



RESEARCH ARTICLE

Quantifying the relationship between prey density, livestock and illegal killing of leopards

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Feodor Lynen Fellowship of the Alexander von Humboldt Foundation, Grant/Award Number: DEU 1220304 FLP-P and 2021-2023; PRIME programme of the German Academic Exchange Service (DAAD) from the German Federal Ministry of Education and Research (BMBF), Grant/Award Number: 57436650

Handling Editor: Matt W. Hayward**Abstract**

1. Many large mammalian carnivores are facing population declines due to illegal killing (e.g. shooting) and habitat modification (e.g. livestock farming). Illegal killing occurs cryptically and hence is difficult to detect. However, reducing illegal killing requires a solid understanding of its magnitude and underlying drivers, while accounting for the imperfect detection of illegal killing events. Despite the importance of illegal killing of large carnivores in comparison with other causes of mortality, its relationship with potential drivers such as livestock density and wild prey abundance is rarely described.
2. Using ranger-collected data (2007–2019) of leopard killing events and data on covariates (livestock density, wild prey abundance, road length, protected area size, elevation) across Iran, we applied a single-visit N-mixture model to jointly model variation in detection probability and expected annualized number of leopard killing events.
3. Over the study period, we estimated 428 leopard mortalities (95% CI 184 to 1,014), which was 45% larger than the observed number. Expected intensity of leopard killing was positively related to protected area size, livestock density and wild prey abundance. Detection of leopard killing was higher in areas with more developed road networks.
4. *Synthesis and applications.* Ranger-based monitoring data on poaching of carnivores are cost effective, but traditional analysis does not take into account imperfect detection. We show that innovative statistics (single-visit N-mixture modelling) can reliably quantify poaching events and address their drivers, at

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large geographical scales. We used the example of the Persian leopard across Iran, but our approach is also applicable to understand killing dynamics of other species. Results suggest that a high frequency of leopard killing is likely to occur in areas with >100 livestock per km² and >450 individuals of wild prey per km². This highlights the need for improved management of livestock grazing and effective measures around high-risk protected areas to mitigate human–leopard conflict and reduce killing of leopards.

KEYWORDS

big cat, carnivore, hierarchical modelling, livestock density, N-mixture, poaching, protected area, wild prey

1 | INTRODUCTION

Many large mammalian carnivores around the world are experiencing population declines, range loss and local extinctions as a result of illegal killing, prey depletion and habitat degradation (Wolf & Ripple, 2016). High requirements for space and wild prey and pressure of intraspecific competition drive large carnivores into unprotected lands where the risk of livestock depredation and human-induced killing is high (Balme et al., 2019). Thus, carnivores are exposed to various human-induced mortality risks such as illegal killing (e.g. shooting, trapping and poisoning; Memarian et al., 2018), and/or road mortalities (Naderi et al., 2018). Such human-induced mortality in unprotected areas may contribute significantly to population declines of large carnivores (Carter et al., 2020).

Conflict between large carnivores and local people over livestock depredation is widely recognized as one of the most significant threats to the survival of large carnivores globally (van Eeden et al., 2017). Over one-third of the global land area is currently used for livestock production (Otte et al., 2012). Retaliatory or precautionary killings by humans in response to livestock predation may seriously affect population sizes of large carnivores (Carter et al., 2016). For example, Jędrzejewski et al. (2017) found that retaliatory killing of jaguars *Panthera onca* in South America was the main driver of their local extirpation. Deficiency in wild prey base and illegal killing of large carnivores have been described as limiting factors for population growth of carnivores (Naude et al., 2020) and wild prey recovery plans are unable to sustain carnivore populations if intensity of illegal killing is high (Bleyhl et al., 2021).

In general, information on the magnitudes of illegal killing and its drivers for large carnivores and other species is extremely limited (Moore et al., 2018). However, such information is needed to facilitate conservation and management plans (Balme et al., 2019), especially at large spatial scales. Deriving illegal killing data from monitoring might undercount the true killing intensity as illegal killing often occurs cryptically and hence its detection is notoriously difficult (Wittemyer et al., 2014). Thus, special attention is required to assess illegal killing intensity with the use of methods that account for imperfect detection (Marescot et al., 2019; Wittemyer et al., 2014). Such assessments are essential to contribute to a better

understanding of the cryptic drivers of carnivore killing and, subsequently, to develop possible mitigation measures (Khorozyan et al., 2015; van Eeden et al., 2017). Having empirical evidence of factors that influence illegal killing can help decision-makers prioritize their conservation efforts effectively (Treves & Karanth, 2003).

One of the drivers of human–carnivore conflict is the abundance of wild prey with conflicting hypotheses on the influence of this factor on conflict intensity. Suryawanshi et al. (2017) found that snow leopard depredation on livestock may increase with more abundant wild prey, as higher numbers of wild prey support a greater number of carnivores. In contrast, Khorozyan et al. (2015) concluded that large carnivores increase depredation on livestock when wild prey biomass/density decreases below a certain minimum threshold.

In this article, we address the issue of illegal killing of the Persian leopard (*Panthera pardus tulliana* Valenciennes, 1856; synonym to *P.p. saxicolor*) in Iran. Although Iran supports a diversity of extant large carnivores the Caspian tiger *P. tigris virgata* and the Asiatic lion *P. leo persica* are already extinct. Illegal killing contributed to the extirpation of both species (Firouz, 2005). The population size of Persian leopards in Iran is not known precisely; however, it is low, and was tentatively estimated to be around 550–850 individuals by Kiabi et al. (2002). This subspecies was once widespread across Southwest and Central Asia and the Caucasus ecoregion (Breitenmoser et al., 2007), but has lost 72%–84% of its range due to various human pressures (Stein et al., 2016). Illegal killing has been recognized as the principal factor causing local extirpation of leopards (Breitenmoser et al., 2007; Kiabi et al., 2002). Human–leopard conflicts are frequently reported in Iran (Babgir et al., 2017; Ghoddousi et al., 2020; Khorozyan et al., 2020; Kiabi et al., 2002; Soofi et al., 2019) and wildlife poaching is widespread in the country (Ghoddousi et al., 2019). During the past six decades (1960–2021), Iran's human population (~85 million) has increased exponentially (www.amar.org.ir), leading to a sharp increase in livestock numbers. A 2011 estimate of livestock numbers was 124 million head (FAO Stats; Amiraslani & Dragovich, 2011). Livestock pastoralism is widespread in Iran and occurs even inside national parks (Soofi et al., 2018). Depredation of livestock by large carnivores is common (Ghoddousi et al., 2016; Soofi et al., 2019).

Multiple studies have applied occupancy modelling for assessing wildlife poaching while simultaneously accounting for imperfect detection (Critchlow et al., 2017; Marescot et al., 2019; Soofi et al., 2018). However, published work has been heavily focused on inferences about occupancy (i.e. spatial extent), rather than of poaching events (O'Kelly et al., 2018). Royle (2004) proposed the N-mixture model, which takes counts ($C_{i,t}$) of independent events detected at each spatial unit i during the survey t and allows for modelling and estimation of abundance over space and time while also accounting for imperfect detection. N-mixture models make an assumption of population closure, that is, abundance does not change during the survey period (Royle, 2004). However, conditions of closed populations can be met in single-visit N-mixture models if at least one unique covariate is available for the detection (p) and abundance (N) parameters (Dorazio, 2014; Sólymos et al., 2012). While multi-visit wildlife monitoring data are rare, single-visit data are common (Sólymos et al., 2012), making the application of such approaches useful for wildlife conservation by reliably estimating the expected abundance from single-visit monitoring data.

In this study, we applied a single-visit N-mixture model (Kéry & Royle, 2021; Sólymos et al., 2012) to jointly model variation in detection probability and expected abundance of illegal killing events. This model regards the true number of illegal killing events as a latent variable, which is analogous to population size in the classical use of the N-mixture model (Royle, 2004). It estimates the latent quantity using observed numbers of illegal killing biased by imperfect detection. We used ranger-collected monitoring data (2007–2019) on the number of illegal killings of leopards across Iran and estimated illegal killing events for a given year and spatial unit. Here, we

- a. quantify the annualized illegal killing intensity of leopards in Iran using ranger-collected data, and evaluate the applicability of a single-visit N-mixture model at large spatial scales.
- b. assess the relationship between illegal killing events of leopards and livestock density and wild prey abundance over time.

2 | MATERIALS AND METHODS

2.1 | Study area

Iran is one of the most biologically diverse countries in Southwest Asia (Firouz, 2005). The country covers 1,648 million km², of which 54% is mountainous rangeland including steppe, 20% is desert, while only 8% is covered by forest (Sagheb-Talebi et al., 2014). Iran has a human population of ~85 million (Statistic Center of Iran 2021, www.amar.org.ir). Elevations range from -28 to 5,670m. The Hyrcanian relic temperate forests, stretching along the southern coastline of the Caspian Sea, and the Zagros semi-arid oak forests in western Iran, are the country's two biodiversity hotspots (Olson & Dinerstein, 2002).

The protected area (hereafter, PA) system in Iran is comprised of five categories: national parks (IUCN category II), natural monuments (cat. III), wildlife refuges (cat. IV), protected areas (cat. V) and no-hunting areas (hereafter, NHA) (unclassified by the IUCN). About 11.1% (excluding NHA) of the Iranian land surface is designated as PAs and is managed by the Iranian Department of Environment (DoE).

The Persian leopard occurs throughout most of Iran (Yusefi et al., 2019). The main wild prey of Persian leopard includes urial (*Ovis vignei* Blyth, 1841), mouflon (*Ovis gmelini*, Blyth, 1841), central Alborz red sheep, which is a hybrid population in the central Alborz Mountains, bezoar goat (*Capra aegagrus* Erxleben, 1777), goitered gazelle (*Gazella subgutturosa* Guldenstaedt, 1778), jebeer or chinkara gazelle (*Gazella bennettii* Sykes, 1831); Persian fallow deer (*Dama mesopotamica* Brooke, 1875), Caspian red deer or maral (*Cervus elaphus maral* Gray, 1850), roe deer (*Capreolus capreolus* Linnaeus 1758), onager (*Equus hemionus onager* Boddaert, 1785) and wild boar (*Sus scrofa* Linnaeus, 1758) (Yusefi et al., 2019).

2.2 | Response variable

We obtained ranger-collected data on the number of illegal killings of leopards across Iran (unpublished data; from 2007 to 2019) from DoE. Rangers in Iran regularly patrol areas and register wildlife sightings and crimes in the logbooks in ranger stations. We regarded the frequency of illegal killing and accidental killing events (an incidence of leopard killing, such as shooting, roadkill or trapping) as the response variable, and did not include natural deaths or deaths where the cause could not be precisely identified. We discarded killing events without location/year data ($n = 51$). Our study did not require ethical approval.

2.3 | Media reports

We also obtained leopard killing data from national public website articles published during the same period. We used media data on leopard killing to compare them with estimates of the true number of killed individuals, given that media is used to help guide public perceptions of wildlife conservation (Nanni et al., 2020).

2.4 | Study design

To define a site in our analysis, we superimposed 20×20 km² grid cells across Iran and spatially assigned all covariates and killing events ($C_{i,t}$) to respective grid cells (i) across years (t) using ArcGIS version 10.7.1 (ESRI USA). This cell size is larger than the average home-range size of Persian leopard (133 ± 66 km²; Farhadinia et al., 2018), so therefore it is appropriate to accommodate at least one individual.

2.5 | Covariates

The covariates in our analyses were selected based on a priori hypotheses and are considered likely to influence human-caused leopard killing events. Below we describe each of these covariates and the rationale for their inclusion in our models according to the framework (Figure 2).

2.5.1 | Covariates of abundance (N)

Here, we describe the covariates which we used exclusively for the abundance (N) model. We included livestock density as a covariate because livestock predation tends to increase when wild prey abundance decreases (Khorozyan et al., 2015). We derived data on livestock (i.e. cattle, sheep and goats) densities from the Food and Agriculture Organization, FAO (<http://www.fao.org>; 2005). Additionally, we included the site-specific ranger-collected wild prey population count data for the 10 herbivore species listed as leopard prey (see above). These prey count data were from 2007 to 2019 both inside and outside of the PAs (DoE) and were collected in winter (November–December) each year. PAs were partitioned into distinct sampling units that were surveyed by at least two to three rangers. For each grid cell, we measured the area size (km^2) covered by PAs of all IUCN categories (including NHAs), because larger PA sizes may support larger populations of carnivores (Santini et al., 2016). To account for the effects of human population density on leopard killing events (Naderi et al., 2018), we included the mean human population density. We obtained this from Gridded Population of the World v.4 at a 1-km spatial resolution from the Socioeconomic Data and Application Center (<http://sedac.ciesin.columbia.edu/data/se>, 2015).

2.5.2 | Covariates of detection (p)

In this part, we describe the covariate which we only included for the detection submodel (p). Data on number of ranger stations across PAs were gathered from Iran's atlas of PAs (Darvishsefat, 2006) and we refined it with the help of local rangers and experts throughout the country to model variation in detection probability of leopard illegal killing events among cells.

2.5.3 | Covariates of both abundance and detection (N, p)

Finally, we introduce the covariates which we used for both abundance and detection submodels (N, p). We calculated the total road length (km) from Open Street Map data (including motorways, primary roads, secondary roads, tertiary roads, trunks and corresponding link roads; <http://download.geofabrik.de> and <https://extra.ct.bbbike.org/>, 2018). We assumed that detection probability and abundance of human-caused killing events may vary as a function of elevation (Kéry & Royle, 2021), hence we included mean elevation

from a 30-m resolution digital elevation model, obtained from the NASA Shuttle Radar Topography Mission (<https://search.earthdata.nasa.gov>). We also considered a quadratic effect of elevation to allow nonlinear changes due to variations of illegal killing rates along the gradients of elevation (Moore et al., 2018).

2.6 | Data analysis

We standardized each site covariate by subtracting its mean and dividing by its standard deviation (Kéry & Royle, 2016) to have unit variance. We checked for multicollinearity of the covariates and excluded covariates if their Spearman's rank correlation $|r_s| \geq 0.7$. Because of perfect correlation ($r_s = 1.00$) among sheep, goat and cattle densities, we kept only sheep as a representative of livestock. The single-season static N-mixture model (Royle, 2004) enables the estimation of expected animal population size (here, total killings) at site i ($N_{i,t}$) and per-individual (killing event) detection probability (p). We used the N-mixture model and regarded each grid cell/year as an independent closed population (Kéry & Royle, 2021) where the population size is the true (unobserved) number of leopard killing events per grid cell and $C_{i,t}$ is the observed number of killing events in the grid cell i during the year t (Figure 2). This data structure fits into the single-visit N-mixture modelling framework, where there are no replicate samples within a year (Sólymos et al., 2012). Such a model is assumed to be estimable for abundance and detection parameters if both parts of the model have at least one continuous ('unique') covariate, that is, a covariate that is not shared by the 'other' submodel (Dorazio, 2014; Sólymos et al., 2012). The N-mixture model is a hierarchical model comprising two parts; an ecological and an observation part (Figure 2). The ecological part of the model (abundance, N) describes variation in the latent (unobserved) true number of leopard killing events for a given cell i and year t :

$$N_{i,t} \sim \text{Poisson}(\lambda_{i,t}),$$

where $N_{i,t}$ is the true number of leopard killing events in cell i ($i = 1, 2, 3, \dots, M$) and $\lambda_{i,t}$ is the expected number $E(N_{i,t})$ of leopard killing events. In addition to the Poisson event frequency model, we also considered a negative binomial (NB) distribution. The observation part of the model is a binomial count model in which we assumed that the number of observed leopard killing events is a binomial random variable:

$$C_{i,t} \sim \text{Binomial}(N_{i,t}p_{i,t}),$$

where $C_{i,t}$ is the number of observed leopard killing events in cell i during year t , and p is the detection probability for each individual killing event. We modelled covariates thought to affect detection probability (p), using a logit-linear model:

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 * X_{\text{ranger stations},i} + \alpha_2 * X_{\text{road length},i} + \alpha_3 * X_{\text{elevation},i},$$

where α_0 is the intercept and $\alpha_{1,2,\dots,3}$ are the coefficients to be estimated (Figure 2).

We modelled the effects of covariates on the expected number of leopard killing events, using the log link function (Figure 2). Specifically, $\lambda_{i,t}$ of each leopard killing in the cell i for the most complex model is described as:

$$\log(\lambda_{i,t}) = \beta_{0,t} + \beta_1 * X_{livestock\ density,i} + \beta_2 * X_{wildprey\ abundance,i,t} + \beta_3 * X_{road\ length,i} + \beta_4 * X_{human\ density,i} + \beta_5 * X_{protected\ area\ size,i} + \beta_6 * X_{elevation,i} + \beta_7 * X_{elevation^2,i},$$

where x_i is the vector of leopard killing-related covariates measured at the i -th site and $\beta_{0,t}$ is a year-specific intercept and $\beta_{1,2,\dots,13}$ are the coefficients to be estimated. We ran models in the R package 'UNMARKED' (Fiske & Chandler, 2011).

2.6.1 | Modelling

We retained at least one covariate that is unique for the p (ranger stations) and N (wild prey, livestock density, protected area size and human population density) submodels. Next, we concurrently expanded both submodels by adding common covariates that affect both p (elevation, road length) and N (road length) and quadratic effects of elevation on both submodels (Sólymos et al., 2012). Finally, we fitted a year-specific

intercept in the model for N (Kéry & Royle, 2021). The candidate models were selected using the Akaike information criterion (AIC) approach (Burnham & Anderson, 2002) by implementing the 'AICCMODAVG' package in R (Mazerolle, 2020). We carried out a bootstrap goodness-of-fit analysis with 1,000 iterations (Kéry & Royle, 2021).

2.6.2 | Quantifying expected numbers of leopards killed annually

We quantified the annual mean number of leopard killing events per grid cell by computing the fitted values from the abundance part of the best-fitting model (Figure 2). Then, to obtain annual numbers of killed leopards (Table 1) we summed up the expected killing events over grid cells (1–4,000) and multiplied by the average number of individuals killed per event (mean = 1.04) (Figure 2). We set the calculation as follows:

$$\lambda_{i,t} = \exp(\beta_{0,t} + \beta_1 * X_{livestock\ density,i} + \beta_2 * X_{wild\ prey\ abundance,i,t} + \dots + \beta_{3,\dots,7} * X_{elevation,i}),$$

where i is the indexed grid cells, betas are the covariates from the best-fitting model and x_i is the value of each covariate in the cell ' i '. We then

TABLE 1 Estimates of negative binomial (NB) abundance and detection parameters of the best-fitting single-visit N-mixture model ($n = 4,000$ grid cells). The mean annual estimated quantities (confidence intervals) represent the total killed leopards in each year. DoE: Iranian Department of Environment. β and α indicate the coefficients estimated for mean abundance (lambda) of leopard illegal killing events and detection probability (p) respectively

Model parameters	Estimate (β)	CI (95%)	Estimated leopard killings (95% CI) per year	DoE counts	Media reports
Abundance (lambda)					
$\beta_{wild\ prey}$	0.07	(0.04, 0.09)			
$\beta_{livestock\ (sheep)}$	0.31	(0.18, 0.44)			
$\beta_{protected\ areas}$	0.36	(0.12, 0.59)			
β_{yr2007}	-6.48	(-7.94, -5.02)	13 (3, 57)	10	2
β_{yr2008}	-5.91	(-6.93, -4.90)	23 (8, 64)	10	2
β_{yr2009}	-5.90	(-6.91, -4.90)	24 (8, 64)	24	6
β_{yr2010}	-5.07	(-5.83, -4.31)	54 (25, 116)	11	5
β_{yr2011}	-5.48	(-6.31, -4.65)	36 (16, 82)	8	2
β_{yr2012}	-6.02	(-7.02, -5.02)	21 (8, 57)	16	6
β_{yr2013}	-5.27	(-6.02, -4.51)	45 (21, 95)	19	19
β_{yr2014}	-5.84	(-6.73, -4.95)	25 (10, 61)	18	20
β_{yr2015}	-5.57	(-6.35, -4.78)	33 (15, 72)	30	20
β_{yr2016}	-5.10	(-5.81, -4.40)	53 (25, 106)	20	13
β_{yr2017}	-5.45	(-6.22, -4.68)	37 (17, 80)	24	19
β_{yr2018}	-5.59	(-6.41, -4.78)	32 (14, 73)	28	8
β_{yr2019}	-5.60	(-6.58, -4.62)	32 (12, 85)	10	5
Detection (p)					
$\alpha_{intercept}$	-0.37	(-1.36, 0.63)			
$\alpha_{road\ length}$	2.26	(1.26, 3.25)			
$\alpha_{elevation}$	-0.35	(-0.73, 0.03)			
Total			428 (184, 1,014)	228	127

calculated the total number of killed leopards as $\sum(\lambda_{ij}) \times \text{mean}$ of leopards killed per event.

2.6.3 | Model identifiability

We checked the sensitivity of the best-fitting model parameters over varying values of likelihood truncation in calculation of the marginal likelihood (i.e. $K = 103, K = 200, K = 400, K = 600, K = 800, K = 1,000; K = \max(C_{it}) + 100$) recommended by Kéry (2018) and Kéry and Royle (2021). This approach ensures that the maximum likelihood estimates are not on the boundary of the parameter space (i.e. with infinite abundance and zero detection; Dennis et al., 2015). We then compared the AIC of these best-fitting models with an increased value of K (Kéry & Royle, 2021).

2.6.4 | Post-hoc analysis

We applied the Kernel probability density estimator using DoE data to compare an approximate age distribution of the killed female

($n = 23$) and male ($n = 20$) leopards. We used one-way ANOVA and Tukey's honest significance difference test (HSD) to compare the means of different group sizes of livestock density (30 individuals per km^2), wild prey abundance (50 individuals per km^2) and protected area size (area = 50 km^2) against predicted leopard killing events. All statistical analyses were performed in R software version 3.3.6 (R Core Team, 2020).

3 | RESULTS

Overall, the ranger-collected data included 240 individual leopards (218 events and 12 events with unknown dates) killed in Iran from 2007 to 2019. The average number of leopards killed per event was 1.04 ($SD = 0.22$, range = 1–3). The causes of mortality were illegal killing (shooting = 77, persecution [i.e. killings which were mainly preventive or retaliatory over livestock depredation] = 34, poisoning = 18), accidental killing (road kills = 33, railroad kills = 1, non-targeted snares = 6), natural (32) and unknown causes (39) (Figure 1). In contrast, our reviews of 1,277 media news articles published from

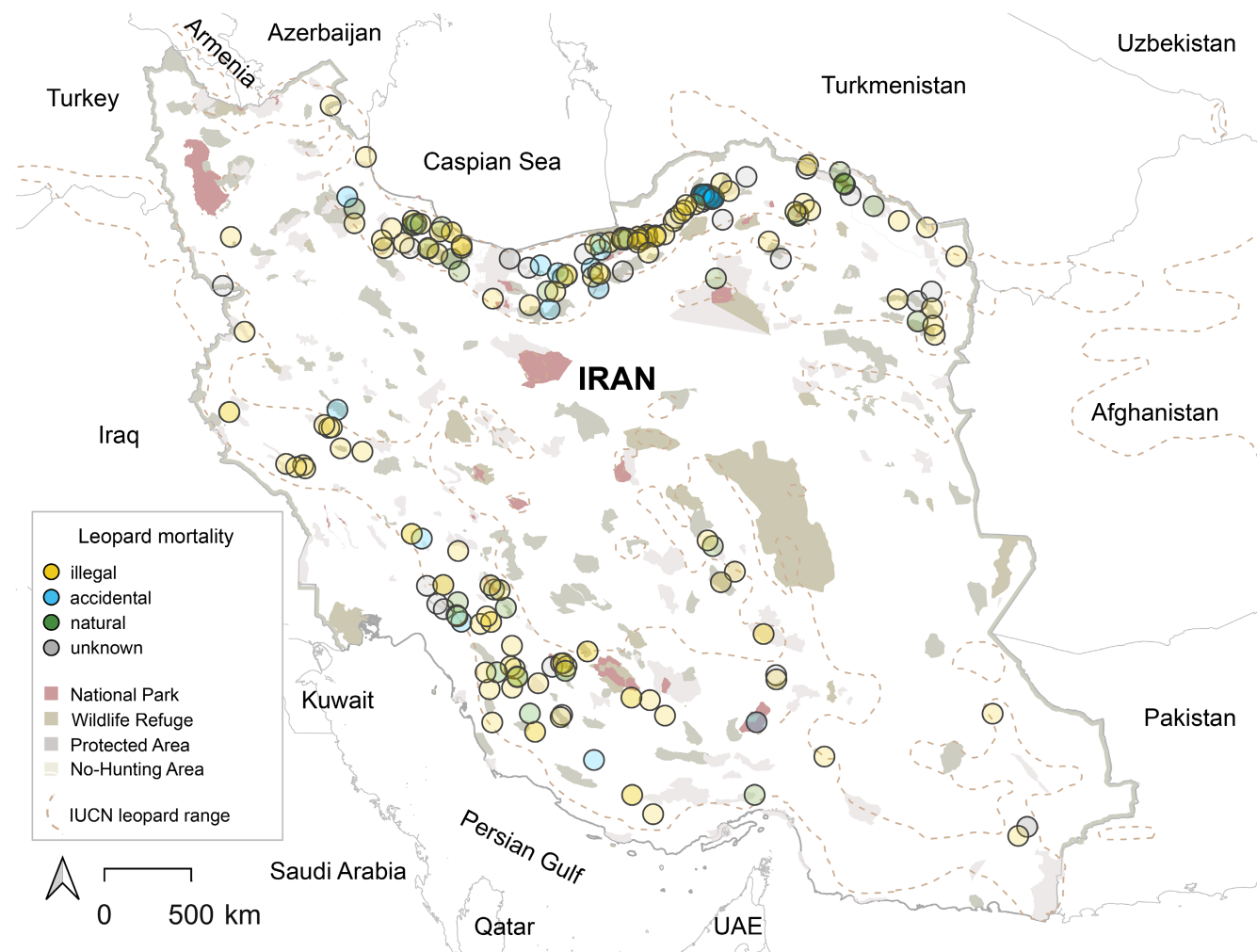


FIGURE 1 Distribution of Persian leopard kill types based on ranger-collected data across Iran during 2007–2019 (based on DoE data 2021; $n = 240$)

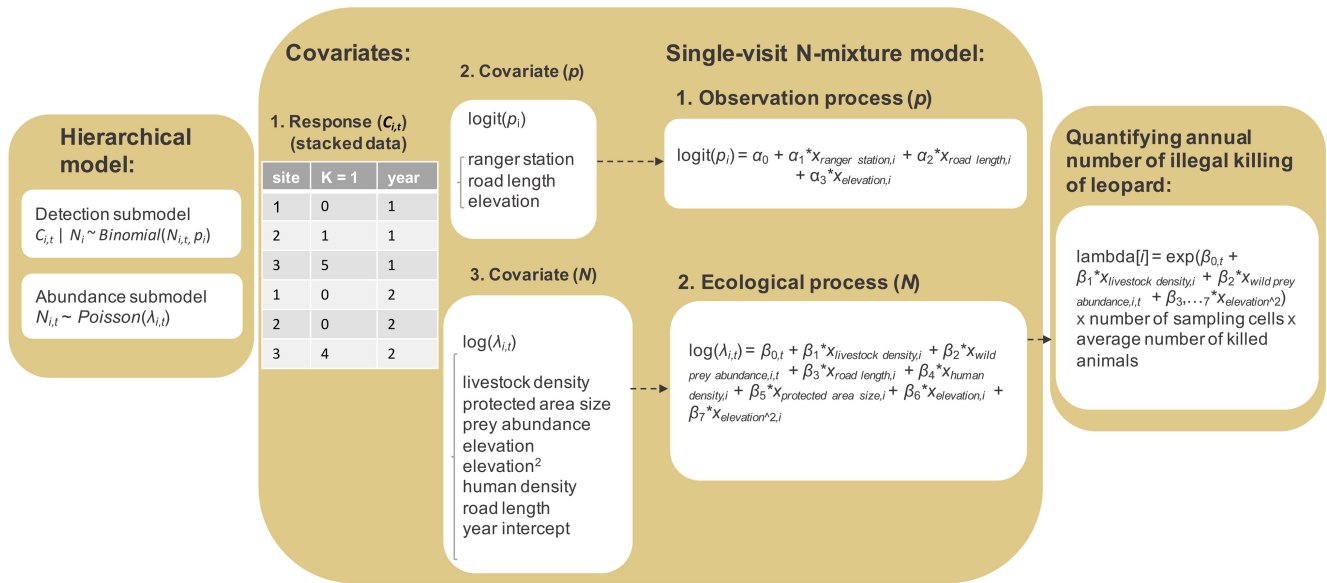


FIGURE 2 A framework fitting our study data to the single-visit N-mixture model to estimate the number of leopard killings

2007 to 2019 led to the detection of only 127 leopards killed across Iran.

Our modelling exercise resulted in 16 models (see Tables S1 and S2), of which only the best-fitting model is presented here. The results of the goodness-of-fit tests indicated that both the NB and Poisson models passed the fit test, but the Poisson model was not selected as the best model (see Table S3; Figure S1). Our abundance model revealed that leopard killing events peaked in the years 2010 (mean 54, 95% CI = 25 to 116) and 2016 (mean 53, 95% CI = 26 to 106) (Table 1, Figure 3). Leopard killing events were positively associated with increased density of livestock ($\beta = 0.31$, 95% CI = 0.18 to 0.44). The numbers of killing events were not significantly different from 0 (Tukey HSD test, $p = 0.29$) when livestock density was between 0 and 100 animals per km² but they doubled significantly with every 50 additional head of livestock (Figure 4a). Likewise, protected area size had the strongest and positive effect ($\beta = 0.36$, 95% CI = 0.12 to 0.59) on leopard killing events (Figure 4b). Wild prey abundance also had a positive influence ($\beta = 0.06$, 95% CI = 0.03 to 0.08) on the number of killing events, which was significantly different from 0 (Tukey's HSD, $p = 0.01$) when wild prey abundance per km² was >450 individuals (Table 1; Figure 4c). Our detection probability (p) model showed that road length had a significant positive effect ($\alpha = 2.26$, 95% CI = 1.26 to 3.25) on detecting killing events (Figure 4d), and elevation had a non-significant negative effect ($\alpha = -0.35$, 95% CI = -0.73 to 0.03) (Table 1). The probability of detecting leopard killing events was moderate in cells with 80km of road and increased to 1 when more than 370km of roads existed within a sampled cell (Figure 4c). The estimated total number of individuals killed was 428 (95% CI = 184 to 1014), which was 45% larger than the DoE count (Figure 3, Table 1). Finally, sensitivity of the choice of K for parameter estimates showed that the maximum likelihood and AIC under the negative binomial model with $K = 103$ ($K = \max(C_{i,t}) + 100$) were identical for higher values of K (see Table S4). The probability density function calculated by the Kernel density estimator showed that female leopards were more likely to be killed by all killing types (accidental, illegal, natural; Figure 5) at younger ages, while male leopards showed a relatively consistent mortality pattern in all age groups (Figure 5). The mean female mortality age was 3.07 years ($SD = 2.06$) and that of males was 5.05 years ($SD 3.23$).

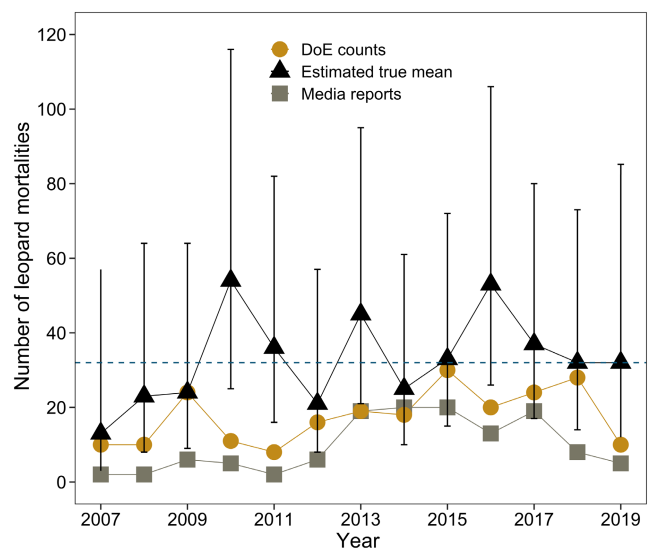


FIGURE 3 Estimated true mean of killed leopards (black-coloured symbol with 95% confidence interval). DoE counts: Yearly number of killed leopards that were reported by DoE for the years 2007–2019 (brown-coloured symbol) and counts (dark grey-coloured symbol) of killed leopards in Iran based on media articles for the same years. The horizontal blue dashed line indicates the expected frequency of killings averaged over the 13-year period

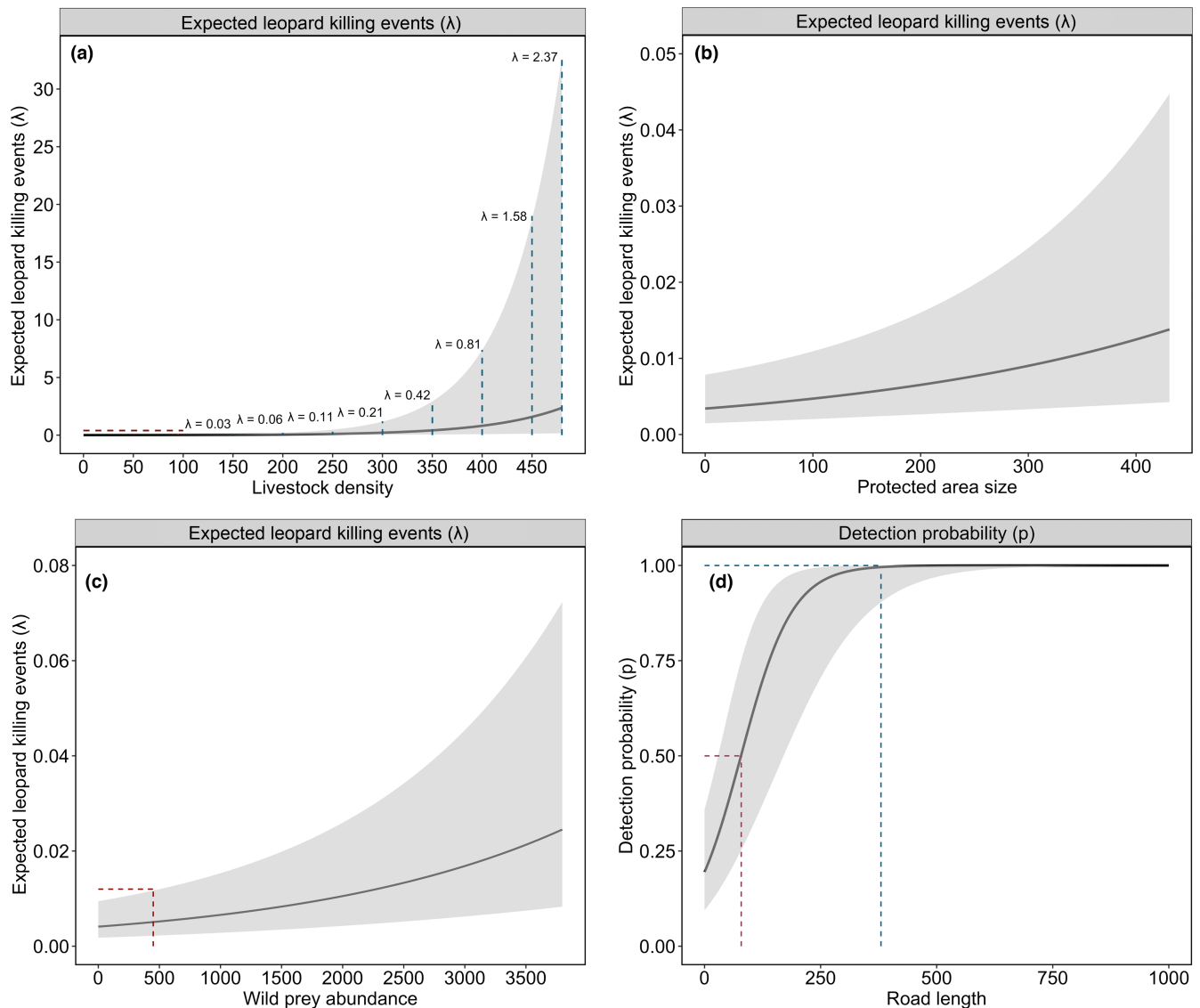


FIGURE 4 Response curves (estimated from the best-fitting model) of expected killing events of leopard in relationship with (a) livestock density (km^2), (b) protected areas size (km^2), (c) wild prey abundance (km^2) and (d) detection with road density (km) under the negative binomial (NB) model for killing event frequency of the Persian leopard. The grey shaded colour illustrates the confidence interval bands and the black line colour shows the mean estimate. (a) The vertical blue dashed lines show the estimated true mean killing events at different livestock densities, and dark red dashed horizontal line shows where kills were not significantly different from 0. (d) The vertical blue and dark red dashed lines on the road lengths illustrate the detection probability of killing events reached to 0.5 and 1

4 | DISCUSSION

Illegal killing has been recognized as one of the major drivers of population declines and extinction of many species, especially large carnivores (Wolf & Ripple, 2016). Using a novel application of the single-visit N-mixture model (Kéry & Royle, 2021), we quantified annual events of illegal leopard killing in Iran, the raw observations of which are expected to be rare and biased by imperfect and heterogeneous detection rates over time and space. Additionally, we evaluated the relationships between livestock density, wild prey abundance and leopard killing events. Our modelling approach allowed for accurate quantification of illegal killing events, while accounting for imperfect detection. The main advantage of this model

is that it estimates the number of non-detected illegal killing events (Royle, 2004). This is especially relevant to wildlife monitoring data in many protected areas, since data are often collected across large spatial units.

Our results showed that leopard killing events increased over the 13-year study period, but the intensity was highest in 2010 and 2016. Our findings differ from those of recent studies investigating mortality of six species of large carnivores, including Persian leopard, using records of DoE (Naderi et al., 2018; Parchizadeh & Belant, 2021). Although these studies extended over a longer time period (1980–2021) than ours (2007–2019), they reported fewer than 100 events of leopard mortality. Our single-visit N-mixture model, which accounts for non-detection of events, produced an

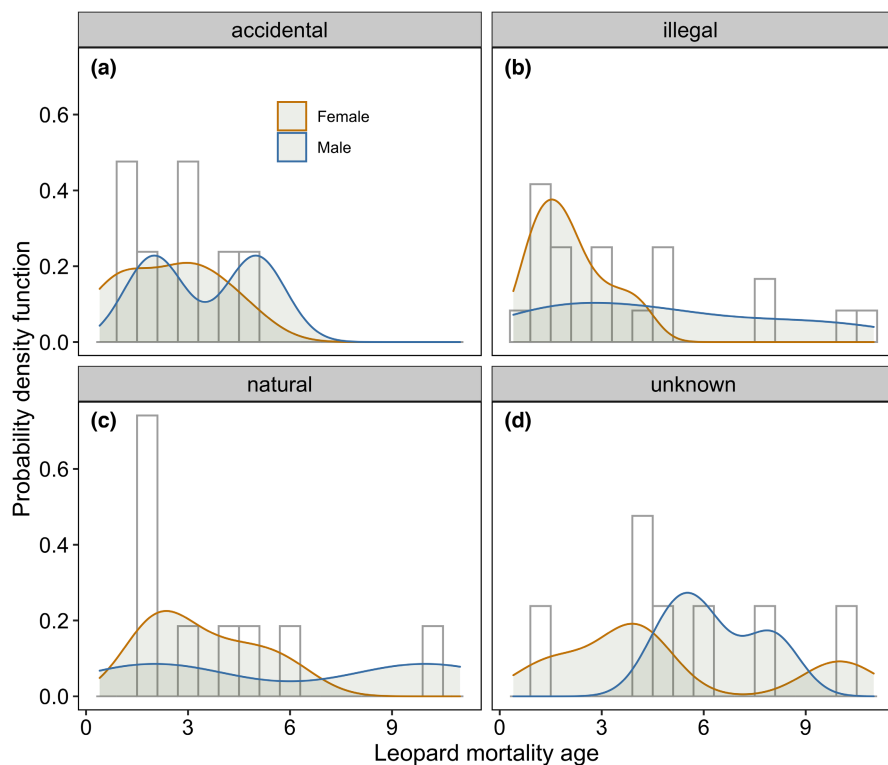


FIGURE 5 Probability kernel density function (y-axis) against approximate illegal killing age (years; x-axis) for female and male Persian leopards in Iran (DoE data)

estimate of 428 leopard deaths over the 13-year study period. This estimate differs not only from that of Parchizadeh and Belant (2021) but also from the mortality counts obtained from both DoE ($N = 228$) and the news media ($N = 127$) (Table 1). Media reports appeared to be infrequent (30%) partially because accessing and locating illegal killing events requires technical skills (Di Minin et al., 2016), leading to imperfect detection.

Our abundance model indicated a higher expected frequency of leopard killing events in larger protected areas. Larger protected areas could accommodate higher populations of leopard and therefore, more dispersal. These factors suggest that leopard killings were triggered by leopard depredation on livestock, which is very common in Iranian protected areas (Soofi et al., 2018). At the same time, leopard killing events increased with wild prey abundance, presumably because leopards were attracted to areas with abundant prey (Suryawanshi et al., 2017), but the magnitude of this effect was low (Figure 4c). Furthermore, we found that the detectability of killing events increased with road length. This may suggest that leopard killing events were more likely to be detected by rangers in areas of greater road length (Carter et al., 2020). Our raw data showed that 54% of leopard killing events were related to shooting and persecution following livestock depredation events, especially in areas with livestock density higher than 100 head per km^2 . Loss of livestock as a valuable asset of local pastoralists may provoke the killing of leopards in retribution for these losses and to prevent future losses. This likelihood suggests that enforcement of grazing management should be a priority for leopard conservation.

Our estimates of leopard killing events show that on average 32 leopards were killed annually across Iran, mostly in the areas with high densities of livestock. Therefore, mitigation of human–leopard

conflict should be a conservation priority (Ghoddousi et al., 2020). A recent analysis of metapopulation dynamics of Persian leopard found that reducing levels of persecution is the principal requirement to enable recolonization of the leopard population in the Caucasus ecoregion (Bleyhl et al., 2021).

Our Kernel density analysis showed that female leopards were vulnerable to illegal killing at younger ages (1–6 years), whereas males showed a relatively similar mortality pattern in all age groups (0–10 years) (Figure 5a–d). This may indicate a potentially serious threat of leopard killing to species survival in Iran as the survival of adult females is a vital determinant of population self-maintenance in big cats (Bleyhl et al., 2021).

Our approach using the single-visit N-mixture model to assess killing of wildlife is novel and potentially useful for dealing with similar conservation threats involving different wildlife species in various regions. Nevertheless a few drawbacks with the approach remain. Knappe and Korner-Nievergelt (2015) have criticized the single-visit models, arguing that these models could be unidentifiable, and that absolute abundance cannot be estimated when the log link function for expected N and p is used. Kéry (2018) proposed a criterion of varying K values, selected by default as $K = \max(C_{i,t} + 100)$ for identifiability of negative binomial N-mixture models. We acknowledge that multi-visit models might be preferable to single-visit N-mixture models when multi-visit data are available. However, single-visit data are often collected (Sólymos et al., 2012), and such data should be analysed to address conservation issues. Thus, understanding killing processes and their effects in real landscapes requires more robust model-based procedures, such as the N-mixture model. The N-mixture model requires the independence of detection events. Our data contained only seven cases where a female with dependent juveniles or juveniles alone were

killed. These dependent events were few, and we believe were unlikely to systematically bias our results.

Illegal killing can adversely affect the survival of large carnivore populations but such killing is notoriously difficult to detect and study due to its cryptic nature. However, assessment and mitigation of illegal killing require a solid understanding of its magnitude, pattern and underlying drivers for the prioritization of conservation management policy. Using ranger-collected data and applying the single-visit N-mixture model, we overcame (at least partly) intrinsic limitations in the study of illegal killing, and we were able to quantify the numbers of leopards killed annually in Iran by using a class of statistical models (the N-mixture model) that allows for the modelling of both abundance and detectability from count data.

ACKNOWLEDGEMENTS

This project would not have been possible without the generous support of local rangers and environmental experts throughout Iran. This project was implemented under permit number 98/170/39717 issued by the Iranian Department of Environment, with funding provided to M.S. by the PRIME programme of the German Academic Exchange Service (DAAD, project No. 57436650) from the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung [BMBF]). MS currently is funded by a Feodor Lynen Fellowship of the Alexander von Humboldt Foundation (award No. DEU 1220304 FLP-P, 2021–2023), Germany. AG appreciates the financial support of the German Research Foundation (DFG; PARCS project #409732304). B.B. gratefully acknowledges funding through BMBF (BMBF, project SoMo 01DK21003). We are grateful to T. Zeppenfeld for his generous methodological advice. All relevant parties involved in the underlying research, who are listed as co-authors or acknowledged here, contributed critically to the drafts and gave their final approval for publication. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We are grateful to Associate Editor M. Hayward, M. Kéry and anonymous reviewers for their constructive comments. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

There is no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.S. and A.R. conceived the idea and designed the methodology; A.T.Q., M.S., M.M., E.H., B.B. and M.F. collected the data; M.S. and A.R. analysed the data, and M.S. produced the graphs; M.S. drafted the original manuscript; M.S., A.R., C.R.P., M.W., I.K.H., A.G.H., B.B., N.B., B.H.K., A.T.Q. and M.F. contributed in the interpretation, editing and revising the article. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R codes are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.gtht76hp7> (Soofi et al., 2022).

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How to cite this article: Soofi, M., Qashqaei, A. T., Mousavi, M., Hadipour, E., Filla, M., Kiabi, B. H., Bleyhl, B., Ghoddousi, A., Balkenhol, N., Royle, A., Pavey, C. R., Khorozyan, I. & Waltert, M. (2022). Quantifying the relationship between prey density, livestock and illegal killing of leopards. *Journal of Applied Ecology*, 59, 1536–1547. <https://doi.org/10.1111/1365-2664.14163>