), Slope (28%), Temperature seasonality (17%), Precipitation of coldest quarter (7%), Vegetation Height (8), Canopy Cover Majority (6%)
	MHRS (6.6 km)	1 km	Slope (60%), Canopy Cover Majority (40%)
	MHRS (6.6 km)	AHRS (4.7km)	Vegetation Height (35%), Slope (18%), Land Cover Majority (17%), Canopy Cover

			Majority (14%), Distance to Roads (10%), Heat Load Index (6%)
	MHRS (6.6 km)	MHRS (6.6 km)	Canopy Cover Majority (26%), Slope (23%), Soil Suborder Majority (14%), Tree Canopy Cover (13%), Heat Load Index (13%), Distance to Water Resources (11%)
White-tailed deer	MDD (224 km)	1 km	Annual precipitation (31%), Precipitation of wettest month (19%), Temperature seasonality (17%), Minimum Temperature of coldest month (12%), Soil Suborder Majority (11%), Land Cover Majority Variation (5%), Precipitation of coldest quarter (5%)
	MHRS (3.1 km)	AHRS (2.2 km)	Soil Suborder Majority (35%), Vegetation Height (33%), Canopy Cover Majority (32%)

a Extent in which random background points are selected: No = no background limitation, MDD = maximum dispersal distance, MHRS = maximum home range size.

b Scale in which all presence points but one are randomly removed: AHRS = average home range size, MHRS = maximum home range size.

Full details of the methodology are available in Goljani Amirkhiz et al. (2018).

Chapter 3

Interview questions in English

Ranch ID:

Gender:

Approximate area:

Number of cattle:

- 0
- 1-50
- 51-150
- 151-300
- 301-1000
- 1000+

General questions:

1. Do you think the population of jaguars should:
 - a. Increase
 - b. Stay the same
 - c. Decrease
2. How much damage have jaguars caused to your livestock in the past?
 - a. None
 - b. A slight amount
 - c. A moderate amount
 - d. A lot
 - e. A great deal
3. How much damage have jaguars caused to your neighbors in the past?
 - a. None
 - b. A slight amount
 - c. A moderate amount
 - d. A lot
 - e. A great deal
 - f. Unsure
 - g. A great deal
 - h. Unsure
4. How likely is it that jaguars will cause damage to you in the next 12 months?
 - a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely
 - d. Neither likely nor unlikely
 - e. Somewhat likely
 - f. Moderately likely
 - g. Very likely
5. How likely is it that jaguars will cause damage to your neighbors in the next 12 months?
 - a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely
 - d. Neither likely nor unlikely

- e. Somewhat likely
- f. Moderately likely
- g. Very likely
- h. Unsure

Willingness to implement/perception of preventative strategies

1. How effective do you think an electric fence to protect cattle would be on your ranch?
 - a. Very ineffective
 - b. Moderately ineffective
 - c. Somewhat ineffective
 - d. Neither effective nor ineffective
 - e. Somewhat effective
 - f. Moderately effective
 - g. Very effective
2. How effective do you think moving cattle nightly to a pen or corral near the house would be to protect cattle?
 - a. Very ineffective
 - b. Moderately ineffective
 - c. Somewhat ineffective
 - d. Neither effective nor ineffective
 - e. Somewhat effective
 - f. Moderately effective
 - g. Very effective
3. How effective do you think integrating criollo cattle into your herd would be to protect against depredations?
 - a. Very ineffective
 - b. Moderately ineffective
 - c. Somewhat ineffective
 - d. Neither effective nor ineffective
 - e. Somewhat effective
 - f. Moderately effective
 - g. Very effective
4. How likely are you to implement an electric fence on your ranch to protect cattle?
 - a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely
 - d. Neither likely nor unlikely
 - e. Somewhat likely
 - f. Moderately likely
 - g. Very likely
5. How likely are you to move cattle nightly to a pen or corral on your ranch?
 - a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely

- d. Neither likely nor unlikely
 - e. Somewhat likely
 - f. Moderately likely
 - g. Very likely
6. How likely are you to integrate criollo cattle into your herd on your ranch?
- a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely
 - d. Neither likely nor unlikely
 - e. Somewhat likely
 - f. Moderately likely
 - g. Very likely

Personal norms

1. Do you think protecting, rather than killing, wildlife on your property would be:
- a. Very harmful
 - b. Moderately harmful
 - c. Somewhat harmful
 - d. Neither harmful nor beneficial
 - e. Somewhat beneficial
 - f. Moderately beneficial
 - g. Very beneficial
2. Do you think protecting habitat on your property that native animals use would be:
- a. Very harmful
 - b. Moderately harmful
 - c. Somewhat harmful
 - d. Neither harmful nor beneficial
 - e. Somewhat beneficial
 - f. Moderately beneficial
 - g. Very beneficial
3. How effective is killing a jaguar compared to implementing a nonlethal strategy at reducing your losses?
- a. Very ineffective
 - b. Moderately ineffective
 - c. Somewhat ineffective
 - d. Neither effective nor ineffective
 - e. Somewhat effective
 - f. Moderately effective
 - g. Very effective

Attitudes and intent to retaliate

1. How many of your neighbors do you think kill jaguars?
 - a. All
 - b. Most
 - c. Some
 - d. Few
 - e. None
2. Do you think killing a jaguar if it has killed multiple calves or foals is justified?
 - a. Very justified
 - b. Moderately justified
 - c. Somewhat justified
 - d. Neither justified nor unjustified
 - e. Somewhat unjustified
 - f. Moderately unjustified
 - g. Very unjustified
3. Do you think killing a jaguar to prevent it killing calves or foals is justified?
 - a. Very justified
 - b. Moderately justified
 - c. Somewhat justified
 - d. Neither justified nor unjustified
 - e. Somewhat unjustified
 - f. Moderately unjustified
 - g. Very unjustified
4. Do you think killing the next jaguar the appears in your property after livestock losses would be:
 - a. Very harmful
 - b. Moderately harmful
 - c. Somewhat harmful
 - d. Neither harmful nor beneficial
 - e. Somewhat beneficial
 - f. Moderately beneficial
 - g. Very beneficial
5. How likely are you to kill the next jaguar you see on your ranch after a depredation?
 - a. Very unlikely
 - b. Moderately unlikely
 - c. Somewhat unlikely
 - d. Neither likely nor unlikely
 - e. Somewhat likely
 - f. Moderately likely
 - g. Very likely

Measuring subjective norms around lethal and non-lethal control

1. How many of the people important to you would disapprove of you killing big cats on your ranch?
 - a. All would disapprove
 - b. Most would disapprove

- c. Some would disapprove
 - d. Few would disapprove
 - e. None would disapprove
2. Most people important to me think that killing big cats is admirable.
- a. Strongly agree
 - b. Moderately agree
 - c. Slightly agree
 - d. Neither agree nor disagree
 - e. Slightly disagree
 - f. Moderately disagree
 - g. Strongly disagree
3. Most people important to me think that implementing a nonlethal strategy is admirable.
- a. Strongly agree
 - b. Moderately agree
 - c. Slightly agree
 - d. Neither agree nor disagree
 - e. Slightly disagree
 - f. Moderately disagree
 - g. Strongly disagree

Measuring behavioral control for lethal and non-lethal control

1. For me, killing the next jaguar that appears on my property would be...
- a. Very difficult
 - b. Moderately difficult
 - c. Somewhat difficult
 - d. Somewhat easy
 - e. Moderately easy
 - f. Very easy
2. For me, implementing a nonlethal strategy (define) on my property would be...
- a. Very difficult
 - b. Moderately difficult
 - c. Somewhat difficult
 - d. Somewhat easy
 - e. Moderately easy
 - f. Very easy

Interview questions in Spanish

ID de la finca:

Género:

Área aproximada de la finca:

Número de ganado bovino:

- 0
- 1-50
- 51-150
- 151-300
- 301-1000
- 1000+

Preguntas generales:

6. ¿Cree que la población de jaguares debería aumentar, mantenerse, y reducirse?:
 - a. Aumentarse
 - b. Mantenerse
 - c. Reducirse
7. ¿Cuánto daño le han hecho los jaguares en el último año?
 - a. Nada
 - b. Muy poco daño
 - c. Daño moderado
 - d. Bastante daño
 - e. Mucho daño
8. ¿Cuánto daño les han hecho los jaguares a sus vecinos en el último año?
 - a. Nada
 - b. Muy poco daño
 - c. Daño moderado
 - d. Bastante daño
 - e. Mucho daño
9. ¿Qué tan probable es que un jaguar le causa daño en los próximos 12 meses?
 - a. Muy improbable
 - b. Bastante improbable
 - c. Moderadamente improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable
 - g. Muy probable
10. ¿Qué tan probable es que un jaguar causa daño a sus vecinos en los próximos 12 meses?
 - a. Muy improbable
 - b. Bastante improbable
 - c. Moderadamente improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable
 - g. Muy probable

Voluntad de implementar y percepción de estrategias

7. ¿Qué tan efectivo cree usted que sería una cerca eléctrica para proteger su ganado?
 - a. Muy inefectivo
 - b. Bastante inefectivo
 - c. Moderadamente inefectivo
 - d. Ni efectivo ni inefectivo
 - e. Poco efectivo
 - f. Moderadamente efectivo
 - g. Muy efectivo
8. ¿Qué tan efectivo cree que sería mover el ganado cada noche a un corral o potrero nocturno cerca de la casa para proteger el ganado?
 - a. Muy inefectivo
 - b. Bastante inefectivo
 - c. Moderadamente inefectivo
 - d. Ni efectivo ni inefectivo
 - e. Poco efectivo
 - f. Moderadamente efectivo
 - g. Muy efectivo
9. ¿Qué tan efectivo cree que sería integrar ganado criollo a su rebaño para evitar eventos de depredación?
 - a. Muy inefectivo
 - b. Bastante inefectivo
 - c. Moderadamente inefectivo
 - d. Ni efectivo ni inefectivo
 - e. Poco efectivo
 - f. Moderadamente efectivo
 - g. Muy efectivo
10. ¿Qué tan probable es que usted implemente una cerca eléctrica en su finca para proteger el ganado?
 - a. Muy improbable
 - b. Bastante improbable
 - c. Moderadamente improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable
 - g. Muy probable
11. ¿Qué tan probable es que usted moviera su ganado cada noche a un corral o potrero nocturno para reducir la depredación?
 - a. Muy improbable
 - b. Bastante improbable
 - c. Moderadamente improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable

- g. Muy probable
12. ¿Qué tan probable es que usted integrara ganado criollo al rebaño para reducir la depredación?
- a. Muy improbable
 - b. Bastante improbable
 - c. Moderadamente improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable
 - g. Muy probable

Normas personales

1. ¿Cree que proteger, en vez de matar, a los animales nativos silvestres en su predio sería:
- a. Muy dañino
 - b. Moderadamente dañino
 - c. Bastante dañino
 - d. Ni dañino ni beneficioso
 - e. Poco beneficioso
 - f. Moderadamente beneficioso
 - g. Muy beneficioso
2. ¿Cree que proteger el hábitat de los animales silvestres nativos en su predio sería:
- a. Muy dañino
 - b. Moderadamente dañino
 - c. Bastante dañino
 - d. Ni dañino ni beneficioso
 - e. Poco beneficioso
 - f. Moderadamente beneficioso
 - g. Muy beneficioso
3. ¿Qué tan efectivo es matar un jaguar o un puma comparado con implementar una estrategia no letal para reducir las pérdidas?
- a. Muy inefectivo
 - b. Moderadamente inefectivo
 - c. Bastante inefectivo
 - d. Ni efectivo ni inefectivo
 - e. Poco efectivo
 - f. Moderadamente efectivo
 - g. Muy efectivo

Actitudes e intención de retaliación

4. ¿Cuántos vecinos suyos cree que han matado jaguares o pumas?
- a. Todos
 - b. La mayoría
 - c. Algunos
 - d. Pocos

- e. Ninguno
5. ¿Cree que sería justificable matar un jaguar si ha matado varios becerros o potros?
 - a. Muy justificado
 - b. Moderadamente justificado
 - c. Poco justificado
 - d. Ni justificado ni injustificado
 - e. Poco injustificado
 - f. Moderadamente injustificado
 - g. Muy injustificado
 6. ¿Cree que sería justificable matar un jaguar para prevenir que mate becerros o potros?
 - a. Muy dañino
 - b. Moderadamente dañino
 - c. Bastante dañino
 - d. Ni dañino ni beneficioso
 - e. Poco beneficioso
 - f. Moderadamente beneficioso
 - g. Muy beneficioso
 7. ¿Cree que matar el siguiente jaguar que aparece en su predio sería:
 - a. Muy dañino
 - b. Moderadamente dañino
 - c. Bastante dañino
 - d. Ni dañino ni beneficioso
 - e. Poco beneficioso
 - f. Moderadamente beneficioso
 - g. Muy beneficioso
 8. ¿Qué tan probable es que usted mata el siguiente jaguar o que usted ve en su predio?
 - a. Muy poco probable
 - b. Moderadamente probable
 - c. Bastante improbable
 - d. Ni probable ni improbable
 - e. Poco probable
 - f. Moderadamente probable
 - g. Muy probable

Normas subjetivas

1. ¿Cuántas personas importantes para usted no aprobarían de que ha matado un grande felino?
 - a. Todos no aprobarían
 - b. La mayoría no aprobarían
 - c. Algunos no aprobarían
 - d. Pocos no aprobarían
 - e. Nadie aprobaría
2. La mayoría de la gente importante en mi vida cree que matar un felino es admirable
 - a. Muy de acuerdo
 - b. Moderadamente de acuerdo
 - c. Poco de acuerdo
 - d. Ni de acuerdo ni desacuerdo

- e. Poco desacuerdo
 - f. Moderadamente desacuerdo
 - g. Muy desacuerdo
3. La mayoría de gente importante en mi vida cree que implementar una estrategia no letal como la cerca eléctrica es admirable
- a. Muy de acuerdo
 - b. Moderadamente de acuerdo
 - c. Poco de acuerdo
 - d. Ni de acuerdo ni desacuerdo
 - e. Poco desacuerdo
 - f. Moderadamente desacuerdo
 - g. Muy desacuerdo

Control de comportamiento para intervenciones letales y no letales

3. Para mí, matar al siguiente jaguar en mi predio sería:
- a. Muy difícil
 - b. Moderadamente difícil
 - c. Poco difícil
 - d. Ni difícil ni fácil
 - e. Algo fácil
 - f. Moderadamente fácil
 - g. Muy fácil
4. Para mí, implementar una cerca eléctrica en mi predio sería:
- a. Muy difícil
 - b. Moderadamente difícil
 - c. Poco difícil
 - d. Ni difícil ni fácil
 - e. Algo fácil
 - f. Moderadamente fácil
 - g. Muy fácil

Table S5. Results for predictive models of retaliation.

Model	Variable	Estimate	90% CI / 75% CI
Past and expected losses to jaguars, number of cattle, and gender predict intention to kill a jaguar.	Past damages	0.25	0.03 - 0.463 / 0.10 - 0.40
	Expected damages	0.12	-0.07 - 0.8 / -0.01 - 0.23
	Number of cattle	-0.08	-0.25 - 0.08 / -0.202 - 0.03
	Gender (Reference = male)	-0.52	-1.09 - 0.08 / -0.93 - -0.09
Past and expected losses to jaguars, attitudes towards retaliation, number of cattle and gender predict intention to kill a jaguar.	Past damages	0.32	0.09 - 0.58 / 0.16 - 0.50
	Expected damages	0.01	-0.18 - 0.20 / -0.12 - 0.14
	Attitudes towards retaliation	0.79	0.50 - 1.11 / 0.59 - 1.00
	Number of cattle	-0.15	-0.37 - 0.04 / -0.29 - -0.01
	Gender (Reference = male)	-0.17	-0.79 - 0.48 / -0.61 - 0.30
Attitudes towards retaliation, subjective norms of killing jaguars, behavioral control of killing a jaguar, number of cattle, and gender predict intention to kill a jaguar. (Theory of Planned Behavior).	Attitudes towards retaliation	0.62	0.34 - 0.94 / 0.42 - 0.83
	Subjective norms of retaliation	0.48	0.28 - 0.68 / 0.34 - 0.62
	Behavioral control of killing a jaguar	0.34	0.07 - 0.61 / 0.16 - 0.53
	Number of cattle	-0.07	-0.26 - 0.12 / -0.20 - 0.06
	Gender (Reference = male)	0.05	-0.55 - 0.65 / -0.35 - 0.47
Past losses to jaguars, attitudes towards retaliation, subjective norms	Past damages	0.26	-0.01 - 0.54 / 0.07 - 0.45
	Expected damages	0.00	-0.21 - 0.22 / -0.14 - 0.15

of killing jaguars, and behavioral control of killing a jaguar predict intention to kill a jaguar. (Theory of Planned Behavior + losses).	Attitudes towards retaliation	0.69	0.39 - 1.03 / 0.47 - 0.92
	Subjective norms of retaliation	0.47	0.27 - 0.68 / 0.33 - 0.61
	Behavioral control of killing a jaguar	0.26	-0.01 - 0.55 / 0.07 - 0.46
	Number of cattle	-0.13	-0.33 - 0.07 / -0.27 - 0.01
	Gender (Reference = male)	-0.13	-0.85 - 0.59 / -0.64 - 0.37
Perceived effectiveness of conflict mitigation tools and behavioral control of implementing them predicts intention to kill a jaguar.	Effectiveness of fencing vs killing jaguars	-0.02	-0.16 - 0.12 / -0.12 - 0.07
	Effectiveness of electric fence	-0.03	-0.16 - 0.10 / -0.12 - 0.06
	Behavioral control to implement an electric fence	-0.20	-0.35 - -0.05 / -0.30 - -0.09
	Number of cattle	-0.02	-0.19 - 0.16 / -0.14 - 0.10
	Gender (Reference = male)	-0.30	-0.86 - 0.26 / -0.696 - 0.096