

CONTRIBUTED PAPER

Harassment-induced changes in lion space use as a conflict mitigation tool

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Abstract

Human-wildlife conflict represents a substantial threat to rural livelihoods and species persistence. Directed harassment (i.e., hazing) is one method for mitigating conflict, though gauging its effectiveness is often complicated by a lack of replication, controls, or effective contrasts. Herein we assessed whether African lions (*Panthera leo*) shifted their space use in response to a hazing program intended to deter lions from community lands adjacent to Hwange National Park, Zimbabwe. Using GPS-collared lions ($n = 16$) from unique prides, we investigated the degree to which individuals exhibited (a) a large-scale response by shifting their home ranges away from community lands, or (b) a fine-scale response by increasingly avoiding areas near households post-program initiation. Responses between “at-risk” (those exposed to the program; $n = 5$) and “protected” ($n = 11$) lions varied, with at-risk males shifting their home ranges to include 12.08% more national park and 9.04% less community lands post-program (median), a shift not replicated by at-risk females nor protected lions. However, the majority of at-risk lions demonstrated increased attraction to households post-program. We demonstrated that while aversive stimulus approaches may alter large-scale space use by individual lions, constraints imposed by social structure and available habitat alternatives will affect the level of effort required to achieve program success.

KEYWORDS

carnivore management, community-based management, hazing, human-carnivore conflict, human-wildlife conflict, lion, lion guardians, *Panthera leo*, resource selection, Zimbabwe

1 | INTRODUCTION

The tradeoff between reward versus risk, or food versus safety, is a primary driver of animal behavior and space use decisions (Brown, 1999; Lima & Dill, 1990). Human-dominated landscapes, such as those involving livestock

rearing, may draw carnivores into conflict with humans by tipping the apparent balance in favor of food over risk, particularly along the margins of productive habitats (Gaynor, Brown, Middleton, Power, & Brashares, 2019; Treves & Karanth, 2003). Carnivores, including top predators, are sensitive to mortality risks imposed by conspecifics,

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competing predators, and humans alike, exhibiting risk-sensitive behavior similar to their prey (Oriol-Cotterill, Valeix, Frank, Riginos, & Macdonald, 2015). Such behaviors include spatial avoidance of areas they perceive as risky or behavioral modifications when using risky areas, such as shifting to more nocturnal behavior to avoid encountering humans (Carter, Shrestha, Karki, Pradhan, & Liu, 2012; Gaynor et al., 2019; Oriol-Cotterill, Macdonald, Valeix, Ekwanga, & Frank, 2015). Seeking to capitalize on such innate responses to perceived risk, use of aversive stimulus approaches such as directed harassment (i.e., “hazing”) has become an increasingly common method for confronting human-wildlife conflict, especially for species of conservation concern, despite limited evidence of the long-term effectiveness of such interventions (Shivik, 2006). As conflict with humans remains one of the largest threats to the persistence of large carnivores (Loveridge et al., 2010; Treves & Karanth, 2003), greater effort towards improving the effectiveness of aversive stimulus approaches to conflict resolution is warranted.

Behaviorally-based interventions to reduce wildlife conflict generally aim to disrupt appetitive behaviors using fear-inducing, sometimes painful stimuli to deter animals from pursuing resources (Shivik et al., 2003). Such stimuli may be auditory (e.g., gunshots, barking dogs, cracker shells [Beckmann, Lackey, & Berger, 2004, Zarco-Gonzalez & Monroy-Vilchis, 2014]), visual (e.g., fladry, strobe lights [Musiani et al., 2003, Darrow & Shivik, 2009]), or physical (pepper spray, rubber bullets [Beckmann et al., 2004, Mazur, 2010]). Most interventions have had inconsistent effects across species and a limited duration of effectiveness (Shivik, 2006), though rigorous evaluations of such programs are lacking (van Eeden et al., 2018). Such efforts are hindered by low sample sizes, in terms of the number of offending individuals, the number of conditioning trials per individual, and number of replicates (Beckmann et al., 2004; Rauer et al., 2003; van Eeden et al., 2018). Another common limitation is an absence of robust experimental design, including the presence of controls and ability to determine treatment effects in the presence of confounding factors (Andelt et al., 1999; Hawley, Gehring, Schultz, Rossler, & Wydeven, 2009; Schultz, Jonas, Skudt, & Wydeven, 2005; van Eeden et al., 2018).

Importantly, animal responses to aversive stimuli are often mediated by environmental context, such as social structure or the availability of habitat alternatives (Gill, Norris, & Sutherland, 2001). This is especially true for territorial species, where spatial shifts are often precluded by the presence of territories already occupied by dominant individuals (Grinnell, Packer, & Pusey, 1995; Mosser & Packer, 2009). Moreover, habituation, a process leading to decreased responsiveness following repeated presentation of a stimulus (Blumstein, 2016), may result

when the stimulus is not sufficiently noxious or consistently applied to sufficient degree to deter unwanted behaviors, or because such unwanted behaviors are firmly entrenched within individuals (Mazur, 2010; Petracca et al., 2019; Shivik et al., 2003; Stander, 1990). Habituation by African lions (*Panthera leo*) to hazing was documented previously (Petracca et al., 2019), where a successful livestock kill was generally followed by repeated depredations regardless of continued hazing—the potential reward in this case apparently greatly outweighing the perceived risk associated with being chased by people. Beyond social factors, encounter rate with the conditioning stimuli, the individual animal's valuation of resources, and the animal's energy state will each affect their perception and response to risk (Brown, 1999; Gaynor et al., 2019; Laundré et al., 2010). The ability to tease apart these drivers is undermined by the small sample sizes generally involved in carnivore behavioral intervention programs (Beckmann et al., 2004; Rauer et al., 2003; van Eeden et al., 2018), a byproduct of the fact that large carnivores generally exist at low density and a relatively small number of those are actually involved in conflict. Moreover, whereas changes in movement behavior over time may be consistent with animal learning, evidence of learning is gained only by comparing animal behavior before and after exposure to the target stimulus, and preferably simultaneously in comparison to a meaningful control.

Herein, we used a pseudo-BACI (Before-After-Control-Impact) design to investigate changes in behavior by African lions following the onset of an aversive conditioning intervention in the community lands adjacent to Hwange National Park, Zimbabwe (hereafter “the park”). The Long Shields Community Guardians Program (hereafter “the program”) employed use of trained staff to chase GPS-collared lions away from community lands and back into the national park. We specifically investigated the degree to which individual lions adopted risk-sensitive behaviors following program inception, namely (a) large-scale spatial avoidance (a shift of seasonal home range to include more of the “protected” park), or (b) small-scale spatiotemporal avoidance via (a) avoiding households or (b) approaching households, but under greater vegetation cover or increasingly in nocturnal hours (i.e., behavioral modification [Frid & Dill, 2002; Gaynor et al., 2019]), with or without a large-scale shift in home range placement. This builds upon a previous work in which we investigated the degree to which individual chases reduced the propensity for problem behaviors in lions (Petracca et al., 2019), and focuses on a “before” versus “after” program initiation framework rather than only on the time period in which the hazing program was active. While we anticipated responses to vary by individual (Petracca et al., 2019; Sih, 2013; Sih, Bell, &

Johnson, 2004), we expected younger animals to exhibit greater behavioral plasticity given their lack of established territories (Schaller, 1972) and thus to be more responsive than older animals to aversive conditioning. Although we focused on African lions, our findings help elucidate general mechanisms underpinning animal responses to fear-inducing stimuli, and our analytical framework is readily adaptable to other species where evaluation of intervention-specific changes in animal behavior is of interest.

2 | METHODS

2.1 | Study area

The study area (15,900 km²) spans Hwange National Park (19°0'S 27°3'E) and surrounding protected areas

and community lands (Figure 1). The park covers 14,600 km² of semi-arid savanna in northwestern Zimbabwe, with altitude varying from 800 to 1,100 m (Loveridge et al., 2009). Mean annual rainfall was 600 mm and highly variable (inter-annual CV of 25%), with water artificially supplied at water points in the dry season (Loveridge, Valeix, Elliot, & Macdonald, 2017) (Figure 1). There are presently two community areas bordering the national park that partially overlapped our study area: Tsholotsho and Mabale Communal Lands, with 4,066 households (3.82 households/km² within communal lands) included in our study area. Residents are mainly subsistence agropastoral farmers, focusing on livestock husbandry (predominantly cattle *Bos indicus*, donkeys *Equus asinus*, goats *Capra hircus* and sheep *Ovis aries*) and the growing of maize, sorghum, millet and legumes (Kuiper et al., 2015; Loveridge et al., 2017).

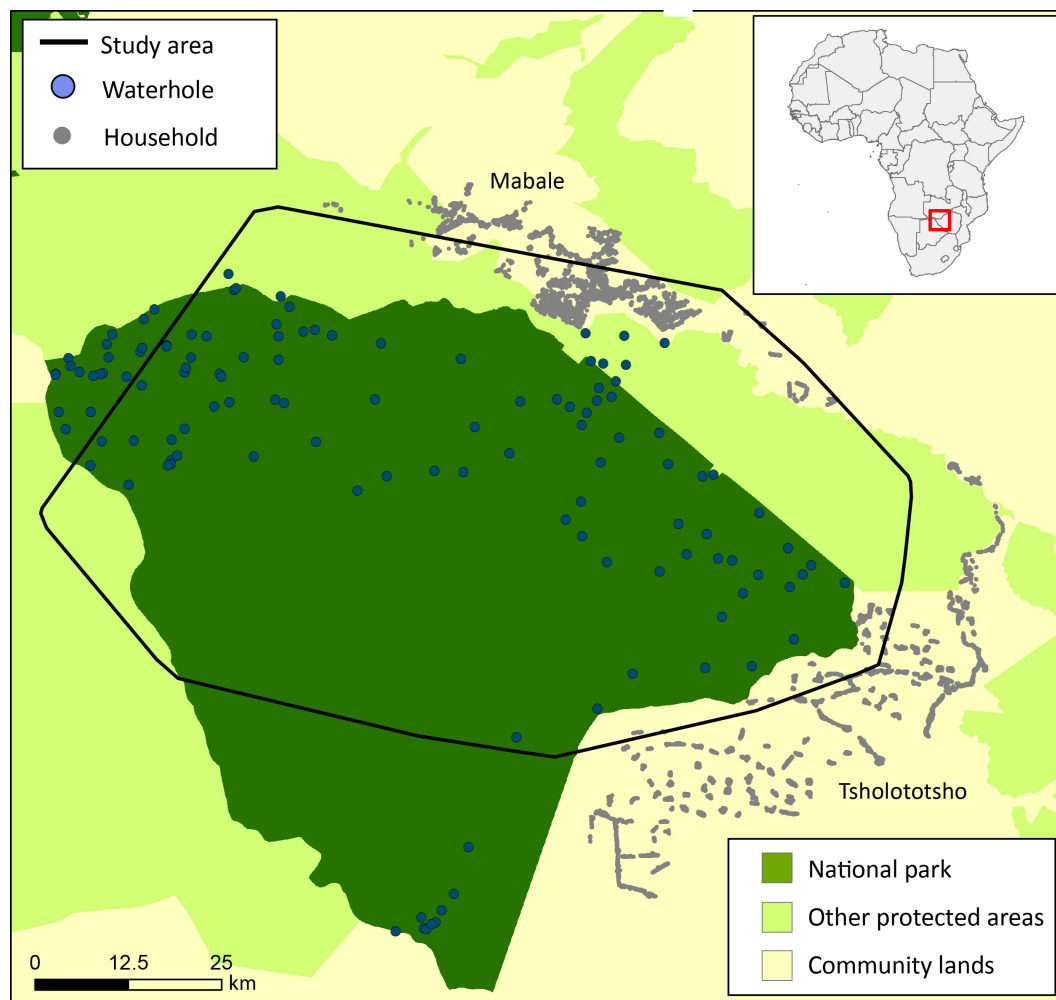


FIGURE 1 Study area (15,500 km²; solid outline) of Hwange National Park, surrounding protected areas (forest lands, conservancy ranches, and safari areas), and community lands (Mabale and Tsholotsho) in western Zimbabwe, comprising the seasonal home ranges ($n = 135$) from 2005 to 2016 of all 16 lions (10 M, 6 F) in the study. Map created in ArcMap v.10.7.1 (ESRI 2020; <https://desktop.arcgis.com/en/>)

The wet (November–April) and dry (May–October) seasons are particularly pronounced in this system and dictate landscape-level water and prey availability (Davidson et al., 2013; Valeix, Loveridge, & Macdonald, 2012). During the wet season, surface water is present throughout most of the park, leading to more widely dispersed wild prey than during the dry season, when prey typically congregate at artificially-supplied waterholes (Davidson et al., 2013). Seasonality also has implications for cattle rearing, as during the wet season (also the crop growing season) cattle are herded closer to the park boundary in order to provide fresh forage and keep them away from the agricultural fields (Kuiper et al., 2015); this presence of cattle near the park boundary has led to heightened depredations by lions during the wet season (Kuiper et al., 2015, Loveridge, Kuiper, et al., 2017). In the dry season, cattle are left to graze in fallow fields closer to households (Kuiper et al., 2015). In both seasons, cattle are generally not supervised or guarded during the day and are brought back to the villages by nightfall (Kuiper et al., 2015). While households generally have a protective livestock enclosure (boma) where livestock are kept at night, the level of fortification varies by household (Loveridge, Kuiper, et al., 2017).

2.2 | Lion monitoring

Lions were immobilized for handling by qualified field staff using standard protocols for the species (Fahlman et al., 2005) (see Appendix S1) and fitted with GPS collars equipped with either UHF or satellite remote downloads (Televilt Positioning, Lindesberg, Sweden; Sirtrack, Hawkes Bay, New Zealand; Africa Wildlife Tracking, Pretoria, South Africa).

From a total of 109 lions collared within the greater study area from 2002 to 2016, criteria for inclusion in this study required collar data for >1 year both before and after the program was initiated in June 2012. As a result, 16 study animals were retained for inclusion in this study—5 adult females, 1 subadult female, 4 adult males, and 6 subadult males at study onset (adult defined as ≥ 4 years of age) (Appendix S2). Importantly, each animal represented a unique pride or coalition. Given exploratory movements out of the study area by one lion (M3) before reaching adulthood, data from this animal were restricted to adult age. Positional data were collected on these animals between 2005 and 2016, yielding a mean of $1,167 \pm 700$ SD collar-days per individual, based on one or more fix schedules: (a) hourly at night (18:00–7:00) with 2–4 additional fixes in day hours ($n = 11$, 50.24% of data) or no day fixes ($n = 4$, 14.30% of data); (b) bi-hourly ($n = 14$, 32.98% of data) or hourly

($n = 1$, 0.24% of data); or (c) every 4 hr ($n = 2$, 2.25% of data). Data from 2005–2011 were largely category 1, while data from 2012 to 2016 were largely category 2; these fix schedules were present in similar proportions in both at-risk and protected lions. When necessary we resampled these data to a common monitoring interval as described later. Following Prokopenko, Boyce, and Avgar (2017), we required ≥ 200 locations/individual/season to be included in our models.

We considered “at-risk” animals ($n = 5$) to be those lions potentially exposed to hazing by (a) coming within 846 m (the average two-hour step length for lions in this study) of a household at least once prior to onset of the intervention program, and (b) having at least two independent incursions into community lands prior to program onset, rather than animals specifically receiving hazing treatments. This definition allowed for potential social transmission of knowledge among lions regarding elevated levels of risk in community lands (Thornton & Clutton-Brock, 2011; van de Waal, Borgeaud, & Whiten, 2013; Whiten, 2005). Likewise, “protected” animals ($n = 11$) were unlikely to have been exposed to hazing, and included collared lions residing largely within the park or adjacent protected areas (rather than community lands). Importantly, these animals were not randomly assigned to treatment versus control categories, with “at-risk” lions considered to already be prone to human-carnivore conflict within community lands while “protected” lions were considered low-risk individuals. Nevertheless, having “protected” lions as a benchmark for comparison is useful for elucidating inherent behavioral flexibility among demographic groups, seasonal variation in lion movements, and direct responses to the hazing program by controlling for resource variation over time.

At program initiation, there were 10 Community Guardians operating in Tsholotsho and Mabale Communal Lands, monitoring GPS-collared lions in real-time via laptop or smartphone each day from sunrise (6:00 hr) to sunset (18:00 hr). Guardians were alerted via text message when a collared lion occurred in close proximity (~ 2 km) to households, and were tasked with pushing the lion(s) into the park by pursuing them on foot, creating a disturbance by making noise and using horns (vuvuzelas). Chases continued during daylight hours and, for safety reasons, were abandoned at sunset.

2.3 | Modeling resource selection

We explored two overarching hypotheses with respect to the potential behavioral responses of lions to initiation of the program:

1. *Leave and take refuge in safer spaces:* The management goal was for lions that make use of community lands to shift their space use into the park. This outcome would yield the greatest reduction in potential lion-human conflict in the region, and would be apparent given an increase in the proportion of seasonal home range area overlapping the park after program initiation.
2. *Stay and reduce risk in place:* Lions might be constrained from moving into the park, where dominant lions already hold territories. As a result, without a shift in home range placement, other means of risk avoidance include (1) lions increasingly avoiding areas close to households after the onset of hazing, or (2) lions continuing to approach households after hazing onset but (a) under denser vegetation cover or (b) increasingly under the cover of darkness.

Home ranges were defined separately by lion and season (e.g., “F1-wet,” “M2-dry,” hereafter known as lion-seasons), with the wet season defined as 1 Nov–30 Apr and the dry season as 1 May–31 Oct (Kuiper et al., 2015). Seasonal data were pooled across years, with a random intercept defined by year.

An at-risk lion entered our analysis with its first GPS location occurring within 846 m (an average lion's two-hour step length) of a household before program initiation (June 2012), with the assumption that the lion was not familiar with community lands (and therefore not “at-risk”) before that point. For both groups, the “before” period spanned November 2005 to May 2012 and the “after” period spanned June 2012–May 2016, though specific entry and exit times varied by individual (Appendix S2). Exit times represented collar failure, animal death, or end of study.

2.4 | Evaluation of large-scale response: home range shift

We were interested in whether “at-risk” lions shifted their range into the park from pre- to post-program periods while controlling for range shifts in comparison to “protected” lions. We hypothesized that, in general, male lions would exhibit greater inter-season movements than females, and that at-risk individuals ($n = 5$ lions, 3 M, 2 F) would show greater differences in home range placement following program initiation compared to protected lions ($n = 11$ lions, 7 M, 4 F).

A kernel density home range was fit to each lion by season (wet and dry), year, and period (before and after program initiation) using R package *adehabitatHR* (Calenge, 2006). To better understand the magnitude of

inter-season movements, core seasonal ranges were delineated using a 50% contour (Laver & Kelly, 2008) and distances between core range centroids (e.g., wet season 2011 to dry season 2011 to wet season 2012) were calculated in R package *sp* (Bivand et al., 2013). Sex-based differences in inter-season movements were analyzed via an unpaired two-samples Wilcoxon rank-sum test using R package *coin* (Hothorn, Hornik, van de Wiel, & Zeileis, 2006).

Seasonal range extents were calculated using a 95% contour (Laver & Kelly, 2008), with the proportion of each seasonal range overlapping (a) the park, (b) “other” protected areas (e.g., forestry lands, safari areas), and (c) community lands calculated in R package *raster* (Hijmans, 2020). Range overlap with the park and community lands were analyzed separately using a one-way repeated-measures ANOVA with main effect of period (before and after) in R package *nlme* (Pinheiro et al., 2018). All ANOVAs were run upon confirming normality and homogeneity of variance of residuals. Lions were analyzed separately by sex and group (at-risk/protected), and lion ID was used as a random effect.

2.5 | Evaluation of small-scale response: resource selection and activity patterns

Given that lions were chased during the daytime only, it is plausible that lions shifted their activity windows to become more nocturnal following the onset of the hazing program. To visualize this potential, we first subset all used lion locations to those separated by exactly 2 hr to avoid possible confounding due to differing time between locations. However, given that data in the “before” period were more biased to locations that occurred at night (18:00–6:00 hr) (88.0% of data, compared to 72.6% for the “after” period; the overall nocturnal bias exists because lions are most active at night [Schaller, 1972] and project leads were most interested in movements during this period), we had to control for this difference in any analysis of nocturnal shift. Thus, we plotted the hour of GPS points by period (before/after) using data (a) at all distances from household, and (b) within 2 km from households (the distance within which lions would be chased by the Guardians) using a kernel density smoother in R package *ggplot2* (Wickham, 2016).

Next, for all lions, we sought to evaluate changes in habitat selection with respect to proximity of households after program initiation. In order to observe changes in selection we held areas available to all lions constant over time, bounded by a minimum convex polygon (MCP) enclosing the GPS locations pooled across all lions and years. This 15,910 km² available area comprised 8%

community lands, 71% park lands, and 21% other protected lands. We drew a sample of available locations at a ratio of 1 used: 1 available point using R package *spdep* (Bivand et al., 2013), which yielded sample sizes sufficient for parameter convergence (Northrup, Hooten, Anderson Jr, & Wittemyer, 2013). Given high variability among individual responses, we fit resource selection functions by lion-season rather than a population-averaged response (Muff et al., 2018).

After controlling for the effects of distance to waterhole and landscape productivity, our models investigated the degree to which lions (a) decreased their use of areas near households or (b) increased use of vegetation cover when near households after program initiation. We investigated the former via selection coefficients for “distance to household” in the before and after periods, and the latter by observing how selection for distance to household changed under scenarios of high and low vegetation cover (a three-way interaction between distance to household, percent tree cover, and period). For each lion-season, we fit a global logistic regression model (use = 1, available = 0) as:

$$w(x) = \exp(\ln(\text{DistWat}) + \text{NDVI} + \text{NDVI}^2 + (\ln(\text{DistHouse}) \times \text{Period}) + \text{PercTree} + (\ln(\text{DistHouse}) \times \text{PercTree} \times \text{Period}) + \gamma_{0y}) \quad (1)$$

where *DistWat* represented distance to waterhole (m), *NDVI* represented daily normalized difference vegetation index (a measure of vegetation greenness), *DistHouse* represented distance to household (m), *PercTree* represented percent tree cover (updated annually), *Period* was a binary covariate representing before ($x = 0$ before June 2012) and after ($x = 1$) initiation of the hazing program, and γ_{0y} was a random intercept of year. Models were fit to each lion and season using package *lme4* in R (Bates et al., 2015).

Households were mapped using high-resolution imagery in GoogleEarth (Loveridge, Valeix, et al., 2017), with proximity to nearest household (*DistHouse*) quantified for each location using R package *raster* (Hijmans, 2020). As water access was likely to influence local prey availability for lions (Davidson et al., 2012, 2013; Valeix et al., 2009), and thereby lion space use and resource selection patterns, we controlled for this factor by quantifying proximity to nearest waterhole (*DistWat*), again in R package *raster* (Hijmans, 2020). Both distance covariates (*DistHouse*, *DistWat*) were natural log-transformed prior to model fitting because we assumed a rapid rather than linear form of distance decay in their influence on lion behavior. To control for site productivity, we sourced *NDVI* data (Vegetation Indices 16-Day L3

Global, 250-m; MOD13Q1 data product, EROS data center), and corrected 16-day values of *NDVI* using the iterative Interpolation for Data Reconstruction method (Julien & Sobrino, 2010)—fitting a smoothing spline and then extracting daily values. To ascribe daily *NDVI* values at available points, we randomly assigned a date from the distribution of used locations for a given lion (Bastille-Rousseau et al., 2015). *NDVI* was normalized to values between 0 and 1 ($[\text{NDVI} - \text{NDVI}_{\min}]/\text{NDVI}_{\text{range}}$) (Prokopenko et al., 2017). We expected lions to select for open savannahs (intermediate *NDVI*) rather than deciduous teak forest (high values) or bare ground (low values), and so fit this variable using a second order polynomial. Lastly, percent tree cover (*PercTree*), a measure of security cover for lions, was sourced annually from the MODIS 44B data product (Vegetation Continuous Fields Yearly L3 Global 250 m) retrieved from the online Data Pool (NASA Land Processes Distributed Active Archive Center, USGS/Earth Resources Observation and Science Center, Sioux Falls, South Dakota).

To visualize changes in selection for areas near households, for a given lion and season we estimated the difference in selection coefficient between the “after” and “before” periods using “after” as a binary variable in Equation (1), rather than as a two-level categorical variable.

We visualized the effect of the three-way interaction used to investigate potentially furtive behavior (i.e., increasingly using cover near households) by (a) setting distance to waterhole and *NDVI* to their means across all lions in each season, (b) varying distance to household from the minimum distance in that season to a maximum of 2 km (the distance from households within which lions would be chased), and (c) plotting the response when percent tree cover was at its 5% and 95% quantiles. The 5% quantiles were 1% and 0% tree cover in the wet and dry seasons, respectively, while the 95% quantile was 19% tree cover in both seasons.

3 | RESULTS

Of the five at-risk lions included in this study, three (F1, F2, M2) were chased a total of 11, 17, and 3 times from January 2013 through March 2016, killing a total of 31, 28, and 5 livestock animals during that period, respectively (see Petracca et al., 2019 for how livestock kills were attributed to individuals). The other two at-risk lions (M1, M3) were very likely chased before the chase database was started (in January 2013, 6 months after program onset) given both lions' presence within community lands in late 2012 (A. Loveridge, pers. comm.).

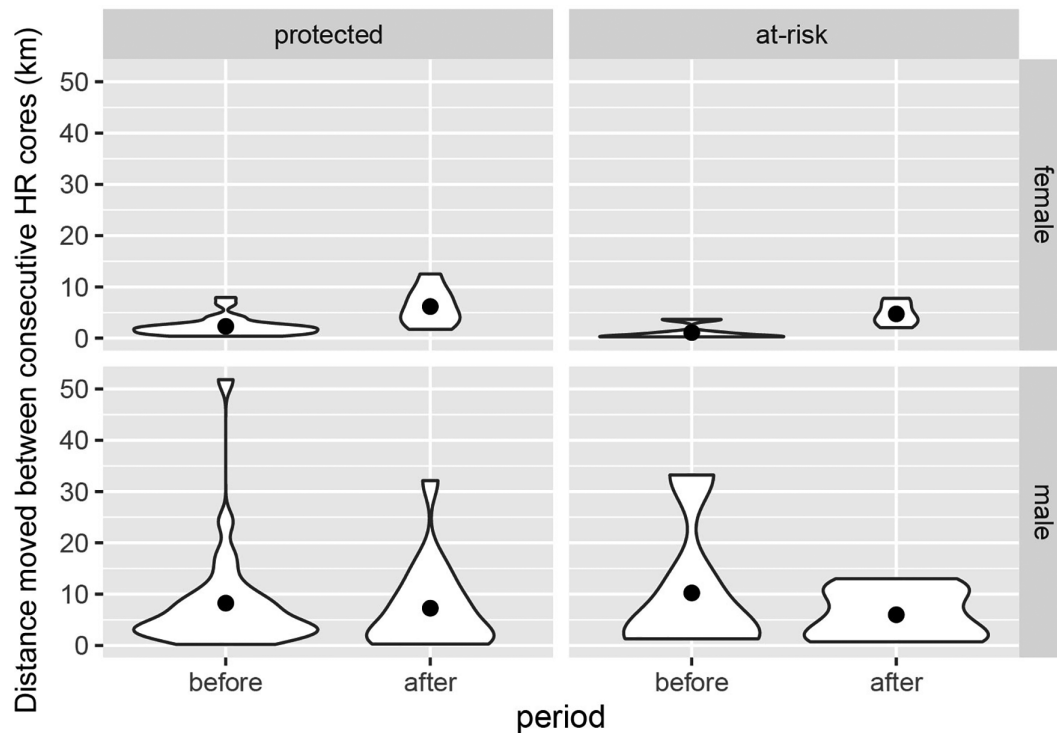


FIGURE 2 Violin plot of distance between consecutive seasonal HR centers (black point represents median) for 16 lions, at-risk ($n = 5$; 3 M, 2 F) and protected ($n = 11$; 7 M, 4 F), before and after initiation of the Long Shields Community Guardians Program around Hwange National Park, Zimbabwe. Plot created in package ggplot2 (Wickham, 2016) in Program R v.3.6.2 (R Core Team 2019)

3.1 | Home range shift

In general, male lions exhibited greater inter-season movements than females, as evidenced by larger mean differences between seasonal home range cores (males: 5.47 km median distance, interquartile range (IQR) [2.24–11.16], $n = 50$ lion-seasons; females: 2.08 km median distance, IQR [1.05–3.96], $n = 41$ lion-seasons; $Z = -3.54$, $p < .001$), with no discernible differences observed pre- versus post-initiation of the program (Figure 2).

The proportion of seasonal home ranges overlapping the park and community lands varied by sex, group, and period (Figure 3; Appendix S4). Importantly, there was a significant main effect of period (before/after) for at-risk males with respect to overlap with the park ($F[1,11] = 14.77$, $p = .0027$), with a near-significant effect for overlap with community lands ($F[1,11] = 4.15$, $p = .07$); main effects of period for the other classes did not approach significance (Appendix S4). More specifically, at-risk males increased the proportion of their home range within the park by 12.08% (median), a result that was $\sim 3\times$ that of the other groups (3.86% for female at-risk, 3.12% for female protected, and a decrease of 1.39% for protected males) (Appendix S4). Increases in the proportion of at-risk male home ranges covered by

the national park appeared to represent a concomitant decrease in use of community lands, given that the increase in home range overlap with the national park (median of 12.08%) was mirrored by a similar decrease in overlap with community lands (median of 9.04%). An opposite response was seen in at-risk females, with home range overlap with community lands increasing by 4.32% (median) (Appendix S4).

3.2 | Activity pattern and resource selection

There was no shift to more nocturnal behavior noted in study lions when <2 km from households (Figure 4). Counter to expectation, there was an increase in use of proximity to households (<2 km) in the day hours (06:00–18:00 hours) in the “after” period (a 33.5% increase in proportion of day points <2 km from households), a finding that was $\sim 2\times$ the baseline increase in proportion of day points across data at all distances from households (15.1%). Of 1,382 total points within 2 km of households, 1,139 (82.4%) were in the wet season.

Resource selection functions could not be fit to two of our protected lions (M6 and M10) due to a distribution of used points that was extreme in its avoidance of

households both “before” and “after” and prevented model convergence. This resulted in a total of 14 lions (5 at-risk [2 F, 3 M], 9 protected [4 F, 5 M]) in our

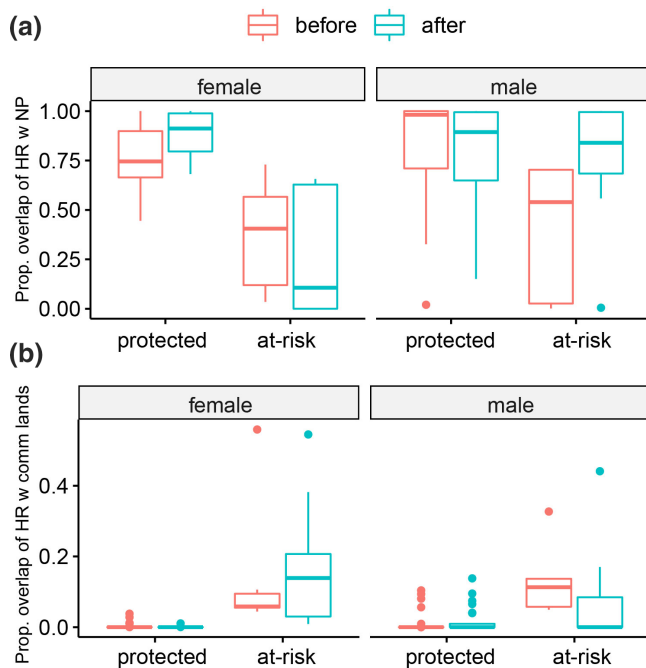


FIGURE 3 Boxplot of proportion of lion seasonal ranges that overlapped (a) Hwange National Park and (b) community lands, before and after initiation of the Long Shields Community Guardians Program in June 2012

analysis of resource selection. Fix rate did not affect the direction or magnitude of our selection coefficients (Appendix S5). When examining outputs from lion-seasons independently (i.e., not taking the difference of “after–before”), the strongest magnitude of selection for proximity to households was shown by four of five at-risk lions (F1, F2, M1, M2; Appendix S6). The notable exception was M3, an at-risk male who exhibited overall household avoidance in both seasons (Appendix S6). When evaluating differences in selection for proximity to households before vs. after, three at-risk lions (F1, F2, M1) showed increased attraction for households in the “after” period (from a 6.19 to 18.58% increase in selection in both seasons), an increase that generally exceeded the random changes in selection observed by protected animals (Figure 5). The remaining at-risk individuals (M2, M3) showed an increase in avoidance of community lands (2.86–11.55%), but the magnitude of change fell within the range exhibited by protected individuals (1.73–39.56%; Figure 5). Of note, however, is that these two at-risk lions displayed this avoidance of community lands while also increasing their seasonal home range overlap with the national park (increases of 12% and 30% for M2 and M3, respectively), a pairing that was not seen in any protected individuals.

There was no demonstrable trend in use of vegetation cover within 2 km of households before vs. after initiation of program in at-risk or protected lions (Appendix S7). After program initiation, we observed a greater overall

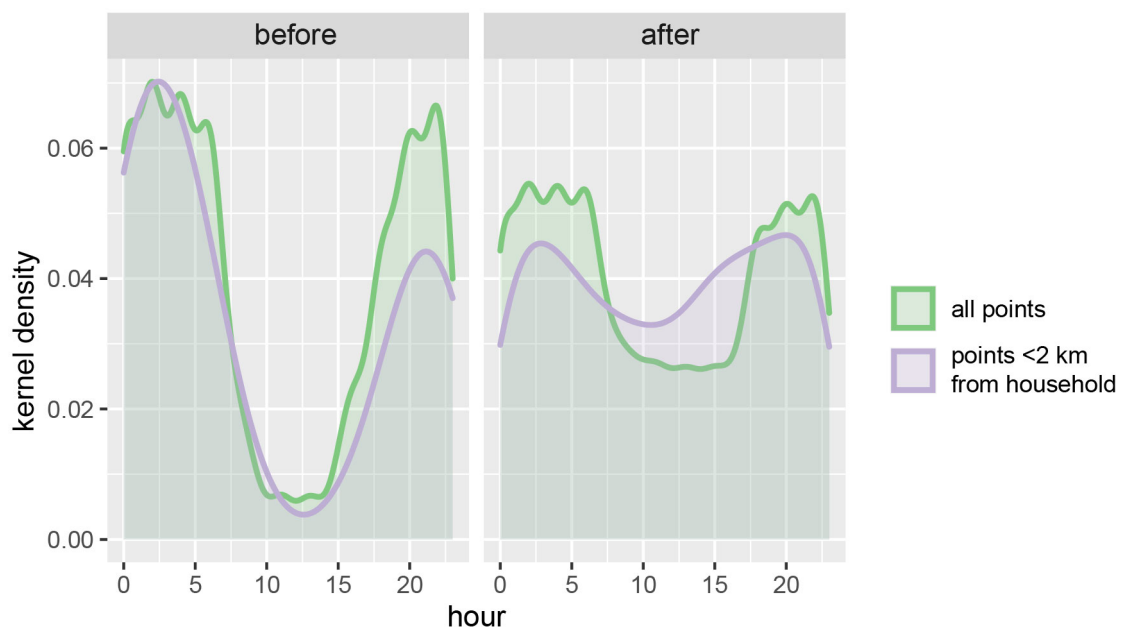


FIGURE 4 Kernel density of used GPS locations (subset to be exactly 2 hr apart) for study lions at (1) all distances and (2) <2 km from households by hour and before/after initiation of the Long Shields Community Guardians Program in June 2012. Data in the “before” period were more biased to locations that occurred at night (18:00–6:00 hr) (88.0% of data, compared to 72.6% for the “after” period), and thus we had to control for this difference

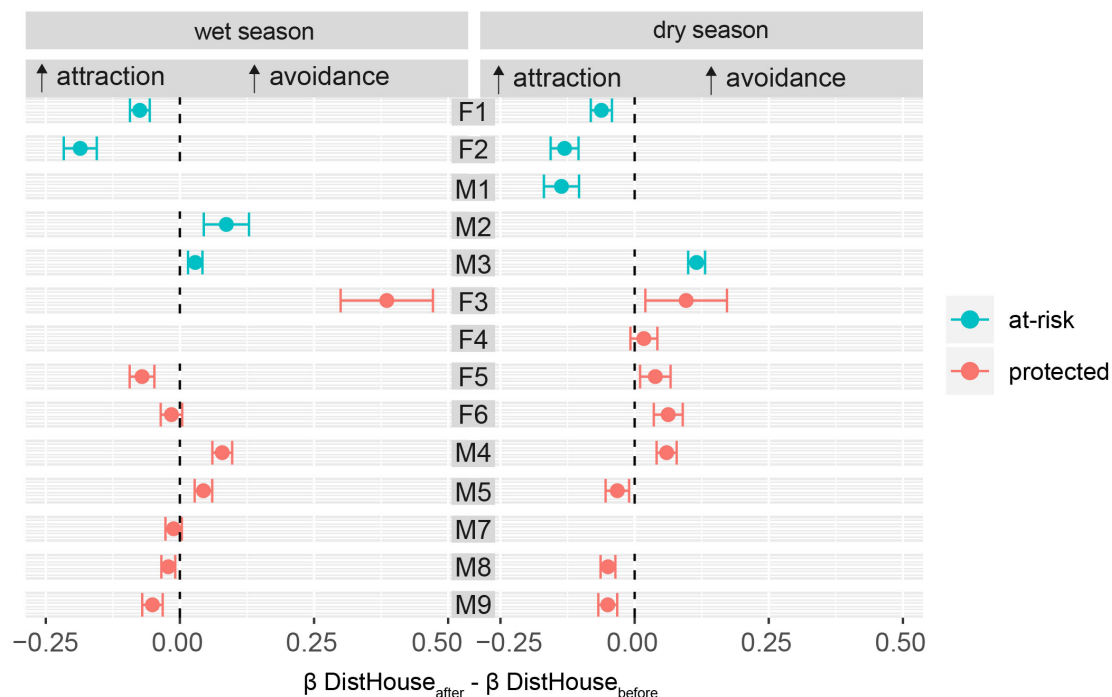


FIGURE 5 Changes in coefficient magnitude for DistHouse (distance to household) by lions within their seasonal ranges post-program initiation. The vertical dashed line at $x = 0$ indicates no difference in selection before versus after program initiation. A positive difference in selection means greater household attraction post-program initiation, while a negative difference in selection means greater household avoidance post-program initiation

difference in selection for denser versus more open cover when in closer proximity to households, particularly in the wet season (a range of change from $\pm 50\%$ in the wet season versus $\pm 25\%$ in the dry season under dense cover), but this difference was observed in protected and at-risk lions.

4 | DISCUSSION

The Hwange lion study is one of the largest and longest-running studies of lion ecology (109 collared lions monitored from 2002 to 2016)—providing the richest available data source for evaluating the effectiveness of hazing as a lion-human conflict mitigation paradigm (Petracca et al., 2019). Even so, efforts to have individuals monitored before and after program onset greatly restricted sample sizes and led to a focus on individual animal differences rather than population-level trends. Although our approach provided a formal and comprehensive framework for assessing the impacts of a wildlife-conflict mitigation effort, we recognize that larger sample sizes will be necessary to fully evaluate the long-term implications of hazing programs for lions and other large carnivores.

The main management implication from our study is that desirable, large-scale shifts in lion space use away

from community lands can be achieved via implementation of hazing, but likely not for all animals involved in conflict. Social context is the likely mediator of why a space use shift was observed in only some individuals, with at-risk male lions more likely than at-risk females and protected lions of both sexes to shift seasonal home ranges into the national park. First, the natural history of female lions differs from that of males, with female lions tending to remain in their natal prides while male lions leave natal prides typically by age four, remaining solo or joining coalitions with other males (Pusey & Packer, 1987; Schaller, 1972). Thus, males, specifically younger, non-pride males, were both expected and observed to have the greatest flexibility to respond to increases in local risk via a large-scale shift in space use. Second, there is a high level of anthropogenic mortality in this system, with 88% of male mortality being anthropogenic and dominated by trophy hunting (Loveridge, Valeix, et al., 2017). The loss of a pride male causes a cascade of effects, including competition among neighboring males for pride ownership (Loveridge, Searle, Murindagomo, & Macdonald, 2007), the eviction of sub-adult males and females (Hanby & Bygott, 1987) and infanticide of the pride's cubs (Loveridge et al., 2007), causing certain individuals to become entrenched in community lands (Petracca et al., 2019). Thus, there are

lions that are likely getting pushed into at-risk areas, with little alternatives to shifting space use.

Given the desire for pride territory among young male lions, it could be that territory acquisition (rather than the hazing program) was the driver behind the observed shift in male home range into the park. However, our contrast groups were similar in age (means of 3.83 years for at-risk, 3.79 for protected) at study onset. In addition, a shift into the park was not necessary for pride acquisition, as two of the three at-risk males that became pride males over the course of the study (M2 and M3 became lone pride males, and M1 was paired with another pride male in a coalition) established pride ranges that overlapped non-park protected areas and community lands. Thus, we did not expect the drive for territory to be a major confounding factor in the home range shifts observed by male lions in response to the onset of hazing.

Young male lions (those <4 years) are the demographic class associated with the highest rate of livestock depredation (Petracca et al., 2019), suggesting that the effectiveness of hazing programs will likely be improved by positively changing the space use and behavioral patterns of young males over other demographic classes. In this regard, the results from the Hwange hazing program, although modest, were promising. Of note is that the program has reduced the number of livestock killed and number of lions killed in retaliation since program inception (Loveridge, 2015)—thus, it is plausible that the hazing of the at-risk males kept them alive long enough to establish a home range and become less conflict-prone pride males. In addition, the presence of an established conflict mitigation program likely dissuades livestock owners from seeking retaliatory kills, a practice that was more frequent before program initiation (Loveridge, 2015). Livestock owners would be particularly reluctant to kill lions that are being monitored, as it is illegal to kill lions without a permit and people are prosecuted for doing so.

Even with these modest successes, the majority of lions (3/5 at-risk, 6/11 protected) displayed greater selection for areas near households after initiation of the hazing program, and the magnitude of change in attraction to areas near households was greater among at-risk lions. In addition, lions did not seem to shift to more nocturnal behaviors after hazing began, but rather came within 2 km of households more frequently during daytime hours (and during the wet season in general, a period associated with greater conflict due to more dispersed and harder to hunt wild prey [Loveridge, Kuiper, et al., 2017; Petracca et al., 2019]). These findings underscore the difficulty of applying hazing techniques to achieve consistent results among highly individualistic animals, and that management of lions entrenched

within communal lands may prove particularly challenging. Importantly, social-spatial context further constrains available lion responses to hazing (Gill et al., 2001), with two “at-risk” lions in this study (M1, F1) maintaining pre- and post-hazing home ranges almost exclusively (>90% of seasonal home range area) outside of the national park. Even so, the successes we observed in establishing household avoidance were among less experienced, younger individuals (M2 and M3; 4 years old at study onset), potentially underscoring the value of early, consistent intervention in the development of potentially problematic behaviors (Rauer et al., 2003). A previous study from this system predicted that even a 1% increase in pairing an unwanted behavior (in this case, a livestock depredation) with a negative stimulus (a chase) may reduce livestock depredations by 12% (95% CI 3–21%) (Petracca et al., 2019)—indicating considerable room for increasing the effectiveness of hazing programs. We hypothesize that hazing interventions might be improved by fine-tuning efforts based on lion sex/age class or spatial context, and encourage adoption of an adaptive management framework to efficiently and reliably gain insights into the drivers of program success.

Ultimately, the potential fitness benefit of depredating livestock may far outweigh the realized cost of being chased via the Community Guardians, especially given that the latter occurs somewhat intermittently and may not be of serious enough intensity to impose a substantial fitness cost (Petracca et al., 2019); as an example, habituation to repeated chasing by people has been a long-standing management issue for elk within Banff National Park (Found, Kloppers, Hurd, & St. Clair, 2018). While lethal removal of problem animals is likely to remain an important part of lion-human conflict mitigation (van Eeden et al., 2018), our study shows that hazing programs might provide another useful tool for managers. Petracca et al. (2019) showed potential for habituation of lions to hazing as currently conducted in this system, but also the potential for meaningful gains in hazing effectiveness given improvements in the onset and consistency with which interventions are delivered. Even so, three of the lions in this study, those that showed attraction to households before and after initiation of the hazing program, were known livestock killers that exhibited chronic “problem” behaviors (Linnell et al., 1999). That females with cubs were among those problem lions is concerning, as social transmission of problematic behaviors from adults to dependent juveniles (Stander, 1990) could perpetuate a cycle of conflict. As a result, strategic removal of recalcitrant individuals, those that do not respond favorably to hazing, will likely remain an important tool for managing human-lion conflict in the region (Linnell et al., 1999; Stander, 1990).

Broadly, our results indicate that hazing can induce large-scale behavioral avoidance of community lands in lions. Although the specific drivers of successful intervention will require study of additional animals to provide greater certainty, our results indicate hazing may be most successful with males, and possibly younger males. In applying lion hazing elsewhere, it is important to consider the accessibility of potential “refuge” habitat (here, the national park) for individual lions to move into but also to recognize that moving may not be an alternative for all problem animals depending upon their social context (Gill et al., 2001). Therefore, hazing should be considered one tool within an integrated effort of approaches (e.g., boma fortification [Kissui, Kiffner, König, & Montgomery, 2019]) to resolve conflict with lions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Lisanne S. Petracca, Jacqueline L. Frair, David W. Macdonald, and Andrew J. Loveridge developed the research question. Guillaume Bastille-Rousseau assisted with model development. Lisanne S. Petracca analyzed the data. David W. Macdonald and Andrew J. Loveridge coordinated the project and secured funding for its execution. Lisanne S. Petracca led manuscript writing with input from Jacqueline L. Frair, Guillaume Bastille-Rousseau, David W. Macdonald, and Andrew J. Loveridge.

DATA AVAILABILITY STATEMENT

R code associated with this paper can be found at https://github.com/lisannepetracca/Petracca_et_al_2021_ConSciandPractice.


ETHICS STATEMENT

Animal handling and care protocols were consistent with guidelines provided in the *Code of Practice for Biologists using Animals*, Department of Zoology, University of Oxford and approved by University of Oxford, Biomedical

Sciences, Animal Welfare and Ethical Review Body (AWERB). Animal handling procedures were carried out by project staff trained and certified by the Zimbabwe Veterinary Association, Wildlife Group in accordance with Statutory Instrument 409 of 1999 (Clause 21A to 21J) amending the Regulations of 1975 to the Dangerous Drugs Act, Zimbabwe (see Appendix S1 for certificate numbers). All procedures were undertaken with the permission of the Zimbabwe Parks and Wildlife Management Authority (see Appendix S1 for permit numbers) and under license from the Zimbabwe Veterinary Association, Wildlife Group (Veterinary Committee) and Medicines Control Authority, Zimbabwe (see Appendix S1 for license numbers).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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