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Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock depredation rate by large carnivores

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Abstract

1. Illegal hunting of ungulates can reduce the prey base of carnivores, which can increase human–carnivore conflict (HCC) through livestock depredation. However, the relationship between ungulate poaching, wild prey abundance and livestock depredation has rarely been empirically studied.

2. We surveyed 18 sites across the Hyrcanian forest in northern Iran; a global biodiversity hotspot under pressure from illegal hunting of ungulates, prey depletion, livestock grazing and HCC. We conducted three field surveys across 1,204 km in 93 4 × 4 km cells to count signs of ungulate poaching as well as encounters with livestock and prey species of the Persian leopard *Panthera pardus saxicolor* and the grey wolf *Canis lupus*. We documented sheep/goat and cattle depredation from interviews with 201 herders and analysed the effects of illegal hunting of ungulates, forest cover, IUCN categories of reserves, elevation, distance to villages, and wild prey and livestock encounter rates on carnivore depredation rates using generalized linear models.

3. Illegal hunting of ungulates was the most influential depredation predictor. An increase in the illegal hunting of ungulates by one sign/km significantly increased depredation by up to four times. We also found significantly lower levels of ungulate poaching in national parks (IUCN category II) compared to protected areas (V), wildlife refuges (IV) and no-hunting areas, though poaching signs were frequently found in most cells (58%). Encounters with livestock was inversely linked to wild prey species, but positively coupled with signs of ungulate poaching.

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4. *Synthesis and applications*. Our study reveals that: (a) an increase in the intensity of illegal hunting of ungulates can intensify livestock depredation by carnivores; (b) future efforts in reducing human-carnivore conflict to acceptable levels require a combination of law enforcement, prey recovery approaches and mitigation measures; (c) it is essential to understand the root causes of poaching to help minimize human-carnivore conflict (HCC).

1 | INTRODUCTION

Most large mammalian carnivore populations are declining rapidly (Ripple et al., 2014; Wolf & Ripple, 2016), mainly due to conflicts with humans, prey depletion and habitat loss (Benitez-Lopez et al., 2017; Maxwell, Fuller, Brooks, & Watson, 2016). High metabolic demands, large home ranges and low wild prey availability in combination with livestock increasingly penetrating into suitable wildlife habitats lead to livestock depredation by large carnivores (Chapron & López-Bao, 2016; Suryawanshi et al., 2017). Livestock grazing is a critical factor that contributes to the decline of wild prey populations, mainly through forage competition or changes in predatory patterns of large carnivores (Ekernas et al., 2017). Consequently, human-carnivore conflicts (HCC) arising from livestock depredation are widespread, causing socio-economic losses to local livelihoods and retaliatory killing of carnivores (Khorozyan, Ghoddousi, Soofi, & Waltert, 2015).

Illegal hunting of ungulates can lead to competition between humans and carnivores over limited prey resources, affecting carnivore survival (Ghoddousi, Soofi, Hamidi, Leumetsberger, et al., 2017) and driving many prey species towards extinction (Benitez-Lopez et al., 2017; Milner-Gulland, Bennett, & SCB, 2003). The scarcity of wild prey abundance may also increase depredation rates as carnivores are forced to shift to alternative prey (Khorozyan et al., 2015). However, high wild prey abundance can have both positive and negative effects on depredation rates, which may differentially affect carnivore conservation (Khorozyan et al., 2015; Suryawanshi et al., 2017). It is hypothesized contrastingly that (a) depredation may arise in areas with high wild prey abundance, which may support higher densities of carnivores (Chetri, Odden, & Wegge, 2017; Suryawanshi, Bhatnagar, Redpath, & Mishra, 2013; Suryawanshi et al., 2017); or that (b) depredation increases in regions suffering from wild prey depletion where predators switch from wild to domestic prey (Khorozyan et al., 2015; Treves et al., 2004). Although there is evidence for both hypotheses, this important conservation issue remains inconclusive (Chetri et al., 2017; Suryawanshi et al., 2017). Generally, it is found that depredation is more closely linked to prey loss than to carnivore densities or landscape protection status (Khorozyan et al.,

2015; Wolf & Ripple, 2016). Ekernas et al. (2017) shows that pastoralists can have dichotomous effects on depredation rates either by reducing predator density (i.e. killing) or by increasing carnivore density as livestock provide a plentiful prey resource capable of supporting high carnivore densities.

The effects of illegal hunting of ungulates on wildlife populations are not easy to study (Milner-Gulland et al., 2003) and, to our knowledge, relationships between ungulate poaching, wildlife occurrence and HCC have rarely been described empirically, especially at broad spatial scales. Existing HCC studies focus mainly on the identification and prediction of high conflict areas (Miller, 2015; Treves et al., 2004). However, to achieve effective and evidence-based conservation measures and to define management priorities, the relationship between illegal killing of ungulates and HCC needs to be understood (Van Eeden et al., 2017).

The Hyrcanian forest in northern Iran provides a useful example to study these relationships, as high levels of illegal hunting and HCC are widespread in this area (Babrgir, Farhadinia, & Moqanaki, 2017; Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017; Khorozyan et al., 2015; Kiabi, Ghaemi, Jahanshahi, & Sassani, 2004; Soofi et al., 2018 b). For example, in Golestan National Park, an important biosphere reserve of the region, ungulate populations have been depleted by 66%–89% since the 1970s (Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017). Previous HCC studies in the Hyrcanian forest suggest that high conflict intensity can be related mostly to prey depletion (Babrgir et al., 2017) or reduction of preferred prey (Ghoddousi et al., 2016).

In this study, we assess depredation by the two large carnivores most responsible for livestock losses in the region, the endangered Persian leopard (*Panthera pardus saxicolor*) and the common grey wolf (*Canis lupus*). We hypothesize that there will be a negative relationship between the rates of illegal hunting of ungulates and wild prey occurrence, which in turn increases livestock depredation levels and thus the conflict rates between humans and large carnivores. Being solitary stalkers, leopards prefer complex habitats with sufficient cover for preying by ambush, while cursorial pack-living wolves tend to hunt more in open habitats (Suryawanshi et al., 2013). Moreover, we also expect that differences in predatory tactics of these carnivores lead to different patterns of livestock depredation (Behdarvand et al., 2014; Garrott, Bruggerman, Becker, Kalinowskiki,

& White, 2007; Imbert et al., 2016; Khorozyan et al., 2017). For instance, leopards are more inclined to prey on larger stock but wolves are mainly adapted to prey on small stock, which may require different conflict management actions (Chetri et al., 2017; Suryawanshi et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study area

The Hyrcanian broadleaved forest expands from the Talysh Mountains in Azerbaijan through the northern slopes of the Alborz Mountains to Golestan National Park in eastern Iran. Elevations range from −28 to 2,800 m a.s.l., mean annual precipitation from 530 mm in the east to 1,350 mm in the west and air temperature from 28°C to 35°C in summer to 1.5°C–4°C in winter (Sagheb-Talebi, Sajedi, & Pourhashemi, 2014). The Hyrcanian forest is part of the Caucasus Biodiversity Hotspot and holds an exceptional diversity of species and landscapes from Asia and Europe that converge in this region (Olson & Dinerstein, 2002). This forest harbours globally significant populations of the endangered Persian leopard and Caspian red deer (*Cervus elaphus maral*) and regionally important populations of the grey wolf, brown bear (*Ursus arctos*), roe deer (*Capreolus capreolus*), bezoar goat (*Capra aegagrus*) and wild boar (*Sus scrofa*) (Karami, Ghadirian, & Faizolahi, 2017). The Iranian part of the

Hyrcanian forest consists of 37 reserves: three national parks (NP, IUCN Category II), two wildlife refuges (WR, Cat. VI), 19 protected areas (PA, Cat. V), 2 national natural monuments and 12 no-hunting areas (NHA; Darvishsefat, 2006). NHAs are established for only a short period of time (*c.* 5 years) to allow the recovery of threatened species (Darvishsefat, 2006). Livestock grazing is banned inside the NPs and in the core zones of the PAs and WRs while ungulate hunting is strictly prohibited in all reserves (Makhdoum, 2008; Soofi et al., 2018b). Domestic animals are allowed to roam in 80% of the total area size of these reserves (except in NPs) and include cattle, sheep, goats, horses and dogs. Around 4 million cattle and small stock (sheep/goat) are herded or graze freely in small herds, with small stock being actively herded and kept in sheds at night (Ghoddousi et al., 2016). Local herders have a traditional right to migrate upwards in spring to find better pastures in highlands but often tend to stay much longer than their grazing permits specify (Soofi et al., 2018b). Cattle are grazed predominantly in forests while sheep/goat (hereafter shoat) are grazed mostly above the treeline (Soofi et al., 2018b).

2.2 | Study design

We selected 18 study sites covering 4,112 km² in total and including 14 reserves (three NPs, eight PAs, one WR, two NHAs) and four nonprotected areas (NPAs) across the Hyrcanian forest in Iran (Figure 1). We placed a grid of 4 × 4 km cells over all study sites. In
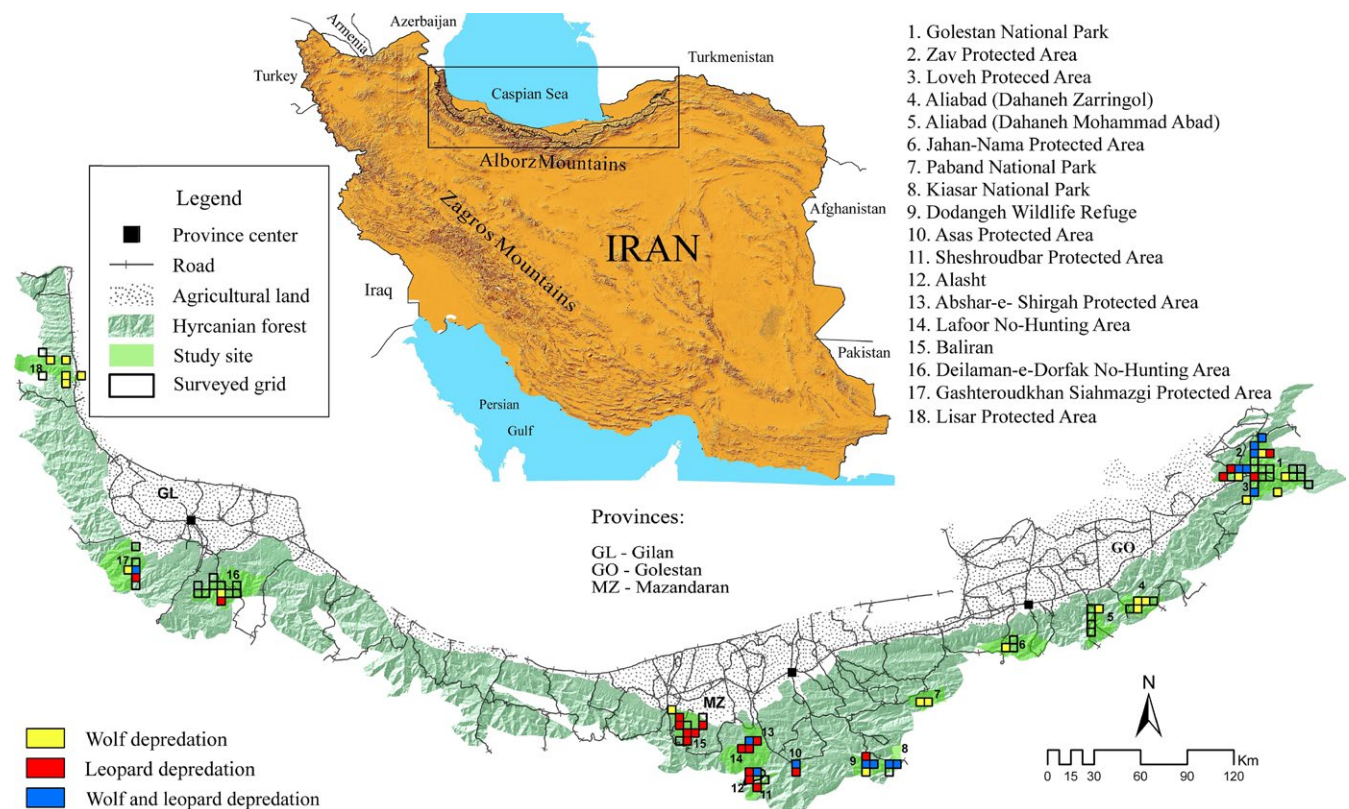
FIGURE 1 Location of 18 study sites throughout the Hyrcanian forest, Iran. In each study site, the quadrats delineate the sampled grid cells (*n* = 93)

each study site, we randomly selected *c.* 45% of the total number of cells as sampling units using Hawth's tools in ArcGIS v.10.2 (ESRI Co., USA; Beyer, 2004). We studied two carnivores (Persian leopard and wolf) and four prey species (red deer, roe deer, bezoar goat and wild boar). Home ranges of Persian leopards vary from 62.9 to 1,098.3 km^2 (Farhadinia et al., 2017) and those of wolves from 53.9 to 120.8 km^2 (Kusak, Majić Skrbinšek, & Huber, 2005). On average, the home ranges of prey are much smaller than those of predators (Karanth et al., 2011). As defining an appropriate cell size is challenging for research in multi-species studies, we chose this cell size as a trade-off between study feasibility and the high space requirements by local large mammals (Soofi et al., 2018b; Yackulic, Sanderson, & Uriarte, 2011).

During three discrete surveys (August–October 2015, February–April 2016 and August–October 2016), teams of 2–3 people who were able to unambiguously identify signs of our target species and those of illegal hunting visited each cell. Each grid cell required a full day to survey, and for distant cells a minimum of 1 day was needed to access them. Surveys during summer/early autumn began roughly at about 07:00 a.m. and ended in late afternoon (20:00 p.m.), but the ending time reduced during winter/early spring (07:00–17:00 p.m.). Variation in sampling effort was caused by limited accessibility of very remote areas, especially during winter, where multiple surveys were not always possible. We walked 1,204 km of trails during 147 field days. Overall, we surveyed 93 cells of which 45 cells were surveyed three times, 21 cells twice and 27 cells once.

2.3 | Surveys of wild prey, illegal hunting of ungulates and livestock signs

In each cell, we walked along randomly selected trails of 2–13 km length and recorded the presence-absence of fresh signs (tracks, scratches, scrapes, feeding and resting places, rubbing posts and wallows) and direct observations (sightings and sounds) of the Caspian red deer, roe deer, bezoar goat and wild boar, which are the main prey species of leopard and wolf (Ghoddousi et al., 2016). Each survey team took photographs of signs for final identification/verification and evaluation of sign freshness. Each type of observed sign was assigned only once to each 200 m trail segment, allowing the standardized presence/absence records of animal signs (Karanth et al., 2011; Gopalaswamy, Karanth, Kumar, & Macdonald 2012). We selected 200 m segments to reduce pseudoreplication and secure independence of sign records on mountain trails, which are generally short and discontinuous. Likewise, direct sightings of individuals, groups and auditory records of animals were registered only once at each trail segment (Laurance et al., 2008). Concurrently, we recorded the occurrence of fresh signs of illegal hunting of ungulates (poacher encounters, fire remains, gun shells without traces of rust and gunshots heard; Laurance et al., 2008) and signs of livestock (observations, corrals/sheds, faeces and tracks of cattle and shoat; Karanth et al., 2011). It was not always possible to determine whether hunting signs belonged to illegal hunting of ungulates or retaliatory killings of predators, but we assumed that most records of poaching

signs were related to ungulate hunting, which is widespread in Iran (Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017). We grouped data from sheep and goats (shoat) as both these species graze together and are equally prone to carnivore attacks (Khorozyan et al., 2017). We rotated team members between grid cells to minimize observer bias (MacKenzie et al., 2006).

2.4 | Surveys of livestock depredation

We asked 201 herders encountered along random trails during the three subsequent survey periods across grid cells to report their livestock losses to depredation during the period of the survey and 3 months before it. During our surveys, part of the reported losses had already been confirmed by environmental experts and a few events were validated by the survey team. Over half of the reports was without confirmation. We used a standardized questionnaire (Table S2) and assumed that respondents were skilled enough to distinguish between leopard and wolf depredation signs (Khorozyan et al., 2017) but discarded ambiguous cases. Predation signs between these two carnivores are very distinct, as leopards kill mainly by strangulation with throat bites whereas wolves do so by laceration of flanks and hind legs.

2.5 | Field and GIS-based variables

We used the numbers of depredation events of cattle and shoat by leopard and wolf in grid cells as two separate response variables. As field-based explanatory variables, we included the occurrences of illegal hunting of ungulates and both wild (i.e. red deer, roe deer, wild boar, bezoar goat) and domestic prey (cattle, shoat). These occurrences were measured as the proportions of 200 m random trail segments with signs present in relation to the total sampling effort (km of trails walked per cell and survey period). We averaged the occurrence estimates of these variables over all survey periods if a cell was surveyed more than once. Additionally, we selected GIS-based variables, which were potentially relevant to depredation: distance from the midpoint of the trails to the nearest village (DV) using the Euclidean distance function in GIS, elevation as the mean elevation from a digital elevation model of 30-m resolution, forest cover as the proportion of forest cover (Google Earth) measured in each cell divided by total cell size, and IUCN categories of reserves among study sites (Table 1; Miller, 2015).

2.6 | Analysis

We applied GLMs to analyse depredation events for each carnivore species (leopard, wolf) as a function of the variables described above. Before model construction, predictors were checked for multicollinearity using the variance inflation factor (VIF) <3 (Zuur, Ieno, & Elphick, 2010). All predictors were centred by dividing them by two standard deviations (Gelman, 2008; Grueber, Nakagawa, Laws, & Jamieson, 2011). We identified outliers as data with Cook's distance >1 and excluded them from the analysis. To

TABLE 1 GIS-based predictor variables, data sources and associated hypotheses regarding their influence on livestock depredation by leopard and wolf in the Hyrcanian forest

Variable	Source	Hypothesis	Reference
Mean distance to village	www.google.com/earth	Larger distance to villages will reduce protection of livestock, thus increasing livestock depredation	Miller (2015)
Mean elevation	http://glovis.usgs.gov	Availability of sheep/goat increases with elevation and availability of cattle decreases with elevation	Miller (2015)
Forest cover	www.earthEnv.org	Higher proportion of forest cover increases livestock depredation due to more cover for leopards and reduces for wolves	Miller (2015)
IUCN categories of reserves	www.protectedplanet.net, World Database of Protected Areas	Higher protection status reduces depletion of wild prey through illegal hunting of ungulates thus indirectly reducing livestock depredation	Miller (2015)

account for imperfect detection of depredation events and to address underestimation of these events with lower sampling effort, we denoted effort_i as an offset in each cell_i (Kery & Royle, 2016). Finally, we modelled the numbers of depredation events for each carnivore as:

$$C_i \sim \text{Poisson}(\text{Effort}_i * \lambda_i)$$

For each grid cell_i, the observed count of depredation events C_i was modelled as a Poisson process, effort (km walked per cell_i) was denoted as an offset, and λ_i was the expected count of depredation events per km in cell_i.

The GLMs represented the following models:

$$\log(\text{Effort}_i * \lambda_i) = \beta_0 \cdot \log(\text{Effort}_i) + \alpha + \beta_1 \cdot x_{\text{poaching},i} + \beta_2 \cdot x_{\text{forest},i}$$
$$+ \beta_3 \cdot x_{\text{reddeer},i} + \beta_4 \cdot x_{\text{roedeer},i} + \beta_5 \cdot x_{\text{boar},i} + \beta_6 \cdot x_{\text{shoat},i}$$
$$+ \beta_7 \cdot x_{\text{IUCN},i} + \beta_8 \cdot x_{\text{DV},i} + \beta_9 \cdot x_{\text{Elevation},i}$$

with α as the intercept and β_n as the coefficients estimated for the offset $\beta_0 = 1$. We measured the goodness-of-fit of the models with McFadden pseudo-R^2 using the PSCL package in R (version 3.3.2, R Core Team, 2016). We used an information-theoretic approach to evaluate models based on quasi-Akaike's Information Criterion corrected for small sample size (QAIC_c) to control for overdispersion (Grueber et al., 2011). For our final inferences, we further applied multi-model averaging in the MuMIn package for R (Grueber et al., 2011) and used candidate models with ΔQAIC <2 using. We considered predictors as significant if their 95% confidence intervals (CI) did not overlap with zero. We measured the relative variable importance (RI; Figure 3) by QAIC_c-weighted standardized coefficients of the original model (Grueber et al., 2011). We calculated the odds ratio $\exp(\beta)$ to quantify the effect size of predictors on the response variables (Table S1). We used Spearman's rho correlation coefficient to measure the relationship between illegal hunting of ungulates and wild prey occurrences. Additionally, we performed ANOVA Tukey's HSD test using MULTCOMP package in R to compare the encounter rates of ungulate poaching and numbers of depredation events between study sites. Finally, we applied ANOVA to compare the numbers of depredation events between different seasons.

2.7 | Sensitivity analysis

Much of our data on depredation rates stemmed from herders and there was no baseline data that could help us in estimating potential bias of herders' reports. Thus, we cannot quantify the accuracy of the collected survey data, but have no reason to believe that any systematic bias could be present in this data. However, reports from herders might not be precise, for example because livestock found dead might incorrectly be classified as predator kill, or because the predator responsible for an actual kill might not have been identified correctly by the herders. To assess the sensitivity of our inferences to such potential imprecisions, we conducted a sensitivity analysis for our models. Specifically, we simulated 99-fold replications of response variables by adding or substracting a random number drawn from a Poisson distribution to the approximate mean of observed depredation events data (with $\lambda = 0.2$). Through these simulations, we wanted to test if the estimates of predictors change compared to the original model. If relative importance of a variable did not change a great deal in these simulation models (i.e. still did not overlap zero; see above), we assumed that variable importance was not simply caused by potential imprecision and that the variable actually had an effect on depredation rates. We refer to the models produced by the sensitivity analysis as simulation models.

3 | RESULTS

Leopards were reported to kill mainly cattle (79%, $n = 115$) compared to shoat (21%, $n = 30$) and only one individual per attack regardless of livestock species. In contrast, wolves were reported to kill mainly shoat (96%, $n = 501$) compared to cattle (4%, $n = 23$). On average, wolves were reported to kill 8.64 ± 1.85 shoat and 1.28 ± 0.19 cattle per attack in a total of 58 depredation events. Herders' reports suggested that both carnivores had a narrow spatial overlap in

depredation (14% of grid cells). Leopards were reported to kill 57% of shoat and 37% of cattle outside reserves, but wolves were reported to kill only 22% of shoat and 30% of cattle outside reserves. Of 142 signs of illegal hunting of ungulates, gunshells were the most common ones (66%, $n = 94$), followed by direct sightings (14%, $n = 14$%), fire remains (12%, $n = 17$) and gunshots heard (8%, $n = 11$). Encounter rates of cattle and shoat were inversely and significantly correlated with wild prey species (Table S3). Cattle (rho = 0.31, $p < 0.000$) and shoat signs (rho = 0.36, $p < 0.000$) were positively correlated with signs of illegal hunting of ungulates.

In leopard models, McFadden pseudo-R^2 was 0.37 for the leopard-cattle model and 0.34 for the leopard-shoat model. We excluded six outliers from Lisar PA because leopard is locally extinct there and three outliers from Asas PA, Lafoor NHA and Baliran (Figure 1). Cattle depredation by leopard increased with illegal hunting of ungulates by 2.83 times ($\beta = 1.04$, 95% CI = 0.49–1.59, Figure 2a), shorter distances to villages ($\beta = -3.81$, 95% CI = −5.10 to −2.52), cattle encounters by 1.84 times ($\beta = 0.61$, 95% CI = 0.29–0.93), elevation by 4.09 times ($\beta = 1.05$, 95% CI = 0.67–2.15) and higher IUCN protection status by 1.85 times ($\beta = 0.62$, CI = 0.07–1.71). RI was 1 in original and simulation models for all these predictors, except for IUCN categories where RI was 0.40 (Figure 3a). Shoat depredation by leopard increased with illegal hunting of ungulates by 3.35 times ($\beta = 1.39$, 95% CI = 0.51–2.34), lower red deer encounter rate ($\beta = -6.50$, 95% CI = −11.81 to −1.20), elevation by 3.67 times ($\beta = 1.30$, 95% CI = 0.26–2.34) and lower IUCN protection status ($\beta = -1.44$, 95% CI = −2.60 to −0.28) (Figure 2b). RI was 1 for illegal hunting of ungulates in original and simulation models, but 0.53 for red deer and IUCN categories and 0.03 for elevation in simulation models (Figure 3b). We did not find a significant difference of leopard depredation on cattle ($F = 0.618$, $p = 0.651$) and shoat ($F = 1.092$, $p = 0.367$) between different IUCN categories. Cattle and shoat depredation by leopard did not differ between seasons (cattle; $F = 2.685$, $p = 0.054$; shoat; $F = 1.626$, $p = 0.217$).

In wolf models, McFadden pseudo-R^2 was 0.29 for the wolf-shoat model and 0.18 for the wolf-cattle model. We excluded three outliers from Baliran, Aliabad and Alasht (Figure 1) and a predictor of red deer encounter rate because of its multicollinearity (VIF = 3.11). Cattle depredation by wolf increased with illegal hunting of ungulates by 3.35 times ($\beta = 1.21$, 95% CI = 0.34–2.09) and IUCN categories by 3.70 times ($\beta = 1.31$, 95% CI = 0.03–2.59) (Figure 2c). RI was 1 for illegal hunting of ungulates, but 0.67 for IUCN categories in simulation models (Figure 3c). Shoat depredation by wolf increased with illegal hunting of ungulates by 2.59 times ($\beta = 0.95$, 95% CI = 0.50–1.41), less forest ($\beta = -1.47$, 95% CI = −2.54 to −0.40), shorter distance to villages ($\beta = -1.15$, 95% CI = −1.99 to 0.31) and
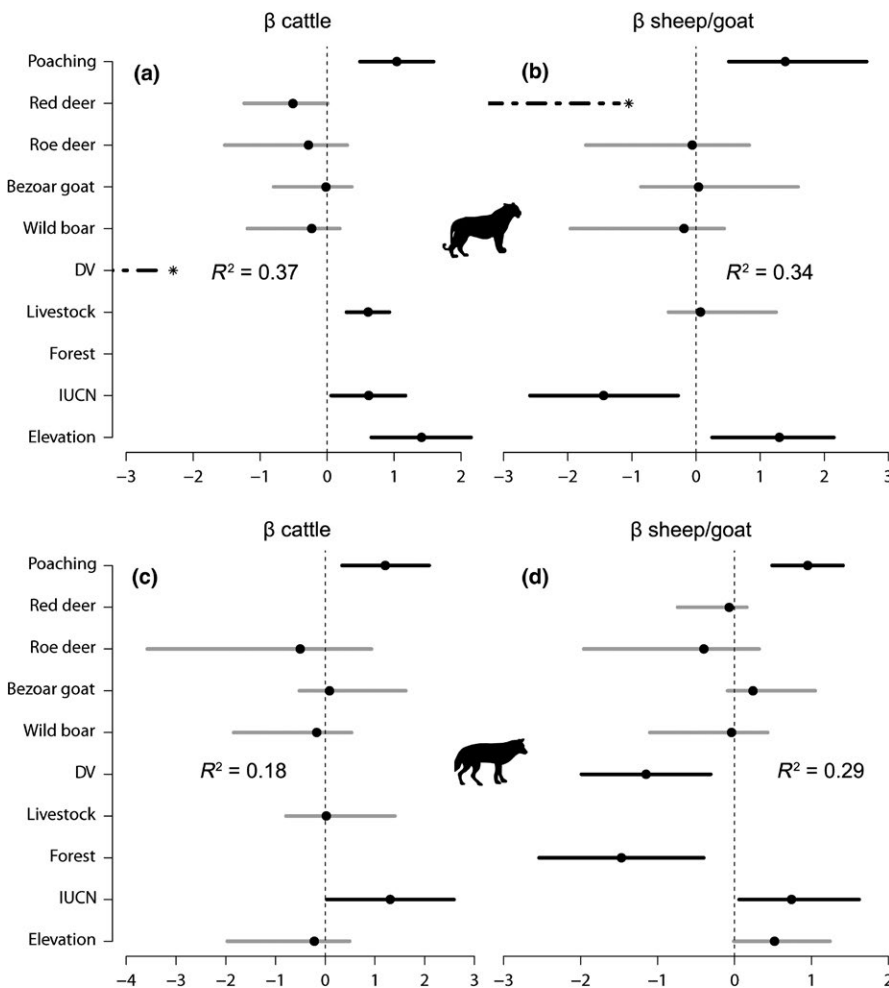
FIGURE 2 Effect sizes (β, black dots) of GLMs after model averaging showing the effects of predictors on livestock depredation by the leopard (a—cattle, b—sheep/goat) and the grey wolf (c—cattle, d—sheep/goat) in the Hyrcanian forest, Iran. Bars around the estimates show a 95% confidence interval, with black bars not overlapping zero. The asterisk (*) indicates that the mean and confidence interval exceed the scale of the figure. DV: distance to village; forest: forest cover; IUCN: protection status of reserves defined by the International Union for Conservation of Nature. The term poaching in the figure refers to illegal hunting of ungulates

IUCN protection status by 2.10 times (β = 0.74, 95% CI = 0.06–1.63) (Figure 2d). RI was 1 for illegal hunting of ungulates and forest, 0.96 for distance to villages and 0.09 for IUCN protection status in simulation models (Figure 3d). Wolf depredation on shoat was significantly higher in PA vs. NHA (F = 4.545, p = 0.019) while wolf depredation on cattle did not differ between IUCN categories (F = 1.05, p = 0.386). Wolf depredation on cattle and shoat did not differ between seasons (cattle: F = 1.014, p = 0.363; shoat: F = 1.626, p = 0.217). Encounter rates of red and roe deer were negatively correlated with encounter rates of signs of illegal hunting of ungulates (Spearman's rho = −0.22, p = 0.027 and rho = −0.25, p = 0.016, respectively).

4 | DISCUSSION

The illegal hunting of ungulates is a cryptic activity that is notoriously difficult to study (Ghoddousi, Soofi, Hamidi, Leumetsberger, et al., 2017; Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017; Laurance et al., 2008; Milner-Gulland et al., 2003). In this paper we address illegal hunting of ungulates in the reserves of the Hyrcanian forest using indirect and direct signs of ungulate poaching. Most commonly, ungulate poaching was detected in the form of gunshells, while fire remains, direct evidence of poaching and gunshots heard were rarely detectable.

We show that an increase in the encounter rate of these poaching signs was associated with a decrease in prey occurrence, which in turn was linked to higher levels of livestock depredation. This pattern was consistent even when we re-analysed data with the exclusion of

the 27 cells which were surveyed only once. Illegal hunting of ungulates was the most influential variable on depredation and its effect size was consistent across all models. More specifically, an increase in the occurrence of illegal hunting of ungulates by one sign per kilometre increased the odds of cattle and shoat depredation rates by leopard and wolf by 3–4 times.

In our study, decreasing red deer availability was significantly associated with increased depredation on shoats by leopards, though the effect size was low. This may result from the fact that red deer are mostly scattered in highlands and live at low densities because of poaching pressure (Kiabi et al., 2004; Soofi, Ghoddousi, et al., 2017). As a result, red deer have low detection rates (Soofi et al., 2018b), but shoat have higher relative abundance at these elevations (Ghoddousi et al., 2016; Imbert et al., 2016). This partially supports the hypothesis by Khorozyan et al. (2015) that large carnivores increase depredation on livestock, such as cattle, sheep and goats, when wild prey abundance is low. Our models indicate that depredation notably increased by leopards in higher elevations, particularly in areas of higher protection levels (IUCN categories II and IV vs. V), higher cattle abundance and lower red deer encounters. It is evident that in the Hyrcanian forest livestock numbering about 4 million heads outnumber wild prey (Sagheb-Talebi et al., 2014).

Likewise, we also found wolf depredation on both shoat and cattle, to increase in areas of higher protection levels. But in absolute terms, the majority of shoat depredation events occurred in the many category V reserves. Out of all study sites, only three had all four species of wild prey, while the other 15 sites lost 1–3 species.
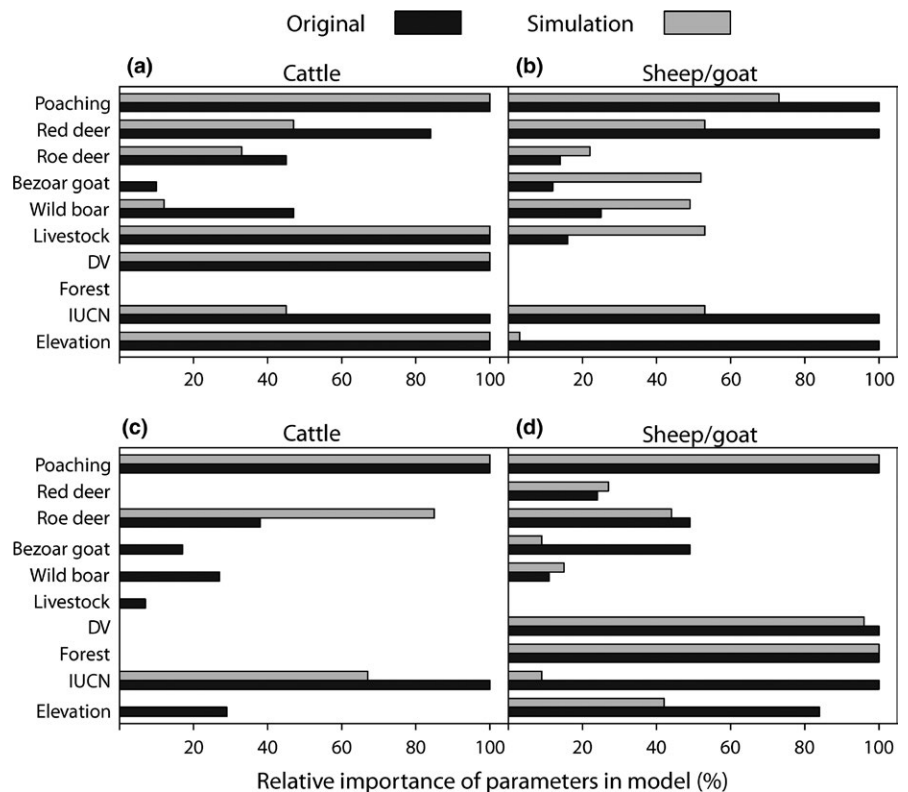
FIGURE 3 Relative importance of predictors in original and simulation models for leopard (a cattle, b—sheep/goat) and wolf (c—cattle, d—sheep/goat) in the Hyrcanian forest. The term poaching in the figure refers to illegal hunting of ungulates

This result may reflect severe local defaunation of reserves in the Hyrcanian forest range.

Wolf depredation on shoat was negatively associated with forest cover, but leopard depredation did not depend on landscapes. We found that leopard depredation on cattle and wolf depredation on shoat was higher in proximity to villages, perhaps because livestock are mostly scattered over the mountainsides and rugged areas near villages where wild prey is less abundant due to human activities (Soofi et al., 2018b).

As expected, leopards were more likely to prey on cattle and wolves tended to prey more on sheep/goat which confirms the differences in the predation strategies of these carnivores: open areas are generally more suitable for wolves which are cursorial predators (Uboni, Smith, Stahler, & Vucetich, 2017), preferring open areas to hunt and killing shoat in open pastures (Behdarvand et al., 2014; Treves et al., 2004). Leopards preyed substantially more on cattle perhaps because cattle were more likely to graze in forest habitat, which is suitable for ambush hunting by leopards. Overall, the power of our models to assess livestock depredation by carnivores varied, especially for the wolf-cattle model, suggesting that in certain conditions other predictors can be important (Treves et al., 2004). A recent study by Ekernas et al. (2017) found that pastoralists in Mongolia increased livestock densities, which, in turn, led to increasing wolf densities and depredation by wolves. In our study, we did not obtain such a clear evidence of a strong relationship between wild prey abundance and livestock depredation, with the exception of a negative association between red deer occurrence and shoat depredation by leopard.

Our results are globally important for mitigation of HCC as they show the large-scale effects of illegal killing of ungulates on livestock depredation. A recent large-scale study also confirms that red deer, roe deer and leopard face strong fragmentation of their distribution areas due to multiplicative effects of anthropogenic threats (Soofi et al., 2018b). Prey recovery and livestock protection plans should be set up especially in areas experiencing high defaunation and which are of high importance for landscape connectivity (Soofi et al., 2018a). For example, disappearance of leopard in Lisar Protected Area threatens the survival of the leopard population in the Caucasus where this species is critically endangered or locally extinct (Breitenmoser et al., 2017).

Overall, our study shows that in the Hyrcanian forest recent intensive illegal hunting of ungulates is coupled inversely with wild prey abundance, with livestock becoming hyperabundant in most localities and leading to high livestock depredation (Babrgir et al., 2017; Khorozyan et al., 2017). The Caspian red deer and roe deer are now extinct from the western parts of the Hyrcanian forest, are only patchily distributed in some reserves and continue to suffer from high levels of illegal killing of ungulates (Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017; Kiabi et al., 2004; Soofi, Egli, et al., 2017; Soofi, Ghoddousi, et al., 2017). The red deer population in Iran may number only around one-fifth of its population size in 1977 (784 vs. 4,350, Kiabi et al., 2004; Soofi, Egli, et al., 2017). Also the bezoar goat increasingly retreats into inaccessible rocky areas and is globally vulnerable (Ghoddousi, Soofi, Hamidi, Ashayeri, et al., 2017; Weinberg et al., 2008). The wild boar is the only abundant prey in the Hyrcanian forest and hunting of this species is rare due to Muslim religious beliefs (Ghoddousi, Soofi, Hamidi, Leumetsberger, et al., 2017).

The high number of signs of illegal hunting in IUCN category V reserves (protected area) implies that enforcement measures have failed so far to curb poaching of ungulates in these areas. A long history of illegal hunting of ungulates and livestock grazing makes it difficult to clearly disentangle their impacts on wild prey abundance. We were not able to account for livestock grazing impacts on wild prey in our modelling which is a caveat to our study. Although, for all wild prey species, we found a negative correlation with livestock abundance, while livestock was positively related to signs of illegal hunting. These correlates may indicate that current livestock grazing facilitates ungulate poaching and additively affects wild prey abundance and depredation risks. That livestock grazing is widespread in category V reserves raises a serious concern as these protected areas cover 66% of all officially protected lands in the Hyrcanian forest. Moreover, overgrazing is common even within national parks (Makhdoum, 2008; Soofi et al., 2018b). Nevertheless, national parks of category II apply the most stringent control of illegal hunting of ungulates and grazing, but they cover only 0.01% of protected lands in the Hyrcanian forest (Soofi et al., 2018b).

Overall, our study is among the first to show that a complex but measurable relationship exists between illegal hunting, wild prey and livestock depredation. Results show the need for conflict mitigation plans alongside the combat against poaching and prey recovery initiatives. Provisions to protect livestock will also have to address differences in the ecology of leopard and wolf depredation, as well as livestock grazing patterns and landscape structure. Our research also shows that there is an urgent need to conduct research on the root causes of illegal hunting to help minimize HCC in the region.

AUTHORS' CONTRIBUTIONS

M.S., A.G., S.S., L.E., B.K., I.K., M.W. and N.B. conceived the ideas and designed methodology; M.S., A.J., M.S., M.A., A.Q., T.G., A.G. and T.Z. collected the data; M.S., T.Z. and N.B. analysed the data; M.S., M.W., N.B. and I.K. led the writing of the manuscript. All

authors contributed critically to the drafts and gave final approval for publication.

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