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The effectiveness of hazing African lions as a conflict mitigation tool: implications for carnivore management

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Abstract. Human–carnivore conflict (HCC) represents one of the greatest threats to rural livelihoods and the persistence of large carnivores. The application of aversive conditioning, the association of unpleasant stimuli with the occurrence of unwanted behaviors, to mitigate HCC has achieved mixed results within and across species, making a better understanding of the factors driving intervention success critical to inform management practices. We explored the degree to which the chasing of African lions (*Panthera leo*) out of no tolerance zones conditions lion behavior to reduce their rate of return into community lands or rate of repeated livestock killing, providing evidence-based understanding of program outcomes. We used data from 15 global positioning system (GPS)-collared lions adjacent to Hwange National Park, Zimbabwe, with each lion receiving 0–17 conditioning treatments, and analyzed the data using recurrent event survival analysis and logistic regression. Chases were most successful (i.e., lion pushed out of the no tolerance zone by sunrise of the following day) in the dry season (i.e., when wild prey were more predictable), in areas closer to the park, and for individuals from smaller and more stable prides (i.e., had not lost a pride male within six months). Adult females and subadult males were more likely than adult males to reenter community lands, and subadult males were most likely to repeatedly depredate livestock. While livestock depredation has decreased since program initiation, the individuals in this study were overall not less likely to enter community lands or depredate livestock in response to chases when chases were considered isolated events. Rather, it was the consistency of deterrence events that proved most important in reducing livestock depredations, likely because of a stronger reinforcement between the undesired behavior and the negative stimulus. However, lions that had previously habitually killed livestock had greater depredation rates even after several conditioning treatments. Aversive conditioning holds promise in the management of carnivores that depredate livestock, but intervention must be consistent, ideally early in the development of problem behaviors, to maximize intervention effectiveness. Methods that separate wildlife from people (i.e., fencing, livestock enclosure fortification), in combination with aversive conditioning, may be needed to provide a sustainable, long-term solution.

Key words: aversive conditioning; conflict mitigation; hazing; human–wildlife conflict; lion; Lion Guardians; livestock; *Panthera leo*;.

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Introduction

An overarching goal of conservation biology is to preserve and restore the world's biodiversity. However, intractable challenges arise for species that pose serious risk to people's livelihoods, in particular for large carnivores and herbivores in impoverished rural areas (Osborn and Parker 2003, Dickman et al. 2011). Livestock depredation is the largest source of conflict between carnivores and people globally (van Eeden et al. 2018*b*), causing substantial financial losses (Dickman et al. 2011) and tangible threats to human safety (Löe and Röskaft 2004, Packer et al. 2005). Over the last 200 yr, habitat loss and fragmentation, combined with changing land uses, have elevated human–wildlife conflict and led to substantial population declines and range contractions for most species of large carnivore, rendering many species at risk of extinction (Ripple et al. 2014). Given burgeoning human populations (Bongaarts 2009) and expanding agricultural frontiers (Green 2005), human–carnivore conflict is likely to intensify in the future, particularly at the edges of protected areas that serve as strongholds for large carnivore populations (Wittemyer et al. 2008). The existing network of protected areas alone is insufficient to ensure the long-term persistence of wide-ranging carnivores (Di Minin et al. 2016), and international pressure is mounting to find non-lethal solutions for mitigating human–carnivore conflict in the working landscapes between protected areas.

Non-lethal options to mitigate human–carnivore conflict are limited largely to physical separation (e.g., fences, enclosures) or deterrents (Shivik et al. 2003). Aversive conditioning in wildlife management is an active mode of deterrent that delivers a punishment (e.g., chasing by dogs or humans, painful stimuli such as capsicum powder and rubber bullets; Shivik 2006) to targeted individuals in response to an unwanted behavior, such as entering a campground or approaching livestock. The goal of aversive conditioning is the association of the punishment with the undesired behavior, and ultimately a cessation of the undesired behavior (Pavlov 1927).

Applications of aversive conditioning in conflict situations have met with varying degrees of success for free-ranging omnivores (Rauer et al. 2003, Beckmann et al. 2004, Mazur 2010), carnivores (Andelt et al. 1999, Schultz et al. 2005, Hawley et al. 2009), and ungulates (Kloppers et al. 2005, VerCauteren et al. 2005, Found and St. Clair 2018). Failures in these applications have been attributed in part to the challenges of implementation, such as the deterrent being insignificant to the animal in terms of fitness cost, or having insufficient reinforcement between the behavior and the punishment, that ultimately lead to habituation, or extinction of the neophobic effect (Shivik et al. 2003, Shivik 2006, Blumstein 2016). Other suggested drivers of mixed outcomes included variation among individuals in terms of their degree of previous positive reinforcement of undesired behaviors (Rauer et al. 2003, Beckmann et al. 2004, Mazur 2010), social status (Rauer et al. 2003, Schultz et al. 2005), personality (Found and St. Clair 2018), or ecological context (e.g., availability of suitable alternatives to the undesired behavior; Blumstein 2016). Two key limitations in gaining proper inference on the effectiveness of aversive conditioning for mitigating conflict include (1) low sample sizes, in terms of the number of offending animals, the number of conditioning trials per individual, and replication (Rauer et al. 2003, Beckmann et al. 2004, van Eeden et al. 2018*b*), and (2) lack of robust experimental design, including the presence of controls and ability to separate treatment effects (Andelt et al. 1999, Schultz et al. 2005, Hawley et al. 2009, van Eeden et al. 2018*b*).

African lions pose a particularly challenging framework for conservation, as they are valued at a global scale but often considered nuisance animals at a local scale (Dickman et al. 2011). However, given a high degree of conflict with people, combined with major efforts to reduce retaliatory killing of lions (Hazzah et al. 2014), the species also provides unprecedented opportunities for gaining deeper insights into the factors influencing the success of aversive conditioning programs. Increasingly, satellite collars are deployed to track movements of lions in real time, providing an opportunity to intervene before a livestock depredation occurs. One such application, the Long Shields Community Guardians Program (LSCGP) around Hwange National Park, Zimbabwe, uses trained local people to intercept collared lions when they come within ~2 km of a household and to initiate a chase to push the offending lion out of community lands. These chases often occur on foot, and are supplemented by blowing horns and making other loud noises. Whereas reductions in retaliatory killing are an important aspect of program success, long-term public support for such a program will likely require reductions in lion visitations to community lands and resulting reductions in actual livestock depredations—outcomes that will depend upon how efficiently and effectively aversive conditioning might overcome recalcitrant behaviors, habituation, and recidivism by lions.

Using data from collared lions at the periphery of Hwange National Park, in combination with records of lion interventions and livestock depredations in surrounding community lands, we investigated lion- and chase-specific factors influencing immediate and longer-term behavioral changes by individual lions following aversive conditioning. Advantages of this study system include monitoring of both male and female lions, as well as subadults and adults (with replicates for each), and having monitored individuals for 3.5–21 months ($\bar{x}$ = 12.5 months), during which individuals experienced 0–17 interventions given 1–73 incursions into community lands. Previous research found that livestock depredation rates have decreased following program implementation in June 2012, from 122 ± 29 depredation events annually from 2010 to 2011 to 40 ± 14 events from 2013 to 2015 (Appendix S5; adapted from Loveridge 2015), and that some individual lions in this region shifted their seasonal ranges away from community lands, although others remained entrenched and became more furtive in their movements (Petracca 2018). Herein, we explore the role of direct experience with aversive conditioning as a potential driver of those large-scale patterns and of active interventions with recalcitrant lions as a means of potentially reducing livestock depredation rates. Given that the quantification of intervention effectiveness is largely lacking among techniques to reduce livestock depredation (van Eeden et al. 2018*a*, *b*), our aim is to not only help refine program effectiveness in this system, but also to gain transferable insights to other species and systems by quantifying the effects of aversive conditioning on the spatial and behavioral ecology of individuals.

Materials and Methods

Study area

The study area (6500 km^2) spans Hwange National Park (hereafter "the Park"; 19°0′ S, 27°3′ E) and surrounding protected areas and community lands (Fig. 1). The Park covers 14,600 km^2 of semiarid savanna in northwestern Zimbabwe, with altitude varying from 800 to 1100 m (Loveridge et al. 2009). Mean annual rainfall is 600 mm and highly variable (inter-annual CV of 30%), with water artificially supplied at various locations in the dry season (Loveridge et al. 2016). There are presently two community areas bordering the national park that partially overlapped our study area: Tsholotsho and Mabale Communal Lands, with 1946 households included within our study area. Livelihoods depend on subsistence agro-pastoral farming practices, focusing on livestock husbandry and the growing of maize, sorghum, millet, and legumes (Kuiper et al. 2015).

Most people within our study are Ndebele, with 99% of people within Tsholotsho speaking Ndebele as a first language, while people in Mabale spoke a mix of Ndebele (48%), Nambya (32%), and other regional African languages (20%; Loveridge et al. 2017*a*). Traditionally, nineteenth-century Ndebele people would have hunted and killed lions as the Maasai do today (Hazzah et al. 2014), though such practices stopped with the advent of the Zimbabwean protected areas system. While Problem Animal Control is now the responsibility of the Zimbabwe Parks and Wildlife Management Authority, illegal retaliatory killing still occurs in the villages via wire snares and homemade gin traps. The more traditional Ndebele villages still build traditional log stockades to protect livestock at night (thought the use of the stockades is inconsistent), while the more recently settled communities to the north of the Park often have very poor livestock enclosures. Livestock herding by children is becoming more uncommon due to an increase in schooling.

Lion and depredation monitoring

Lions were immobilized for handling by qualified field staff using standard protocols for the species (Fahlman et al. 2005) and fitted with global positioning system (GPS) collars equipped with either ultra-high frequency (UHF) or

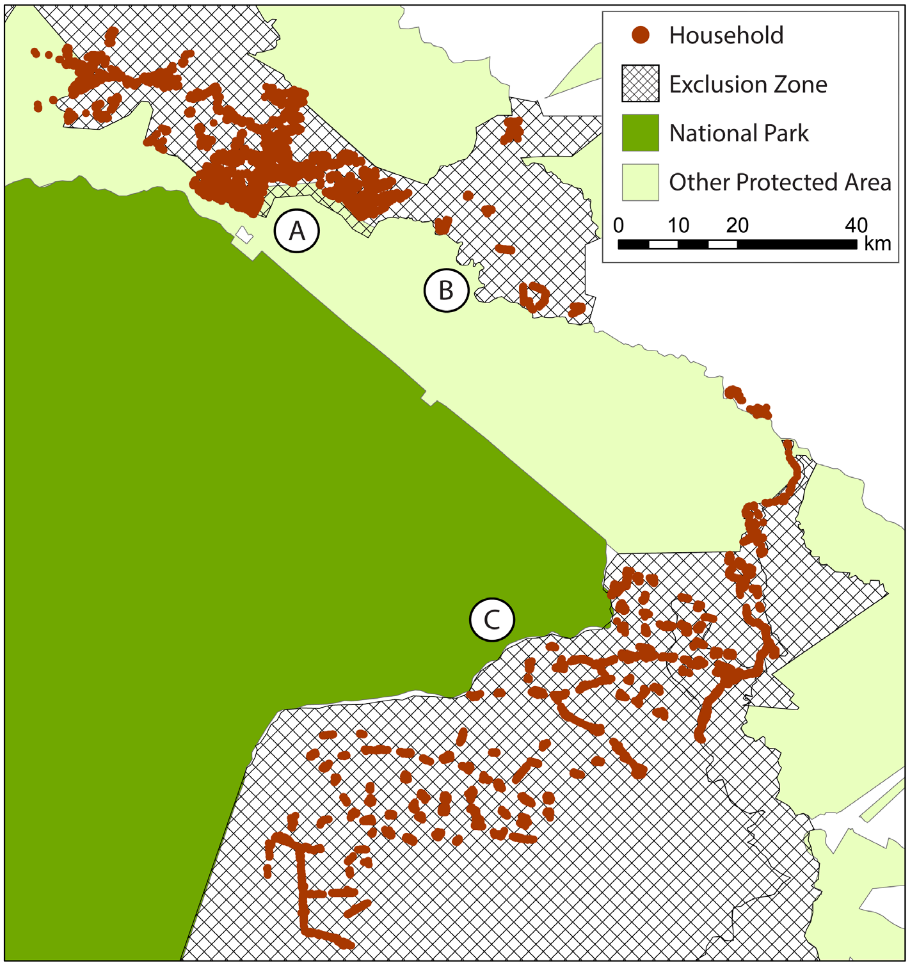

Fig. 1. Location of Exclusion Zone outside Hwange National Park, Zimbabwe. A chase by the Community Guardians would be initiated if a lion had GPS coordinates within this zone. The Exclusion Zone extends 2 km into (A) the Sikumi Forestry Area in Mabale Communal Lands but otherwise conforms to the boundary of (B) the Village Resettlement Area in conservancy lands and (C) Tsholotsho Communal Lands.

satellite remote downloads (Televilt Positioning, Lindesberg, Sweden; Sirtrack, Hawkes Bay, New Zealand; Africa Wildlife Tracking, Pretoria, South Africa). See Appendix S1 for more information on animal handling and ethical care.

From a total of 98 lions collared within the Park and greater study system, 15 (three adult females, six adult males, and six subadult males at study onset; adult is ≥4 yr of age) met the criteria for inclusion in our study, which were (1) being members of unique prides/coalitions (2) having home ranges that did not exclusively fall within the Park (i.e., overlapped community lands to some degree), and (3) having GPS data when the Community Guardians were actively chasing lions (i.e., within the period from January 2013–March 2016). The collaring of only one individual per pride/coalition was desirable for both logistical (e.g., greater geographic coverage) and statistical (e.g., independence of inference) reasons, and should be considered in the application of our methodology to other social species for which it is common to collar more than one member of a social group (e.g., wolves). Positional data were collected on these animals from January 2013 to March 2016 ($\bar{x}$ = 377 ± 170 SD collar-days per individual) using one or more fix schedules: (1) bi-hourly (81.33% of data, 12 individuals), (2) hourly (11.52% of data, four individuals), (3) hourly at night (18:00–7:00) with 2–4 additional fixes in day hours (3.86% of data, three individuals), and (4) every four hours (3.29% of data, one individual). We created regular trajectories of original GPS locations (Δt = 2 h) using adehabitatLT in Program R (Calenge 2006).

As of June 2012, there were 10 Community Guardians operating in Tsholotsho and Mabale Communal Lands. The Guardians (eight men, two women) were hired based on nominations by the traditional chieftainship. They were tasked with monitoring lions each day from sunrise (6:00 h) to sunset (18:00 h), and chasing GPS-collared lions as soon as lion individuals entered the Exclusion Zone (Fig. 1). Their goal was to push lions out of the Exclusion Zone and in the direction of the Park. The Exclusion Zone included community lands and extended 2 km into Sikumi Forest, which serves as a buffer between community lands and the Park in Mabale, and also included an area of resettled villages in conservancy lands east of Mabale. See Appendix S2 for more information on the Community Guardians' field protocol.

Evaluating program success

We divided criteria for evaluating program success into short-term lion responses (e.g., success of individual chase events) vs. longer-term lion behaviors (e.g., return times and depredation propensity). Over the short term, we defined the success of a chase event as the target lion moving out of the Exclusion Zone by sunrise (07:00) on the day following the intervention. Lions are generally more active in darkness (Schaller 1972) and may be reluctant to move substantially during daylight when active hazing of the animal would occur, likely due to both higher temperatures (Schaller 1972) and higher risk of persecution by humans in daytime hours (Oriol-Cotterill et al. 2015). If the animal remained within the Exclusion Zone at sunrise, we considered the previous day's chase to have failed and designated a new chase event if the Guardians continued a chase the following morning. To identify the determinants of a successful chase, we fit mixed-effects logistic regression models using the R package lme4 (Bates et al. 2015), specifying individual lion as a random intercept.

Longer-term indicators of program success were considered to be diminished propensities for reentering the Exclusion Zone or committing livestock depredation. For these analyses, we used a recurrent event, gap time survival framework (Kleinbaum and Klein 2011), specifying the event as an Exclusion Zone reentry in the first case or as a livestock depredation recurrence in the second case.

Candidate Cox proportional hazards models were fit using the R package survival (Therneau 2015), with the data clustered by individual lion and stratified by the Exclusion Zone entry number for that individual or depredation number, depending on the analysis. Study onset was set as 13 January 2013, the start of that year's collaring period. Gap times were calculated in days, after censoring consecutive days spent within the Exclusion Zone; thus, if a lion entered the Exclusion Zone on Day 1, stayed for Days 1–5, left on Day 6, and reentered on Day 7, that time difference would be 7–6 = 1. Data were right-censored when there was no subsequent event (either Exclusion Zone reentry or depredation recurrence) at the end of the collaring period (i.e., Event = 0 for those gap times).

We organized candidate covariates for both analyses into categories related to the intervention process itself: early intervention, positive vs. negative reinforcement, and factors associated with social or environmental resistance (Table 1; also see Appendix S3). We had a priori hypotheses to justify the inclusion of each covariate (see Appendix S3), considered the covariate effects to be additive within and across covariate categories, and used backward model selection to retain informative covariates as described below.

For each of our three analyses—chase success, rate of reentry, and depredation recurrence—we started with a global model that included uncorrelated sets of candidate covariates (covariate pairs having $r < 0.6$; Hebblewhite et al. 2014) and then used a stepwise approach to model selection using Akaike information criterion corrected for small sample size (AIC_c) to rank candidate models (Burnham and Anderson 2002); not all covariates were used across all analyses (see Appendix S3). In each case, we removed variables one at a time to determine each covariate's influence on AIC_c and evaluate its importance relative to our a priori hypotheses. We stopped covariate removal when the exclusion of covariates led to model ΔAIC_c values >2.0, meaning

Table 1. Covariates hypothesized to influence chase success and rates of repeated Exclusion Zone reentry or livestock depredations by GPS-collared lions outside Hwange National Park, Zimbabwe.

Early intervention	Positive reinforcement	Negative reinforcement	Social resistance	Environmental resistance
Animal is known livestock killer (1/0)	Home range size	Chase event in response to previous Exclusion Zone reentry (1/0)$^{T-1}$	Demographic class	Wet season (1/0) (in this season, wild prey are more dispersed)
Depredation number at which intervention began	Cumulative number of depredation events	Chase event in response to previous livestock depredation (1/0)$^{T-1}$	Loss of pride male in the past six months (1/0)	Temperature at chase onset (°C)
	Cumulative number of livestock killed	Level of reinforcement against Exclusion Zone reentry	AgeClass × Male Loss	Hot weather (1/0)
	Depredation occurrence in last 72 h (1/0)	Level of reinforcement against depredation recurrence	Subadult (1/0)	Distance to Hwange NP at chase initiation
	Depredation occurrence on previous Exclusion Zone reentry (1/0)$^{T-1}$	Cumulative days being chased	Pride size	
	Number of hours spent in Exclusion Zone prior to chase onset	Proportion of home range that falls within Exclusion Zone (Relative Risk Familiarity)	Single lion (1/0)	
			Cub presence (1/0)	

Notes: Covariates denoted by superscript "$T-1$" are relevant to the previous entry or depredation (time $T-1$); all others apply to the current entry or depredation (time T). See Appendix S3 for more information on each covariate and associated a priori hypotheses.

that each remaining covariate had substantial explanatory value. For the time-to-event models, we only included those models that met the proportional hazards assumption as determined by scaled Schoenfeld residuals (Kleinbaum and Klein 2011). Ultimately, the strength of support for a given candidate model was determined using AIC_c values, in which models with $\Delta AIC_c < 2$ units difference from the highest ranked model were considered to have greatest support. All covariates in these top models are presented for their explanatory value. However, due to the uncertainty in some covariate relationships, we used the most parsimonious top model to describe effect sizes and to create our figures in order to highlight only the covariate effects with consistent, unequivocal support.

Results

Determinants of chase success

A total of 72 chases of 12 different lions ($\bar{x} = 6 \pm 5$ SD chases per individual) recorded by the Community Guardians between 13 January 2013 and 16 March 2016 were included in our analyses. The three lions that were not chased had low frequency of entry to the Exclusion Zone (1.67 ± 1.15 times per individual) and entered the Exclusion Zone at night. Of the 72 chases, 56% ($n = 40$) were successful (animal moved out of Exclusion Zone by 07:00 next morning), whereas 44% ($n = 32$) failed. Successful chases were split almost evenly between lions leaving the Exclusion Zone by 18:00 of the chase day (corresponding to the end of Community Guardian patrols; $n = 22$, 55%) or leaving sometime before 07:00 of the following morning ($n = 18$, 45%). There was evidence of habituation after the 10th chase, with Chases 1–5, 6–10, and 11–17 having success rates of 61.54% ($n = 39$), 60.00% ($n = 20$), and 30.77% ($n = 13$), respectively.

Probability of chase success was positively associated with closer proximity of chase initiation to the Hwange National Park boundary (i.e., a lesser distance to chase the lion), smaller pride size, pride stability, and the dry season (a time when wild prey are more predictable and

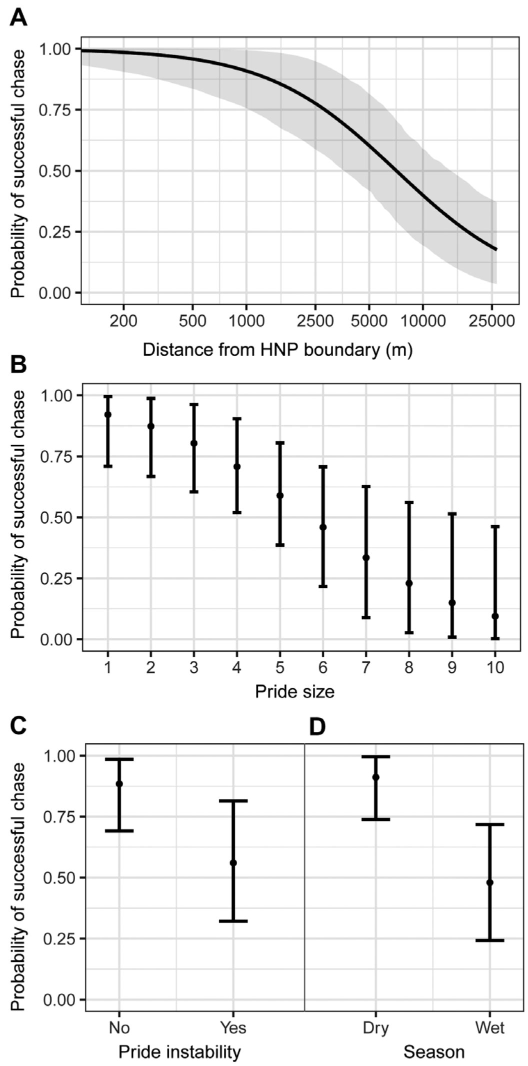

Fig. 2. Probability of chase success by the Long Shields Community Guardians at the periphery of Hwange National Park, Zimbabwe, where chase success is defined as pushing the target lion out of the Exclusion Zone by sunrise (07:00) of the day following chase initiation. Top explanatory variables were (A) distance of chase initiation from the boundary of Hwange National Park, (B) pride size (number of adults and subadults in the pride), (C) pride instability (whether or not a pride male had died in the last six months), and (D) season.

livestock are not herded close to the Park boundary; Davidson et al. 2013, Kuiper et al. 2015; Fig. 2; Tables 2, 3; Appendix S4). The 95% CIs of these coefficients did not overlap 0, indicating confidence in the direction of these effects (Table 3). As distance from the Park boundary decreased from 25 to 5 km to 500 m, the probability of chase success increased from 0.18 (95% CI = 0.04–0.37) to 0.60 (0.42–0.81) to 0.96 (0.84–1.00; Fig. 2). Chase success was markedly higher for coalitions of 1–2 individuals ($\bar{x}$ = 0.90, combined 95% CI = 0.67–1.00) compared to prides of 8–10 individuals ($\bar{x}$ = 0.16, combined 95% CI = 0.09–0.56; Fig. 2). Lastly, chase success was greater in times of pride stability (0.88; 95% CI = 0.69–0.98) vs. instability (0.56; CI = 0.32–0.81), and in the dry season (0.91; CI = 0.74–0.99), a time when wild prey are more predictable compared to the wet season (0.48; CI = 0.24–0.72; Fig. 2). There was some evidence that greater relative risk familiarity (i.e., the proportion of an individual's home range that overlaps the Exclusion Zone) was associated with greater chase success, but this relationship was statistically uncertain (i.e., the 95% CI overlapped 0; Appendix S4).

Determinants of time to Exclusion Zone reentry

There were 361 entries into the Exclusion Zone detected by GPS collar locations from 15 individual lions during this study. Thirteen lions entered the Exclusion Zone repeatedly ($\bar{x}$ = 26 ± 24 SD reentries/lion), while two individuals (both adult males, aged 6.5 and 7.5 yr) did not reenter the Exclusion Zone after their first entry. Following an Exclusion Zone departure (with or without intervention), the median time to return to the Exclusion Zone was 3 d (SD = 23), and reentering lions spent a median duration of 10 h (SD = 48 h) inside the Exclusion Zone. Of 337 reentries, only 10.4% (n = 35) were followed by a chase event within the subsequent 48 h, and 31.4% of these (n = 11) required 2–6 d of consecutive chases, underscoring the need for repeated intervention in more difficult cases. For the reentries not followed by a chase event (n = 302), nearly half (46.4%) occurred at night (from 18:00 to 6:00), when the Community Guardians were not on patrol.

While there was statistical uncertainty in the top models predicting rate of Exclusion Zone reentry, the only variable with unequivocal statistical support was demographic class (Table 4). In particular, adult females had a risk of Exclusion Zone entry that was 2.21 times that of adult

Table 2. Model selection table for two top candidate models (i.e., models within 2 ΔAIC_c from the top model) explaining probability of success of chases ("success" is defined as pushing the target lion out of the Exclusion Zone by sunrise (07:00) of the day following chase initiation) by the Community Guardians outside Hwange National Park, Zimbabwe, using a logistic regression framework.

Regression model	K	ΔAIC_c	w_i
RelativeRiskFamiliarity + PrideInstability + PrideSize + Wet + DistPark	7	0	0.3
PrideInstability + PrideSize + Wet + DistPark	6	0.62	0.22

Notes: For each model, we identify the predictors (Regression model), number of parameters (K), delta AIC_c (ΔAIC_c), and AIC_c weights (w_i), with the highlighted model the chosen top model due to being the least parameterized model within 2 ΔAIC_c from the top model. Included variables were the proportion of an individual's home range that overlapped the Exclusion Zone (RelativeRiskFamiliarity), if a male lion had died within the last six months (PrideInstability), the number of adults and subadults in the pride (PrideSize), if it was the wet season (Wet), and distance from the national park boundary at which the chase was initiated (DistPark). Please see Appendix S4 for table with all candidate models.

males (95% CI = 1.71–2.87), and subadult males had a risk that was 1.57 times higher than that of adult males (1.19–2.07; Fig. 3, Table 5). There is some evidence that risk of Exclusion Zone entry was higher given a chase intervention on the previous Exclusion Zone reentry, less consistent reinforcement of deterring this behavior, pride instability, and greater relative risk familiarity, but given the overlap of the 95% CIs with 1, more data are needed to clarify these relationships (Appendix S4).

Determinants of time to next livestock depredation

Over the study period, there were 233 reported livestock depredation events attributable to lions around Hwange National Park, leading to the loss of 318 animals (182 cattle, 87 goats, 43 donkeys, five sheep, one dog). Of the 12 lions that were chased, three lions (one subadult male, two young adults aged 4 and 5) did not depredate livestock after program initiation, while the remaining nine lions were either chronic livestock predators (n = 6), with an average of 14 ± 7 SD depredation events/individual, or killed livestock only once (n = 3). These nine lions were responsible for over half of the reported depredations (50.21%; n = 117 events), of which 23.08% were followed by a chase event in the subsequent 48-hour period. In total, our collared lions depredated 173 animals (83 cattle, 68 goats, 22 donkeys) over the 3-yr study period. The median time between recurrent depredations by a given individual was 8 d (SD = 28).

Table 3. Top model explaining probability of success of chases ("success" is defined as pushing the target lion out of the Exclusion Zone by sunrise (07:00) of the day following chase initiation) by the Community Guardians outside Hwange National Park, Zimbabwe, using a logistic regression framework.

Variable	β	95% CI	Odds ratio (e^{β})
(Intercept)	15.36	7.01, 29.38	
PrideInstability	−1.79	−3.68, −0.32	0.17
PrideSize	−0.52	−1.14, −0.14	0.59
Wet	−2.41	−4.67, −0.73	0.09
DistPark	−1.18	−2.37, −0.48	0.31

Notes: Included variables were if an adult male lion had died within the last six months (PrideInstability), the number of adults and subadults in the pride (PrideSize), if it was the wet season (Wet), and distance from the national park boundary at which the chase was initiated (DistPark). We present the estimated coefficients, 95% confidence intervals, and odds ratios.

The best predictors of rate of livestock depredation recurrence were subadult status, cumulative number of livestock killed, reinforcement of deterring entries to the Exclusion Zone, and familiarity with community lands (Table 6). In particular, the risk of a repeated livestock depredation was 2 × higher for subadults (95% CI 1.44–2.78) vs. adults (Table 7; Fig. 4). Moreover, the risk of livestock depredation increased by 15.0% [4.4–26.7%] with each additional animal killed at time t (Table 7). Importantly, for every 1% increase in the percentage of Exclusion Zone reentries associated with a chase, the risk of livestock depredation decreased by 12.3% [2.5–21.1%] (Table 7). Lastly, for each 1% increase in overlap of the animal's home range with the Exclusion Zone, the risk of livestock depredation decreased by 3.9% [1.8–6.1%] (Table 7); these results indicate that one cannot judge the probability of a lion becoming a problem simply by its range overlap with community lands, nor does it

Table 4. Model selection table for seven top candidate models (i.e., models within 2 ΔAIC_c from the top model) explaining rate of lion reentry to the Exclusion Zone outside Hwange National Park, Zimbabwe, using a recurrent event survival model with a gap time framework.

Survival model	K	ΔAIC_c	w_i
ChasedPrevEntry + NonEntryReinforcement + Class + PrideInstability	5	0	0.15
NonEntryReinforcement + Class + PrideInstability	4	0.03	0.15
NonEntryReinforcement + Class	3	0.36	0.13
Class	2	0.80	0.1
ChasedPrevEntry + NonEntryReinforcement + Class	4	0.89	0.1
PrideInstability + Class	3	1.28	0.08
ChasedPrevEntry + RRFamiliarity + NonEntryReinforcement + Class	5	1.71	0.06

Notes: For each model, we identify the predictors (Survival model), number of parameters (K), delta AIC_c (ΔAIC_c), and AIC_c weights (w_i), with the highlighted model the chosen top model due to being the least parameterized model within 2 ΔAIC_c from the top model. Included variables were if the previous reentry was associated with a chase event (ChasedPrevEntry), the percentage of Exclusion Zone reentries that was followed by a chase event (NonEntryReinforcement), demographic class (i.e., adult male, adult female, subadult male; Class), if an adult male lion had died within the last six months (PrideInstability), and the proportion of an individual's home range that overlapped the Exclusion Zone (RelativeRiskFamiliarity, here "RRFamiliarity"). Please see Appendix S4 for table with all candidate models.

mean that lions cannot/should not occupy community lands at all. There was some evidence that being chased earlier in a sequence of depredations by a target individual reduced that lion's future rate of depredation and that being chased after a previous depredation incident did the opposite; however, given the overlap of the 95% CIs with 1, these relationships are statistically uncertain (Appendix S4).

Discussion

A challenge of aversive conditioning programs is attempting to engender a long-lasting shift in animal behavior by increasing the cost associated with a given behavior, especially when the behavior leads to a valuable food resource such as livestock, in an otherwise resource-limited environment. Outside Hwange National Park, Zimbabwe, overall rates of livestock depredation have decreased since initiation of the LSCGP (Appendix S5; adapted from Loveridge 2015), and some lions have exhibited large-scale shifts in space use to avoid community lands (Petracca 2018). Of the 12 lions that were chased in this study, three (1/4) failed to depredate any livestock over the course of the study. For the remaining nine animals, we did not find that individual chases by the Guardians (i.e., chases considered as isolated events) reduced their rate of reentry into community lands or rate of future livestock depredations. Rather, it was the consistent application of chase interventions (i.e., higher proportion of entries intercepted by the Guardians) that proved most important in reducing depredation rates and was weakly associated with reduced rates of Exclusion Zone reentry,

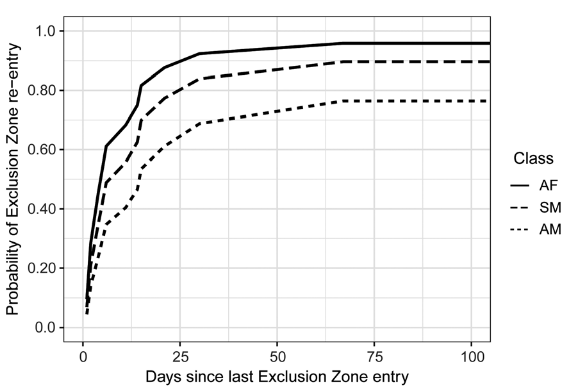

Fig. 3. Probability of Exclusion Zone reentry by lions at the periphery of Hwange National Park, Zimbabwe, based on demographic class (subadult male, adult female, adult male). Survival models used a recurrent event, gap time framework.

Table 5. Top model explaining rate of lion reentry to the Exclusion Zone outside Hwange National Park, Zimbabwe, using a recurrent event survival model with a gap time framework.

Variable	Hazard ratio (HR)	95% CI of HR
Class: AF	2.214	1.711–2.865
Class: SM	1.570	1.191–2.068

Notes: The included variable was demographic class (adult male, adult female, subadult male). We present the estimated hazard ratios and hazard ratio 95% confidence intervals.

Table 6. Model selection table for three top candidate models (i.e., models within 2 ΔAIC_c from the top model) explaining rate of livestock depredation by lions outside Hwange National Park, Zimbabwe, using recurrent event survival models with a gap time framework.

Survival model	*K*	ΔAIC_c	w_i
ChasedPrevDep + InterventionTiming + RRFamiliarity + TotalAnimalsKilled + NonEntryReinforcement + Subadult	6	0	0.24
ChasedPrevDep + RRFamiliarity + TotalAnimalsKilled + NonEntryReinforcement + Subadult	5	0.16	0.22
RRFamiliarity + TotalAnimalsKilled + NonEntryReinforcement + Subadult	4	1.59	0.11

Notes: For each model, we identify the predictors (Survival model), number of parameters (*K*), delta AIC_c (ΔAIC_c), and AIC_c weights (w_i), with the highlighted model the chosen top model due to being the least parameterized model within 2 ΔAIC_c from the top model. Included variables were if the previous reentry was associated with a livestock depredation (ChasedPrevDep), the depredation number of a given animal at which that animal first experienced a chase (Intervention Timing), the proportion of an individual's home range that overlapped the Exclusion Zone (RelativeRiskFamiliarity, here "RRFamiliarity"), the total number of animals killed by that individual (TotalAnimalsKilled), the percentage of Exclusion Zone reentries that was followed by a chase event (NonEntryReinforcement), and if the lion was a subadult (Subadult). Please see Appendix S4 for table with all candidate models.

Table 7. Top model explaining rate of livestock depredation by lions outside Hwange National Park, Zimbabwe, using a recurrent event survival model with a gap time framework.

Variable	Hazard ratio (HR)	95% CI of HR
RelativeRiskFamiliarity	0.961	0.939–0.983
TotalAnimalsKilled	1.150	1.044–1.267
NonEntryReinforcement	0.877	0.790–0.975
Subadult	2.002	1.443–2.777

Notes: The included variables were the proportion of an individual's home range that overlapped the Exclusion Zone (RelativeRiskFamiliarity), the total number of animals killed by that individual (TotalAnimalsKilled), the percentage of Exclusion Zone reentries that was followed by a chase event (NonEntryReinforcement), and if the lion was a subadult (Subadult). We present the hazard ratios and hazard ratio 95% confidence intervals.

suggesting that consistent exposure to stimuli is essential for an intervention to be successful (Rauer et al. 2003, VerCauteren et al. 2005). Of note is that only about 10% of known lion entries into the Exclusion Zone resulted in a chase, leaving opportunity for greater reinforcement between the undesired behavior and the negative stimulus. In our study, the positive reinforcement of a successful livestock depredation by a lion seemed to outweigh the cost of being chased, resulting in longer, multi-day chase sequences by the Guardians, evidence of habituation, and ultimately to an increased depredation propensity. The potential gains of a high-quality resource have led to increased risk tolerance in other species (Gaynor et al. 2019).

Our observations of recalcitrant individuals are in line with the idea of the problem animal, in which some animals are prone to repeated livestock depredations, while others do not engage in this behavior, or do so rarely (Stander 1990, Linnell et al. 1999). Interestingly, individuals with greater familiarity of community lands (indexed by the proportion of an individual's home range that intersected the Exclusion Zone) had a lower propensity for Exclusion Zone reentry and livestock depredation, indicating that we cannot identify potential problem animals simply based on the geography of their ranges. A possible explanation for our findings is that familiarity with a high-risk environment assisted in its safe navigation (Brown 2001). However, problem lions, once identified, became increasingly problematic, given the positive association between cumulative number of animals killed and heightened risk to next depredation. The difficulty of deterring nuisance behaviors in individuals that have a long history of positive associations with said behaviors is well established, with those individuals developing fixed nuisance behaviors (Linnell et al. 1999, Rauer et al. 2003, Beckmann et al. 2004, Mazur 2010). In our study, lions that were repeat livestock killers had killed an average of ~29 animals (max = 56), evidence of the positive feedback loop that may occur when a reward ensues from problematic behaviors. Despite the high rates of livestock killing by a few individuals, overall depredation rates outside the Park are considered intermediate compared to areas in sub-Saharan Africa with higher livestock losses (e.g., Maasailand, Kenya; Western et al. 2019).

Social context played an important role in both the short- and long-term effectiveness of aversive conditioning in this study. Subadult male lions tend to be bolder in their use of risky landscapes (Elliot et al. 2014, Loveridge et al. 2017*b*), a trend reported in other carnivore species (Bunnefeld

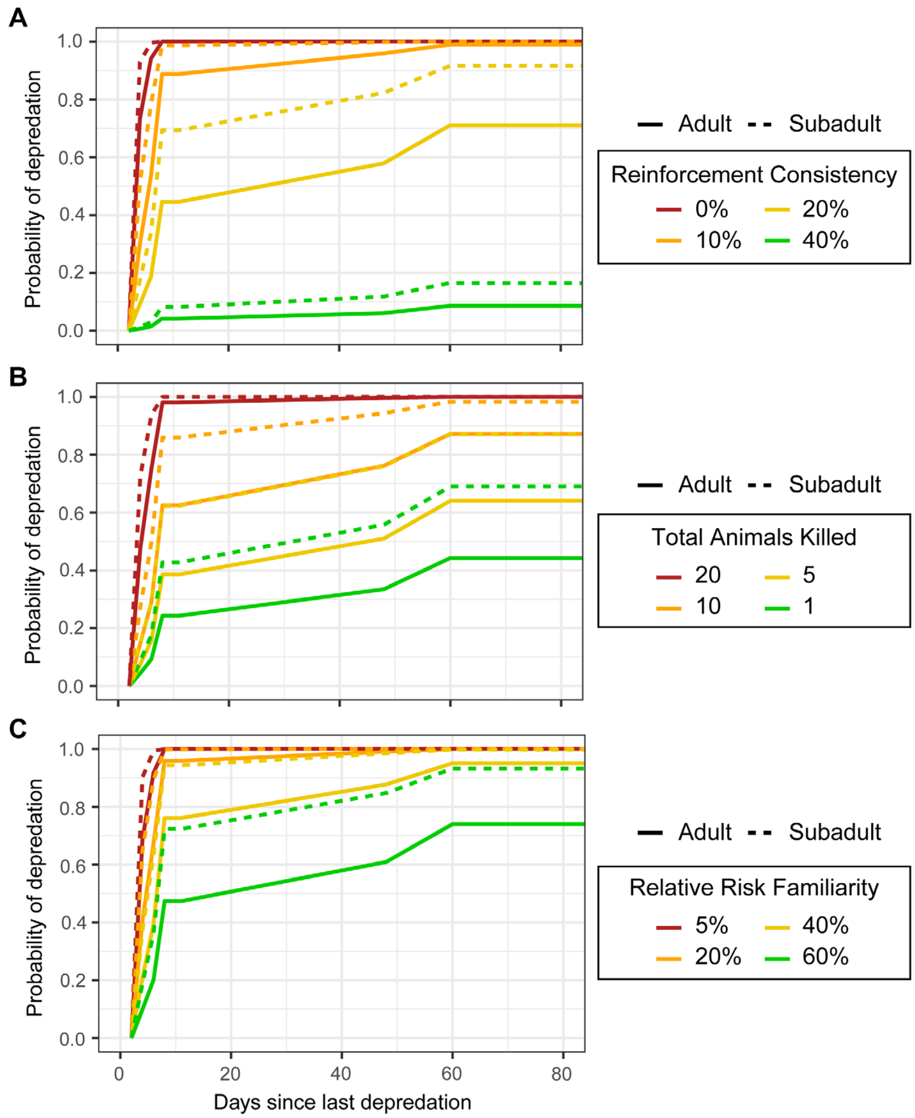

Fig. 4. Probability of livestock depredation recurrence given top multivariate survival models for lions at the periphery of Hwange National Park, Zimbabwe. Survival models used a recurrent event gap time framework. The top multivariate model incorporated (A) reinforcement consistency (the percentage of Exclusion Zone reentries followed by a chase), (B) cumulative number of animals killed by a given individual at the time of the depredation, and (C) relative risk familiarity (the proportion of an individual's home range that intersected the Exclusion Zone). For each plot, the nontarget variables were held at their mean (reinforcement consistency = 8.93%, total animals killed = 16.74, relative risk familiarity = 25.95%).

et al. 2006, Nellemann et al. 2007). In our study, subadult males were the demographic class most likely to commit depredations but also the most likely to respond favorably to aversive conditioning (as subadults were likely those in smaller prides, i.e., coalitions of 1–2 lions). The three chased individuals that failed to depredate livestock were either subadult (n = 1) or young adult (n = 2; age = 4 and 5 yr), highlighting the amenability of younger individuals to behavioral conditioning (see also Petracca 2018). Another important social driver of reentries into the Exclusion Zone and reductions in chase success was pride instability, the loss of a pride male over the previous six months (in this study area, 88% of male mortality was anthropogenic and dominated by trophy hunting; Loveridge et al. 2017*b*). Loss of a pride male is a cause of social upheaval, leading to competition among neighboring males for pride ownership (Loveridge et al. 2007), potential eviction of subadult males and females that are not yet at sexual maturity (Hanby and Bygott 1987), and, commonly, infanticide of the pride's cubs (Loveridge et al. 2007). Our results indicate that during periods of social upheaval, largely caused by the removal of pride males due to trophy hunting (Loveridge et al. 2017*b*), subordinate individuals may be increasingly displaced into community lands (where adult males are less likely to occur) and less likely to leave even when chased (mean of 88% and 56% chase success in times of pride stability and instability, respectively). In turn, this displacement of subordinate individuals into community lands likely led to the elevated livestock depredation rates observed in subadults. Given a greater propensity to become problem animals, as well as to display positive behavioral shifts following conditioning, we suggest that younger lions should be a priority for Community Guardian interventions. In general, early intervention in an animal's history of unwanted behaviors is desirable (Rauer et al. 2003), as it prevents the learning of positive associations with such behaviors.

Conclusions

Aversive conditioning programs have promise in the mitigation of human–wildlife conflict, with our results suggesting that it is intervention consistency that will have greatest impact on reducing occurrence of problematic behaviors in carnivores. In the case of the LSCGP, our findings show that even a 1% increase in pairing an unwanted behavior (in this case, a livestock depredation) with a negative stimulus (a chase) can reduce livestock depredations by 12% (95% CI 3–21%), underscoring that even small improvements in effort can have substantive impacts. In savanna ecosystems, greater effort may be required in the wet season, a period associated with less chase success in this case because (1) carnivores are more dependent on livestock in the wet season, as the hunting of wild prey is more difficult due to more dispersed water sources (Loveridge et al. 2017*a*), and (2) livestock are often herded closer to park boundaries in the wet season (Kuiper et al. 2015). Attention must also be paid to problematic behaviors occurring at night, when chase interventions are unsafe but when most livestock depredations occur (and, in our case, when nearly half of missed Exclusion Zone reentries occurred; Loveridge et al. 2017*a*). An aversive conditioning program is labor-intensive and demands long-term, consistent effort to lower risk of unwanted behaviors, much less to eliminate said behaviors. Thus, supplements and/or alternatives to aversive conditioning (e.g., livestock enclosure fortification, Kissui et al. 2019; and fence construction, Packer et al. 2013; but see also Creel et al. 2013) may be worthy of consideration from a financial and logistical standpoint to further reduce conflict between people and carnivores.

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Literature Cited

Andelt, W. F., R. L. Phillips, K. S. Gruver, and J. W. Guthrie. 1999. Coyote predation on domestic sheep deterred with electronic dog-training collar. Wildlife Society Bulletin 27:12–18.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beckmann, J. P., C. W. Lackey, and J. Berger. 2004. Evaluation of deterrent techniques and dogs to alter behavior of "nuisance" black bears. Wildlife Society Bulletin 32:1141–1146.

Blumstein, D. T. 2016. Habituation and sensitization: new thoughts about old ideas. Animal Behaviour 120:255–262.

Bongaarts, J. 2009. Human population growth and the demographic transition. Philosophical Transactions of the Royal Society B: Biological Sciences 364:2985–2990.

Brown, C. 2001. Familiarity with the test environment improves escape responses in the crimson spotted rainbowfish, *Melanotaenia duboulayi*. Animal Cognition 4:109–113.

Bunnefeld, N., J. D. C. Linnell, J. Odden, M. A. J. van Duijn, and R. Andersen. 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. Journal of Zoology 270:31–39.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Creel, S., et al. 2013. Conserving large populations of lions - the argument for fences has holes. Ecology Letters 16:1413-e3.

Davidson, Z., M. Valeix, F. Van Kesteren, A. J. Loveridge, J. E. Hunt, F. Murindagomo, and D. W. Macdonald. 2013. Seasonal diet and prey preference of the African Lion in a waterhole-driven semi-arid savanna. PLOS ONE 8:e55182.

Di Minin, E., R. Slotow, L. T. B. Hunter, F. Montesino Pouzols, T. Toivonen, P. H. Verburg, N. Leader-Williams, L. Petracca, and A. Moilanen. 2016. Global priorities for national carnivore conservation under land use change. Scientific Reports 6:23814.

Dickman, A. J., E. A. Macdonald, and D. W. Macdonald. 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 108:13937–13944.

Elliot, N. B., S. A. Cushman, A. J. Loveridge, G. Mtare, and D. W. Macdonald. 2014. Movements vary according to dispersal stage, group size, and rainfall: the case of the African lion. Ecology 95:2860–2869.

Fahlman, A., A. Loveridge, C. Wenham, C. Foggin, J. M. Arnemo, and G. Nyman. 2005. Reversible anaesthesia of free-ranging lions (Panthera leo) in Zimbabwe. Journal of the South African Veterinary Association 76:187–192.

Found, R., and C. C. St. Clair. 2018. Personality influences wildlife responses to aversive conditioning. Journal of Wildlife Management 82:747–755.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of fear: spatial patterns of risk perception and response. Trends in Ecology & Evolution 34:355–368.

Green, R. E. 2005. Farming and the fate of wild nature. Science 307:550–555.

Hanby, J. P., and J. D. Bygott. 1987. Emigration of subadult lions. Animal Behaviour 35:161–169.

Hawley, J. E., T. M. Gehring, R. N. Schultz, S. T. Rossler, and A. P. Wydeven. 2009. Assessment of Shock Collars as Nonlethal Management for Wolves in Wisconsin. Journal of Wildlife Management 73:518–525.

Hazzah, L., S. Dolrenry, L. Naughton, C. T. T. Edwards, O. Mwebi, F. Kearney, and L. Frank. 2014. Efficacy of two Lion conservation programs in Maasailand, Kenya. Conservation Biology 28:851–860.

Hebblewhite, M., et al. 2014. Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biological Conservation 178:50–64.

Kissui, B. M., C. Kiffner, H. J. König, and R. A. Montgomery. 2019. Patterns of livestock depredation and cost-effectiveness of fortified livestock enclosures in northern Tanzania. Ecology and Evolution 9:11420–11433.

Kleinbaum, D. G., and M. Klein. 2011. Survival analysis: a self-learning text. Third edition. Springer, New York, New York, USA.

Kloppers, E. L., C. C. St. Clair, and T. E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. Ecology and Society 10:31.

Kuiper, T. R., A. J. Loveridge, D. M. Parker, P. J. Johnson, J. E. Hunt, B. Stapelkamp, L. Sibanda, and D. W. Macdonald. 2015. Seasonal herding practices influence predation on domestic stock by African lions along a protected area boundary. Biological Conservation 191:546–554.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: Do "problem individuals" really exist? Wildlife Society Bulletin 27:698–705.

Löe, J., and E. Röskaft. 2004. Large carnivores and human safety: a review. Ambio 33:283–288.

Loveridge, A. J. 2015. Hwange Lion Research Project Annual Report. Hwange Lion Research Project, Dete, Zimbabwe.

Loveridge, A. J., T. R. Kuiper, R. H. Parry, L. Sibanda, J. E. Hunt, B. Stapelkamp, L. Sebele, and D. W. Macdonald. 2017*a*. Bells, bomas and beefsteak: complex patterns of human-predator conflict at the wildlife-agropastoral interface in Zimbabwe. PeerJ 5:e2898.

Loveridge, A. J., A. W. Searle, F. Murindagomo, and D. W. Macdonald. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biological Conservation 134:548–558.

Loveridge, A. J., M. Valeix, G. Chapron, Z. Davidson, G. Mtare, and D. W. Macdonald. 2016. Conservation of large predator populations: demographic and spatial responses of African lions to the intensity of trophy hunting. Biological Conservation 204:247–254.

Loveridge, A. J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz, and D. W. Macdonald. 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography 32:953–962.

Loveridge, A. J., M. Valeix, N. B. Elliot, and D. W. Macdonald. 2017*b*. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. Journal of Applied Ecology 54:815–825.

Mazur, R. L. 2010. Does aversive conditioning reduce human-black bear conflict? Journal of Wildlife Management 74:48–54.

Nellemann, C., O.-G. Støen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation 138:157–165.

Oriol-Cotterill, A., D. W. Macdonald, M. Valeix, S. Ekwanga, and L. G. Frank. 2015. Spatiotemporal patterns of lion space use in a human-dominated landscape. Animal Behaviour 101:27–39.

Osborn, F. V., and G. E. Parker. 2003. Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. Oryx 37:80-84.

Packer, C., D. Ikanda, B. Kissui, and H. Kushnir. 2005. Lion attacks on humans in Tanzania - Understanding the timing and distribution of attacks on rural communities will help to prevent them. Nature 436:927–928.

Packer, C., et al. 2013. Conserving large carnivores: dollars and fence. Ecology Letters 16:635–641.

Pavlov, I. P. 1927. Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex. Oxford University Press, London, UK.

Petracca, L. S. 2018. Spatial and behavioral ecology of large carnivores at the human-wildlife interface: Insights for species conservation within and between protected areas. Doctoral dissertation, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, USA.

Rauer, G., P. Kaczensky, and F. Knauer. 2003. Experiences with aversive conditioning of habituated brown bears in Austria and other European countries. Ursus 14:215–224.

Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago, Illinois, USA.

Schultz, R. N., K. W. Jonas, L. H. Skuldt, and A. P. Wydeven. 2005. Experimental use of dog-training shock collars to deter depredation by gray wolves. Wildlife Society Bulletin 33:142–148.

Shivik, J. A. 2006. Tools for the edge: what's new for conserving carnivores. BioScience 56:253–259.

Shivik, J. A., A. Treves, and P. Callahan. 2003. Nonlethal techniques for managing predation: primary and secondary repellents. Conservation Biology 17:1531–1537.

Stander, P. 1990. A suggested management strategy for stock-raiding lions in Namibia. South African Journal of Wildlife Research 20:37–43.

Therneau, T. 2015. A Package for Survival Analysis in S. version 2.38. https://CRAN.R-project.org/package=survival

van Eeden, L. M., M. S. Crowther, C. R. Dickman, D. W. Macdonald, W. J. Ripple, E. G. Ritchie, and T. M. Newsome. 2018*a*. Managing conflict between large carnivores and livestock. Conservation Biology 32:26–34.

van Eeden, L. M., et al. 2018*b*. Carnivore conservation needs evidence-based livestock protection. PLOS Biology 16:e2005577.

VerCauteren, K. C., J. A. Shivik, and M. J. Lavelle. 2005. Efficacy of an animal-activated frightening device on urban elk and mule deer. Wildlife Society Bulletin 33:1282–1287.

Western, G., D. W. Macdonald, A. J. Loveridge, and A. J. Dickman. 2019. Creating landscapes of coexistence: do conservation interventions promote tolerance of lions in human-dominated landscapes? Conservation and Society 17:204.

Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. Science 321:123–126.

Supporting Information

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