A novel application of hierarchical modeling to decouple sampling artifacts from socio-ecological effects on poaching intensity

Abstract

Poaching is a global driver of wildlife population decline, including inside protected areas (PAs). Reducing poaching requires an understanding of its cryptic drivers and accurately quantifying poaching scales and intensity. There is little quantification of how poaching is affected by law enforcement intensity (e.g., ranger stations) versus economic factors (e.g., unemployment), while simultaneously accounting for imperfect detection. Using extensive data of poaching events (i.e., seizures) and censuses of nine ungulate species across the PAs and unprotected lands of Iran from 2010 to 2018, we developed a single-visit hierarchical (N-mixture) model to accurately estimate annual poaching of Iranian ungulates and to differentiate between social and ecological effects on annual poaching intensity. We found that poaching detectability increased with numbers of ranger stations. A recent surge in poaching (2013-2018) coincides with rising unemployment rate. We estimated that 19727 ungulates (95% confidence interval 11178–36195) were poached across the country during 2010-2018. Poaching intensity was positively related to unemployment rate, road density, and ungulate abundance. Our simulations demonstrated that the Poisson and Negative binomial N-mixture models had adequate performance when the conditions of Sólymos et al. (2012) were satisfied, in particular, when at least one covariate is unique to both the detection and abundance parts of the model. Overall, we suggest that single-visit models offer unique insights into

understanding the link between poaching intensity, economic conditions, and law enforcement in large-scale landscapes while accounting for imperfect detection of poaching events.

Keywords: Economic status, illegal killing, large mammals, N-mixture model, protected areas, ranger station

1. Introduction

Illegal exploitation of wildlife is occurring at an unprecedented rate and is a leading driver of global population declines and local extinctions of wildlife (Dirzo et al., 2014; Ripple et al. 2015). The unlawful harvest of wildlife (hereafter poaching) takes multiple forms, typically being undertaken by locals with a variety of motivations (Montgomery, 2020). However, economic factors tend to predict illegal activities better than approaches based solely on environmental variables (Wittemyer et al., 2011; Challender and MacMillan, 2014). Specifically, the unemployment rate is a key metric, representing the state of economic growth and development in a region (Mohseni & Jouzaryan, 2016). This metric serves as a useful proxy for assessing and understanding illegal exploitation rates (Dobson and Lysane, 2008; Wittemyer et al., 2011). Barnes et al. (2016), for instance, analysed historical data indicating that populations of large mammals could increase in countries with stable economic conditions despite high human population densities.

Poaching is also facilitated by the presence of roads allowing human access to remote areas (Benítez-López et al., 2017, Carter, 2020). Road access has exposed wildlife, regardless of remoteness, to modern hunting techniques, including firearms, motor vehicles, and, or, snares, markedly expediting the intensity of poaching in many areas (Carter et al., 2020). Globally, but especially in Asian countries, road networks are rapidly growing, contributing significantly to large mammal population declines by reducing habitat quality even within protected areas (hereafter PAs) and increasing

poaching exposure (Carter et al., 2020).

Despite its detrimental effects on wildlife populations, few studies have examined the relationship of poaching events (i.e., counts of seizures) with both the efficacy of law enforcement (e.g., number of ranger stations) and economic trends (e.g., unemployment rate) (Milner-Gulland et al., 2003, Dobson and Lysane, 2008, Wittemyer et al., 2014). Particularly in southwest Asia, data on poaching are only locally available (Soofi et al., 2018; Ghoddousi et al., 2019) and may be reported in a non-systematic manner during regular wildlife patrols by rangers (Egli, 2015).

PAs play a fundamental role in protecting biodiversity from illegal exploitation (Watson, Dudley, Sharma et al. 2014; Segan and Hockings, 2014). To be effective for species conservation, wildlife populations within PAs require regular monitoring at an appropriate scale and frequency to detect any changes in key parameters (Nichols and Williams, 2006). The management of PAs requires law enforcement to halt poaching activities (Hilborn et al., 2006). However, PA managers typically are hindered in this task by multiple barriers, including inadequate resources (e.g., ranger stations, rangers), economic instability (e.g., unemployment, poverty; Ghoddousi et al., 2017), and insufficient strategies for addressing poaching problems (Milner-Gulland et al., 2003). Many of these challenges arise from the clandestine nature of poaching, making its detection notoriously difficult and costly (Wittemyer et al., 2014). In Africa and Asia, law enforcement interventions to detect and control poaching typically involve active patrols by armed rangers who are usually based in nearby ranger stations (Critchlow et

al., 2017). Provision of rangers can be the single highest expenditure of many PAs (Moore et al., 2014; Plumptre et al., 2014). If it occurs, poaching may likely be frequently detected in areas that hold an adequate coverage of active ranger stations (Plumptre et al., 2014, Ghoddousi et al., 2019); however, it may remain undetected if enforcement is insufficient or lacking (Soofi et al., 2018).

A critical challenge to understanding causes and effects of poaching is the difficulty in measuring it accurately and in an unbiased way (Burn et al., 2011; Marescot et al., 2019). Importantly, due to its illegality and social context, poaching events are seldom detected perfectly, leading to negatively biased observations of poaching seizures. Thus, spatial counts of poaching events represent a negatively biased representation of the true frequency of events. Moreover, spatial and temporal heterogeneity in the probability of detecting poaching events is expected due to variation in social and ecological factors. Thus one cannot expect the count of individual poaching events to be an unbiased index of poaching intensity. Absolute poaching assessment methods are often not cost-effective, especially at large spatial scales.

In the past decades, multiple statistical methods have been developed to account for imperfect detection in sampling wildlife populations (e.g., Pollock, 1974; Otis et al., 1975; MacKenzie et al., 2002; Royle, 2004, Kéry and Royle, 2016). So far, these methods have not been routinely applied to the analysis of poaching data. In the context of poaching, a series of studies have relied on relative differences in counts or on occurrence (detection/non-detection) data of poaching while accounting for detection

errors (Sharma et al., 2014; Marescot et al., 2019). Royle (2004) proposed an alternative approach that is known as the N-mixture model, a model that takes biased counts of events collected across multiple spatial units and simultaneously estimates both detection and abundance. This class of model enables estimation of animal population abundance over time and space (Sólymos et al., 2012).

Here, we apply a single-visit N-mixture model to estimate the true number of poaching events for a given year and spatial unit (Royle 2004; Sólymos et al., 2012). The model regards the true number of poaching events as a latent variable (analogous to population size in the classical use of the N-mixture model) and estimates the latent quantity using observed counts of seizures biased by imperfect detection. The model accommodates explicit covariates in both the 'abundance' (i.e., true number of poaching events, *N*) model and the model describing variation in the detection (p) of poaching events (Sharma et al., 2014; O'Kelly et al., 2018), even if such covariates affect both abundance and detection (Kéry, 2018). Earlier studies have demonstrated that hierarchical models for single-visit surveys are identifiable when covariates for both detection and abundance parameters are available, with at least one distinct ("private") covariate for each (Lele and Byne, 2012, Sólymos et al., 2012; Kéry, 2018).

122 In this study, we use an extensive dataset of seizures of illegal killing of ten ungulate
123 species across protected and unprotected areas of Iran based on media reports. We
124 combine these data with ranger-collected census data, as well as several socioeconomic
125 variables. We use the single-visit N-mixture model (Sólymos et al., 2012; Kéry and
126 Royle, 2021) to estimate the effects of PAs, unemployment rate, and ungulate population
127 abundance on poaching intensity and effects of ranger stations and elevation on detection
128 of poaching events across all species from 2010 to 2018, while simultaneously
129 accounting for imperfect detection. In addition, we quantify law enforcement efforts in
130 PAs, systematically describe poaching events and quantify population trajectories of the
131 study species.

132 ## 2. Materials and Methods

133 ### 2.1. Study area and focal species

134 Iran is a country located in southwest Asia that covers an area of ~1,648,195 km^2 and
135 contains portions of the Palearctic, Saharo-Arabian, and Oriental zoogeographic realms.
136 The country includes a wide range of habitat types (Yusefi et al., 2019), and it contains
137 two major mountain ranges, the Alborz Mountains in the north and the Zagros Mountains
138 in the south (Figure 1a). Since 1957, the establishment of PAs in Iran increased rapidly to
139 11% of its land area (Iran Department of Environment, hereafter DoE, www.doe.ir;
140 Figure 1b). The PA system in Iran is composed of four IUCN-based (International Union
141 for Conservation of Nature) categories: national parks (NP, Cat. II), natural monuments
142 (Cat. III), wildlife refuges (WR, Cat. IV), and protected areas (PA, Cat. V). No-hunting

areas (NHAs) is a country-specific (non-IUCN) reserve type created by the DoE in the 1990s, with the aim of population recovery of threatened species (Darvishsefat 2006; Figure 1b). Iran has a wide variety of mammalian herbivores threatened by poaching, of which nine species we focus on in this article. The species arranged by family are; Bovidae: – urial (*Ovis vignei* Blyth, 1841), mouflon (*Ovis gmelini*, Blyth, 1841), central Alborz red sheep, a hybrid population (*O. vignei* × *O. gmelini*) 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); Cervidae: Persian fallow deer (*Dama mesopotamica* Brooke, 1875), Caspian red deer or maral (*Cervus elaphus* ssp. *maral* Gray, 1850), roe deer (*Capreolus capreolus* Linnaeus 1758); and Equidae: onager (*Equus hemionus* ssp. *onager* Boddaert, 1785) (Yusefi et al., 2019) (Figure 2).

2.2. Response variable

We systematically compiled data on known poaching events (seizures) of the focal species by searching keywords (in Persian) in the Google search engine, including all combinations of 'poaching,' 'poacher,' 'arrest of poachers,' 'shooting,' in Iranian national and international media news websites during 2005 to 2019 (see Table A1). These searches included events at the city, county, and province levels. We registered and georeferenced the location of every poaching event using Google Earth Pro. Across all studied species, we pooled poaching event data and used the observed count of poaching events as the response variable. A 'poaching event' here refers to an occasion where

rangers caught the poachers in the act of killing or capturing animals over a particular time during patrols inside a PA or an occasion where poached animals were confiscated at the residence of poachers (as defined by Montgomery (2020)). Data on the number of killed animals (e.g., female and male animal and age groups) were included when available. Additionally, we recorded the method of capture used for each poaching event (i.e., firearm, steel trap, chase and capture by motorcycle, live trapping of newborns, or hunting dogs).

2.3. Statistical Modeling

We regard the observed count of poaching events $C_{i,t}$ as a binomial random variable with parameter '*p*' being the probability that a poaching event is reported and with binomial sample size $N_{i,t}$ being the true but unknown "population size" of poaching events. This conceptual view is consistent with the N-mixture model (Royle 2004) but, since we have only a single count for each year, the situation is equivalent to the single-visit N-mixture model (Sólymos et al., 2012).

The N-mixture model is a hierarchical model consisting of two components. The first component is the ecological model describing variation in the latent (unobserved) population size $N_{i,t}$, which in the present context is the true but unobserved frequency of poaching events:

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

where, N_i is the latent poaching state in cell i $\{i = 1, 2, 3, \ldots, M\}$ and $\lambda_{i,t}$ was the expected count of poaching events in cell i and year t. We model covariate effects on the log-transformed $N_{i,t}$ (see below). In addition to the Poisson event frequency model, we also consider a negative binomial (NB) distribution and compare the two models using Akaike Information Criterion (AIC). The second component of the model is a binomial thinning model in which we assume that the observed number of poached animals is a binomial random variable:

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

where $C_{i,t}$ *is* the number of observed poaching events in cell i during year t, and p is the detection probability for each individual poaching event. We model covariate effects that describe variation in detection probability on the logit-transformed parameter. The models were fitted in the R package 'unmarked' (Fiske and Chandler, 2011).

2.4. Covariates

To spatially assign the counts of poaching events into PAs and unprotected areas, we superimposed grid cells of 20 × 20 km^2 throughout Iran. Poaching events ($C_{i,t}$) were extracted per grid cell (i) across years (t). The choice of cell size was an approximate compromise between: (a) patrolling efforts (ca. 20 km) of rangers (e.g., using car, horse riding, foot patrols) around their assigned ranger stations, (b) and movement patterns of poachers, which tend to hunt animals mainly in areas nearby their settlements (Ghoddousi et al., 2016; Marescot et al., 2019).

2.4.1. Covariates on abundance (*N*)

We included protected area size (IUCN categories including NHAs and unprotected areas) since poaching pressure may vary with reserve size (Daskin and Pringle, 2018). We further extracted human population density from the Gridded Population of the World v.4 at a 1-km spatial resolution (data from the Socioeconomic Data and Application Center http://sedac.ciesin.columbia.edu/data/se). These data were available for 2005, 2010, 2012, and 2015. We included human population density as a covariate on *N* as it has been linked to higher exploitation of wildlife (Daskin and Pringle, 2018). We obtained unemployment rates from 2005 to 2018 from the Ministry of Economic Affairs and Finance (www.databank.mefa.ir) of Iran and included all people aged >15-yr not employed or self-employed during the reference week. We included unemployment rate since economic downturns can lead to escalation of wildlife poaching (Wittemyer et al., 2011).

We obtained the site-specific ranger-collected population census data of nine species from 2010 to 2019 both inside and outside of the PAs (DoE). We used annual count data (censuses) routinely provided by rangers within each PA in winter (November-December). During censuses, the areas are divided into distinct sampling routes that are surveyed by at least 2-3 experienced rangers. Depending on the area of the PA, surveys

222 take approximately 1-3 days (Egli, 2015). We assumed that poaching might often occur
223 in areas with higher ungulate density (Brodie et al., 2015).

224 2.4.2. Covariate on detection and abundance (p, N)

225 We included covariates that affected both p and N. We obtained ranger station data from
226 Iran's atlas of PAs (Darvishsefat, 2006; DoE 2021; Figure 1c), and refined them through
227 personal correspondence with Iranian rangers, conservationists and scientific experts. We
228 included the number of ranger stations (in each cell) since it has been shown that ranger
229 stations have been coupled with higher law enforcement measures and detection of illegal
230 activities (Critchlow et al., 2017; Ghoddousi et al., 2019; Shokri et al. 2020).

231 To account for the effects of terrain on poaching events (Brodie et al., 2015), we included
232 mean elevation from a 30-m resolution digital elevation model obtained from the NASA
233 Shuttle Radar Topography Mission (https://search.earthdata.nasa.gov). We included
234 elevation because we assumed that elevation might affect the patrol efforts of rangers
235 and, therefore, may lead to lower capture rates. We also assumed that elevation might
236 influence poaching intensity since poachers often focus on areas where animal abundance
237 is higher (Brodie et al., 2015). Additionally, we considered the possibility of a quadratic
238 effect of elevation to allow non-linear change due to variations of poaching events in
239 gradients of elevation (Critchlow et al., 2017). We also measured the total road density
240 per cell from Open Street Map data (including motorways, primary roads, secondary
241 roads, tertiary roads, trunks, and corresponding link roads from

http://download.geofabrik.de/ and https://extract.bbbike.org/; Figure 1d; 2018). We used this variable since roads are known to facilitate poaching activities (and hence N) and may also influence detectability of poachers by rangers (Benítez-López et al., 2017).

We checked for multicollinearity among covariates and excluded variables for which Spearman's correlation coefficients were |rho| $r \geq 0.70$. All site covariates were standardized; as for the survey covariates, the unemployment rate was centered, and the square root, as well as log transformation, were applied to ungulate abundances and road density, which were highly skewed. Finally, the ranger station variable was used on its natural scale ranging from 0 ranger stations to 17 (per cell). We restricted our poaching data to the years from 2010 through 2018; this allowed us to improve the consistency and matching (year) of the explanatory variables. All the spatial data preparations were performed in ArcGIS v.10.7.1 (ESRI 2016).

2.5. Single-visit N-mixture model assumptions

The N-mixture model has several important assumptions that must be met for the approach to be used effectively and reliably. The first assumption is that local populations of the focal species are closed during sampling. That is, population size must not change between repeated samples (Royle 2004). This assumption is satisfied in the single-visit N-mixture design because the sampling is instantaneous. In addition, the single-visit N-mixture model requires that at least one unique covariate is available for both detection (p) and abundance (N) submodels (Sólymos et al. 2012).

2.6. Model Selection

We kept at least one unique covariate in both detection submodel (ranger stations) and the abundance model (linear effects of four different IUCN categories, ungulate abundance, unemployment rate and human population density). We then simultaneously expanded both submodels by including common covariates (elevation, road density), and then considered models with quadratic effect (elevation^2) and a year intercept on abundance submodel (*N*). In addition, we also allowed the detection (*p*) intercept to vary among years (alpha0) (Kéry and Royle, 2021). Finally, we considered the best model according to AIC. Thus, the most global model for each parameter was:

$$\log(\lambda_{i,t}) = \beta_{0,t} + \beta_1 . x_{national\ park,i} + \beta_2 . x_{wildlife\ refuge,i} + \beta_3 . x_{protected\ area,i} + \beta_4 . x_{no\text{-}hunting\ area,i} + \beta_5 . x_{elevation,i} + \beta_6 . x_{elevation\hat{}2,i} + \beta_7 . x_{road\ density,i} + \beta_9 . x_{unemployment,i,t} + \beta_{10} . x_{ungulate\ abundance,i,t} + \beta_{11} . x_{ranger\ stations,i}$$

and

$$\text{logit}(p_{i,t}) = \alpha_{0,t} + \alpha_1 . x_{elevation,i,t} + \alpha_2 . x_{road\ density,i,t} + \alpha_3 . x_{ranger\ stations,i}$$

We selected the candidate models according to AIC using the 'AICcmodavg' R package (Mazerolle, 2019). We carried out a bootstrap goodness-of-fit analysis with 99 iterations (Kéry and Royle, 2020). We considered the effect size as significant if the 95% (CI) of the mean coefficient did not overlap with zero (Kéry and Royle 2016).

281 2.7. Quantifying expected number of poached ungulates annually

282 We estimated the annual mean number of 'poaching events' per grid cell by
283 exponentiating both the intercept estimated for each year plus the beta coefficients of the
284 covariates in the best-fitting model. We multiplied the sum of the resultant value by the
285 total number of cells (1 to 3931). Finally, we calculated the annual total 'poached
286 animals' by multiplying the mean (1.74 SD = 1.46; CIs) poached animals per poaching
287 event by the total 'poaching events' (Table 1).

288 2.8. Model identifiability

289 Knape and Korner-Nievergelt (2015) have argued that the detection probabilities in
290 single-visit surveys could be non-identifiable and that absolute abundances cannot be
291 estimated when log-link functions for both expected abundance and detection probability
292 are employed. Kéry (2018) later recommended that the negative binomial N-mixture
293 model must be examined for identifiability of the parameters. We, therefore, examined
294 the sensitivity of the best-fitting model parameters over varying levels of likelihood
295 truncation in the calculation of the marginal likelihood (i.e., K = 107, K = 200, K = 400)
296 recommended by Kéry (2018) and Kéry and Royle (2021). This approach ensures that the
297 maximum likelihood estimates are not on the boundary of the parameter space (i.e., with
298 infinite abundance and zero detection; Dennis et al., 2015). We compared the AIC of
299 these best-fitting models with an increased value of K.

300 2.9. Simulation study

To evaluate the ability of our model to estimate true poaching intensity from biased counts, we conducted several simulation scenarios. We simulated data under the following model:

$N_i \sim Poisson\ (\lambda_i)$, with log $(\lambda_i) = \beta_0 + \beta_{1 * unemployment\ rate}$

$C_{ij} | N_i \sim Binomial\ (N_i, p_{ij})$ with logit $(p_{ij}) = a_0 + a_{1 * ranger\ stations}$

For the parameter values, we used those estimated from the data. We fitted three simulations as follows: (1) First, we simulated Negative binomial (NB) data and then fitted the NB model. (2) Next, we simulated Poisson data and then fitted the Poisson model. (3) We also simulated NB data and fitted NB model with moderate over-dispersion parameter ($a = 1$). These simulations were fitted under Poisson distribution in the 'unmarked' R package (Fiske and Chandler 2011), where we regarded the covariates that affected distinctly the detection (a_1) and abundance model (β_1) and ran 200 simulations using all sites (M = 3931, with a single replicate J = 1) (Sólymos et al. 2012; Kéry and Royle, 2016) discreetly for each model. The parameter values for the NB model were: (1) the intercept ($\beta_0 = –1.50$) of the abundance model, unemployment rate ($\beta_1 =$ 2.00), and (2) the intercept ($a_0 = –2.50$) of the detection model, number of ranger stations ($a_1 = 2.00$) and over-dispersion parameter (alpha = –2.25). We did similar parameter settings for the Poisson mixture model ($\beta_0 = 1.25$, $\beta_1 = 2.00$, $a_0 = 2.40$, $a_1 = 1.60$). We also ran NB simulations with a moderate value of the over-dispersion parameter ($a = 1$). For each simulation, we calculated the bias and 95% confidence interval (CI) coverage

for each parameter, that is, the proportion of the CI, which included the true value (Royle 2004). We also calculated the mean estimated total population size (number of poached events in our case) which was compared to the simulated value.

2.7. Population trajectory metrics

We quantified population trajectory metrics for the focal species at two points in time. Historical ungulate abundance data (censuses) came from De-Vos (1975), and modern data (censuses) were from the years 2010-2018. For some species (e.g., maral), we relied on additional literature (Kiabi 1987, Kiabi et al., 2004). Population trajectories (λ) were calculated as the annualized finite rate of population change:
λ[Y2-Y1] = (N[Y2]/N[Y1])^(1/(Y2-Y1)) where Y2 and Y1 are the years in which population abundances were reported. Thus, $\lambda = 1$ indicates a stable population, $\lambda > 1$ denotes a growing population, and $\lambda < 1$ indicates a diminishing trend (Daskin and Pringle, 2018).

2.8. Post-hoc analysis

We compared the differences in poached quantities amongst species seizure records using the Kruskal-Wallis test. Dunn's z-test statistic approximation (1964) with a Bonferroni adjusted p-value was used for pairwise comparisons among multiple groups ('dunn.test' R package) (Dinno, 2017). Lastly, we examined the difference between the number of seizures inside PAs, at poachers' residences, and cases where the poachers escaped using

341 a Wilcoxon rank-sum test. We compared the ratio of the estimated true mean to the mean
342 observed ("media report") data and the yearly mean counts of DoE.

343 3. Results

344 3.2. Single-visit N-mixture model results (*N*)

345 The abundance submodel suggested that the number of poaching events per year
346 increased in each year until it reached a peak in 2014 and then slightly decreased in each
347 subsequent year (Figure 3a). In 2014 we estimated 3701 animals were poached (95% CI
348 2055–6666) throughout Iran (Figure 3a; Supplementary file, Table A2). We found that
349 the unemployment rate had a significant positive effect (β = 1.26, 95% CI 0.51–2.00) on
350 the intensity of poaching (Table 1). Likewise, poaching events increased with greater
351 ungulate abundance (β = 0.08, 95% CI 0.07–0.09) but ranger stations appeared
352 insignificant in determining poaching events (β = –0.08, 95% CI –0.10, 0.07) (Table 1).
353 Road density had a positive (β = 0.22, 95% CI 0.12–0.31) influence on poaching events
354 (Table 1). Elevation had an insignificant influence on poaching events. Poaching
355 intensity increased inside no-hunting areas (β = 0.14, 95% CI 0.07–0.21) and category V
356 areas (β = 0.16, 95% CI 0.09–0.23) (Table 1).

357 Using the 'abundance' (poaching intensity) parameter estimates from the best fitting-
358 model, our estimated total number of poached animals was 19727 (95% CI 11178–
359 36195). The total count of DoE, 15741 poached animals (Figure 3a, Supplementary file,
360 Table A2), was within the confidence interval range of the true estimate. However, the

mean number of yearly poached animals (1749) reported by DoE and our observed mean counts of the media reports (189) both under-counted the true poaching by 20% and 91%, respectively, relative to the model-based estimates, which account for imperfect detection (Figure 3a). The goodness-of-fit results indicate that our NB model fits well. By contrast, the Poisson mixture model did not provide an adequate fit (see Table A3, A4; Figure A1). The results were not changed by increasing K from 107 to 200 and then 400, indicating that the parameters are well estimated and identifiable in the sense of Kéry (2018). Likewise, the AIC of these models were also identical (Table 1, Table A5).

3.3. Single-visit N-mixture model results (p)

Detection probability (p) of poaching events in the best-fitting model positively (β =1.88, 95% CI 0.28, 3.49) increased as the number of ranger stations went up (Table 1; Figure 3b). However, elevation had an insignificant effect on the detection of poaching events (β = 0.22, 95% CI –0.13, 0.57) (Table 1).

3.4. Simulation results

The average true poaching events for the simulated realizations under the Poisson mixture scenario was 10383 (SD = 107). The mean estimated across all 200 simulation realizations was 10454 (SD = 795) poaching events suggesting near unbiasedness for estimating the total population size. The Poisson mixture performed well in terms of CI coverage achieving nearly the nominal 95% coverage for model parameters. Likewise, the NB model yielded good performance with slightly worse CI coverage compared to

381 the Poisson mixture model. Similarly, the true population size of poaching events (8217
382 SD = 177) in the NB model was substantially close to the true poaching events (8230 SD
383 = 96) under the moderate over-dispersion parameter. Although both NB mixtures
384 scenarios led to smaller numbers of true poaching events compared to the Poisson
385 mixture model (Table 2). The estimated effects of number of ranger stations and
386 unemployment rates in all simulation scenarios were nearly unbiased (Table 2; for
387 details, see Supplementary file, Table A6, A7, A8).

388 3.4. Population trajectory metrics

389 The population (censuses) declines experienced by our study species showed
390 considerable interspecific variation (Table 3). The most frequently poached species, the
391 bezoar goat, experienced a decline of 9% ($\lambda = 0.91$) compared to the 1975 estimate
392 (66328 vs. 80000; Table 3). Despite the evidence of poaching, the overall population size
393 of the three wild sheep species appeared to be stable (83597 vs. 75000; $\lambda = 1.06$; Table 3;
394 Figure 4a) compared to historical estimates (De-Vos, 1975). Among the *Ovis* species, the
395 central Alborz red sheep was poached most frequently (Figure 4b). The maral showed the
396 most dramatic decrease in estimated population size, dropping by a 59% compared to the
397 population in 1977 ($\lambda = 0.41$; 747 vs. 5430).

398 3.5. Post-hoc analysis results

399 Our review of media articles over 15 years (n = 2165) provided evidence of 1177
400 poaching events involving nine ungulate species (except fallow deer) and the (hybrid)

central Alborz red sheep (Supplementary file, Figure A2). Across all species, the average poaching intensity was estimated to be ~1.74 individuals (SD = 1.46, 95% CI 1.66–1.82) per poaching event from 2005 to 2019, with no significant change over time. Rangers encountered a total of 2368 poachers during this period, of which 2009 (SD = 2.34, 85%) were apprehended. Among these, 268 poachers had previous convictions.

The mean poacher group size per hunting event was 1.71 (SD = 1.24), and this size did not change significantly across years. The majority of detentions occurred during patrols in and around reserves (n = 775, 66%), whereas 28% of detentions occurred at the poachers' residences (n = 324). Finally, in 0.1% (n = 78) of cases, poachers were able to escape while rangers seized their catches. These proportions were significantly different ($\chi^2 = 658.2$, $P < 0.00$) (Supplementary file, Figure A3).

The 148 terrestrial PAs (Cat. II, IV, V) and 105 NHAs and off-reserve areas included in the analyses had a total of 400 ranger stations (1 per 488.67 km^2) ranging from 0 to 17 stations per area. The category II areas had the greatest coverage of ranger stations (1 per 214.24 km^2) followed by category V (1 per 413.27-km^2), category IV (1 per 897.60 km^2), and NHAs (1 per 771.97-km^2). However, about 39% of all NHAs, consisting of 72% of off-reserve areas and 13% of category V areas, lacked any ranger stations. By contrast, all areas of the strictest IUCN categories (Cat. II, IV) contained ranger stations (range 1-10 stations).

4. Discussion

Overexploitation (including illegal harvest) has been identified as one of the major drivers of defaunation worldwide (Dirzo et al., 2014). Here we used a type of hierarchical model, the single-visit N-mixture model, to examine the factors associated with poaching intensity, given there are only observed counts of poaching events, which are expected to be biased by imperfect and heterogeneous detection rates over space and time. Our results show that poaching intensity increased each year (Figure 5) until it reached a peak in 2014 across the country.

Our single-visit N-mixture model suggests that capture of poachers is positively associated with unemployment rate at the provincial scale. Overall, poaching was widespread across Iran (Figure 6) while strongly affected by the temporal and spatial changes in unemployment rates at provincial scales. An earlier study suggests that the poaching of ungulates in Iran's oldest national park ('Golestan NP') was motivated mainly by poverty, hunting for the meat market, pleasure, tradition, and conflict ('reprisal') with park rangers (Ghoddousi et al., 2019).

A plausible approach to reduce poaching intensity in our study area will be to undertake economic interventions and the allocation of resources that target provinces with high rates of unemployment (Mohesni and Jouzaryan 2016). A similar study on elephant poaching in Africa indicated that elephant poaching could be reduced if corruption and poverty were reduced simultaneously (Hauenstein et al., 2019).

We found that ungulate poaching intensity was positively associated with high road densities, suggesting that roads increase opportunities for poachers to access ungulate populations. Roads are well known to facilitate poaching activities and assist in the transport of meat into urban markets (Benítez-López et al., 2017). We also found evidence that poachers were reported to use motorcycles for capturing species adapted to arid plains, including goitered gazelle, jebeer gazelle, and onager. Nearly 41% of poached gazelle of both species were shot or captured by poachers using motorcycles, underlining the risks posed by extending road networks both inside and outside PAs across Iran. Road development not only increases mortality within PAs through poaching it also potentially reduces the carrying capacity of ungulates populations in PAs (Ripple et al., 2015).

An important finding from our research is that poaching occurred both inside and outside of PAs. However, poaching was most commonplace in higher category V areas and unclassified reserves (i.e., NHAs and unprotected lands). While these reserves (IUCN category V, NHA, and unprotected lands) collectively encompass ~64% of Iran's total protected lands, alarmingly, over 46% of them lacked ranger stations. Thus, ungulate populations in these PAs without ranger stations can be more vulnerable to poaching.

We found no significant association between the strictest IUCN categories (Cat. II, IV) and poaching events. By contrast, despite the large combined area of NHAs (36%), they experienced a high intensity of poaching, suggesting that this category urgently needs

460 enhanced, consistent law enforcement measures and associated infrastructure to
461 effectively limit poaching.

462 Our model highlights that a high detection probability of poaching occurred in areas with
463 the highest number of ranger stations (e.g., with four ranger stations per 400 km^2
464 detection probability of poaching is nearly perfect), suggesting that higher densities of
465 ranger stations do increase patrol presence and law enforcement. Poaching may go
466 undetected in areas where ranger stations are less common, particularly where
467 enforcement measures are inadequate or lacking (Plumptre et al., 2014), which can
468 effectively reduce the size of PAs over time (Dobson and Lysane, 2008). We
469 acknowledge that poaching detectability in practice relies on optimum ranger patrol
470 efforts (Critchlow et al., 2017). We found that poaching intensity was positively
471 associated with high ungulate density. A plausible explanation for this pattern is that local
472 hunters seek out areas with higher ungulate abundances. This process could lead to
473 greater poaching pressures and future local extinctions and declines of ungulate
474 populations in these PAs.

475 Our post-hoc results showed that rangers seized 71% of poachers during anti-poaching
476 patrols within PAs with the remainder of captures (29%) taking place at the poachers'
477 residences. To alleviate poaching pressures, rangers have relied on developing networks
478 of informants around PAs, which has led to increased seizures in poachers' residences.
479 However, this type of capture did not significantly differ from other seizures (i.e.,
480 reserve-caught, escaped poachers). Rangers in Iran also relied on internet applications

481 (e.g., Instagram) for detecting wildlife crimes. Further, the Iranian DoE is seeking to
482 discourage poaching by adopting newly increased fines for wildlife crime (Article 3 [of
483 the hunting law from 1967] was introduced in July 2019). Evidence from elsewhere
484 shows that prevention of poaching is more dependent upon the increased rate of
485 detections rather than harsher sentences (Hilborn et al., 2006, Dobson and Lysane, 2008).
486 Therefore, increased fines should not come with a reduction in detection efforts. Our
487 results suggest that the use of media news to tally total poaching activity tended to
488 undercount the mean true kills by 91%, while the yearly mean counts from the Iranian
489 Department of Environment appeared to underestimate the true poaching rate by 20%.

490 The majority of the ungulate species we assessed showed downward population
491 trajectories over a period from the mid 1970s to censuses carried out in 2010-2018.
492 However, there was considerable variation in population trajectories across species. No
493 poaching of the Persian fallow deer was detected, most likely because the species only
494 persists within captive breeding sites (n = 12). In comparison, despite the rarity of maral,
495 this deer faces notable poaching pressure. As a result, most maral populations occur
496 inside reserves with higher levels of protection (Soofi et al., 2017; Shokri et al., 2020).
497 We acknowledge that these census data may be biased as the total count approach does
498 not accommodate non-detection bias (Egli, 2015), although we believe the interpretation
499 of these data as indices to abundance is reasonable.

500 We conclude that the single-visit N-mixture modelling approach used in this study offers
501 unique insights to disentangle sampling artifacts from socio-ecological effects

influencing poaching intensity and to quantify poaching in large-scale landscapes. However, application of the single-visit N-mixture has several caveats. Knape and Korner-Nievergelt (2015) have argued that the detection probabilities in single-visit sampling are non-identifiable in some cases. For example, absolute abundances cannot be estimated when log-link functions for both expected abundance and detection probability are employed. As a consequence, if the available data were obtained by multi-visit sampling designs, the dynamic N-mixture model would be preferable to the single-visit N-mixture model, since it provides explicit information about detection probability. However, for poaching systems that lack rigorously designed monitoring programs, data collected under such alternative and more informative sampling designs is often uavailable. Thus, the study of poaching processes and their effects in real landscapes requires more intensive model-based procedures such as the single-visit N-mixture model.

Our simulation study suggests that the Poisson and negative binomial N-mixture models both produce approximate unbiased estimates of model parameters and total population size of poaching events. Even, when we regarded the negative binomial mixture with moderate over-dispersion parameter, the results remained unbiased. These patterns are in agreement with earlier findings (Sólymos et al. 2012). Therefore, we suggest that the single-visit N-mixture models can be useful in the monitoring of poaching processes, because it provides a means for correcting detection error, particularly for large-scale and long-term monitoring datasets such as ranger collected data for which multiple visit

523 covariates are rarely available. However, to ensure reliable application of single-visit N-
524 mixture models, it is important that at least one covariate is unique to both the detection
525 (*p*) and abundance (*N*) submodels (Sólymos et al. 2012). In addition, when the negative
526 binomial N-mixture model is being applied, it must be examined for identifiability of the
527 parameters (Kéry 2018). This test ensures that the maximum likelihood estimates are not
528 on the boundary of the parameter space (Dennis et al., 2015).

529 Our results suggest that an increase in law enforcement can improve the detection of
530 poaching events; however, this approach must be combined with the establishment of
531 multiple community based livelihood alternatives if it is to be successful in the long-term
532 (Hoffmann et al. 2015). The current scale of large ungulate poaching in our study area
533 suggests that without a two-pronged focus on law enforcement and community-based
534 economic interventions, large ungulates will continue to decline and may disappear from
535 many areas in our study area in the near future.

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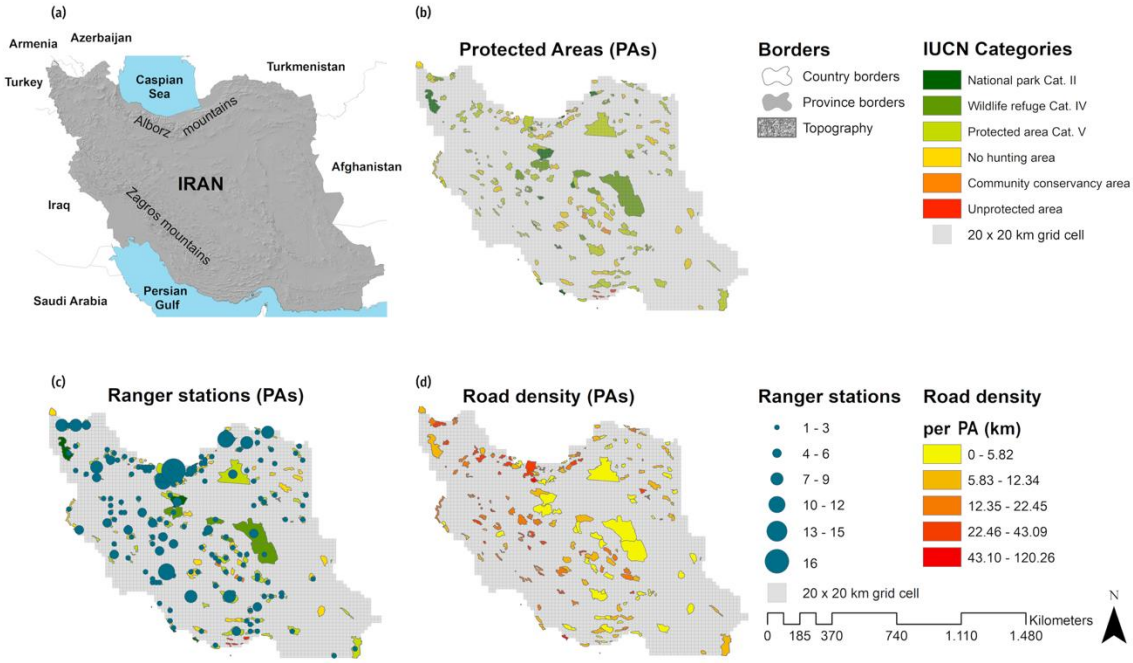

Figure 1. Map of Iran (a), protected areas (b), number of ranger stations (c), and road density across protected areas (d).

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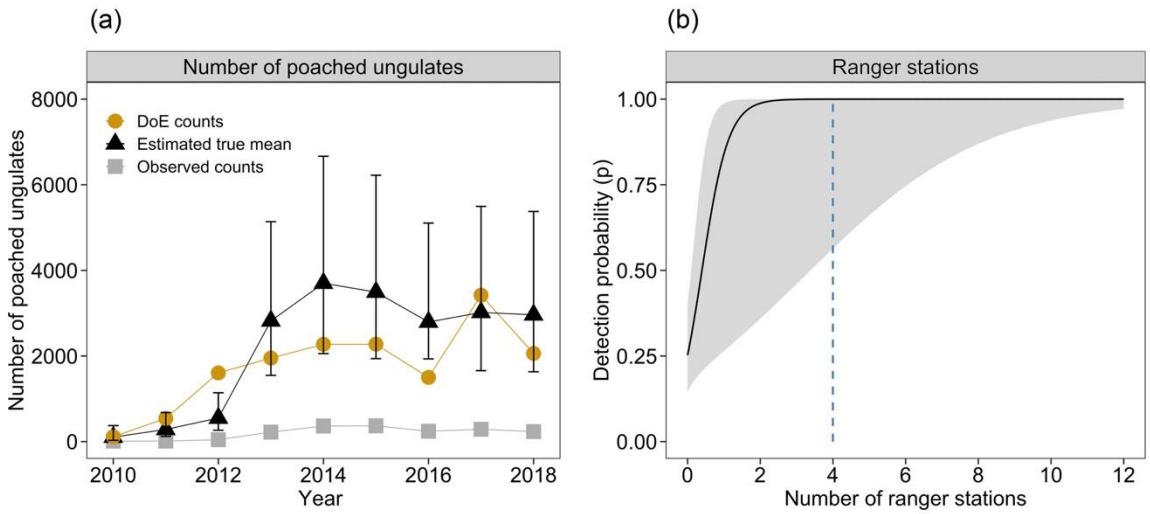
712 Figure 2. Iran's threatened ungulate species. Circles represent the regional IUCN Red
713 List status (VU, vulnerable; EN, endangered; CR, critically endangered). Photo credits:
714 mouflon, Persian fallow deer (a,i; F. Eskandari), urial, bezoar goat, goitered gazelle,
715 jebeer gazelle (b,c,d,e; H. Moqimi), onager (f; H. Fahimi), and maral and roe deer (g,h;
716 H. Tizrooyan).



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719 Figure 3. (a) Estimated true mean of poached animals (black line with 95% confidence
720 interval), DoE counts: annual number of poached animals that were seized by rangers for
721 the years 2010-2018 (red line) and observed number of poached animals in Iran based on
722 media articles for the same years (green line). (b) Expected detection probability of
723 poaching events in Iran, in relation to the number of ranger stations (per grid cell of 400-
724 km^2, the dashed line indicates the highest detection probability of poaching captures at 4
725 ranger stations).

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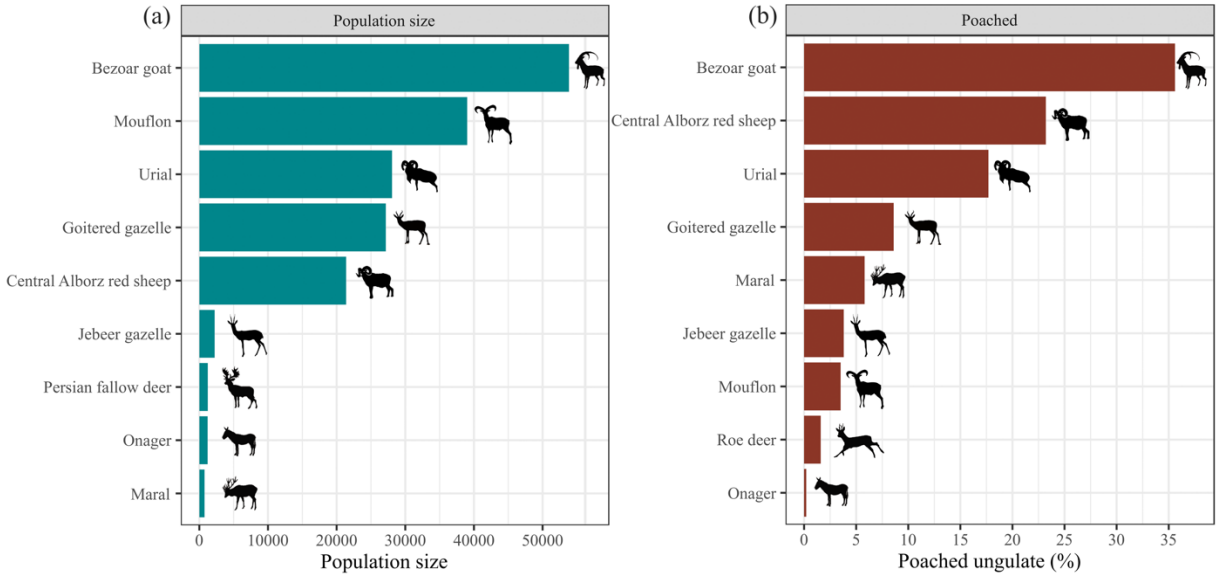
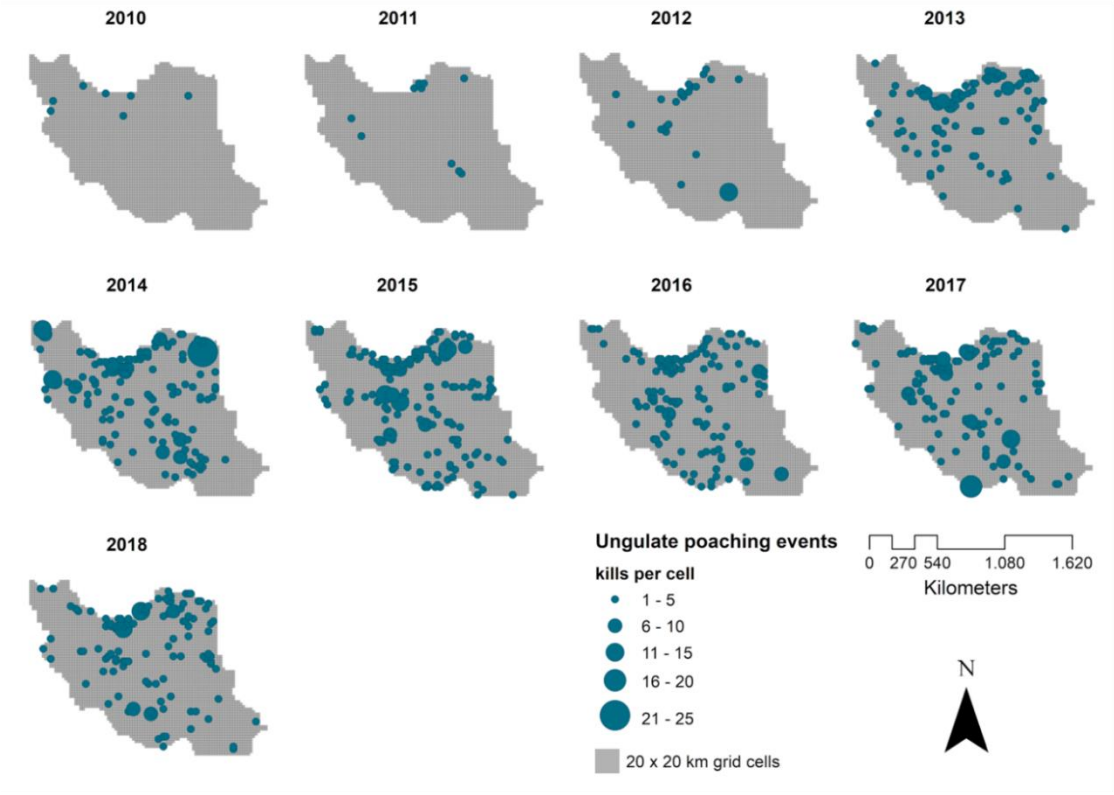


Figure 4. (a) represents the total counts (population abundance) of nine ungulate species (plus a hybrid population, the central Alborz red sheep) in Iran in 2018 (source DoE). A population count for roe deer was not available. (b) represents the relative percentages of the poached quantities during the years 2005-2019.



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739 Figure 5. Trends of poaching events (counts of seizures) identified in media reports for

740 nine ungulate species throughout Iran during the years 2010-2018.

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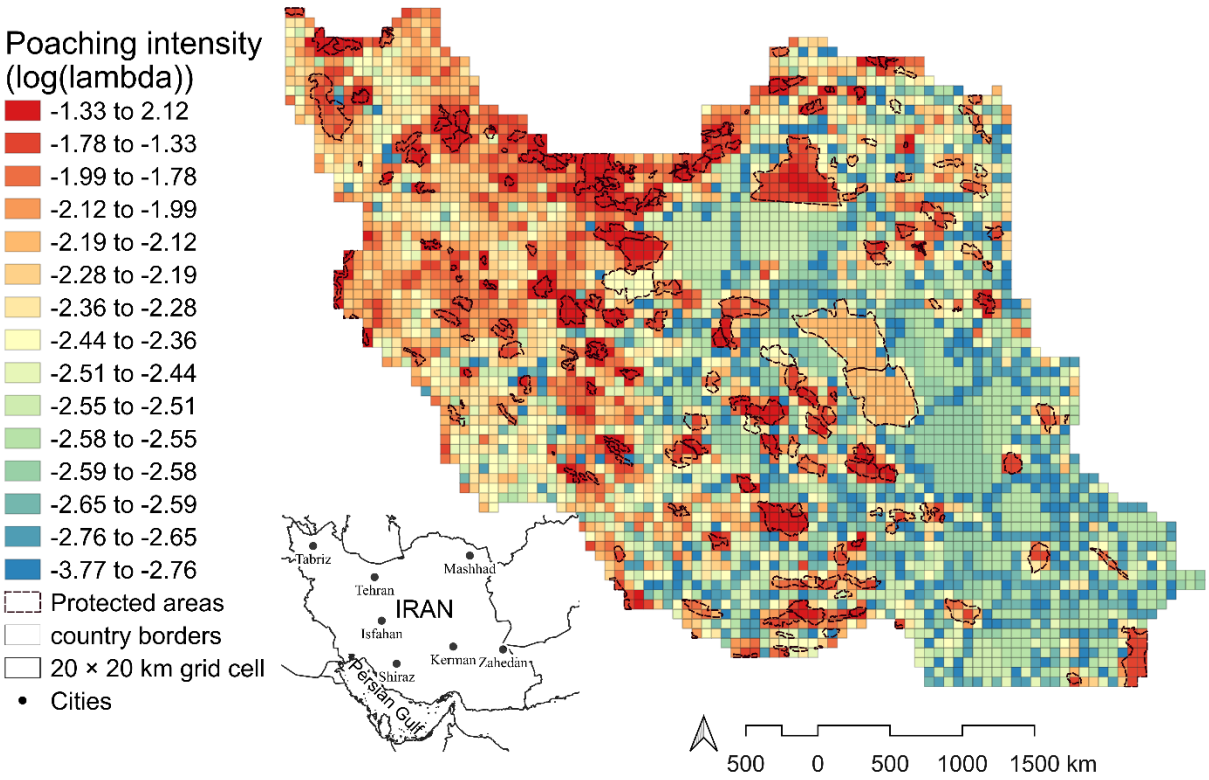

Figure 6. Poaching intensity (log scale) of nine ungulate species and plus a hybrid population in 2014 in 3931 400-km^2 grid cells across Iran, predicted by the single-visit N-mixture model. Poaching intensity is the product of the full set of covariates both in abundance (*N*) and detection (*p*) parameters of the best-fitting model.

751 Table 1. Estimates of negative binomial (NB) abundance (lambda) submodel and
752 detection submodel parameters and the mean (confidence intervals) annual poached
753 quantities for the best fitting NB model (single-visit N-mixture model; n = 3931 grid
754 cells) of the ungulate poaching (count) data in Iran during the years 2010-2018. β and α
755 indicate the coefficients estimated for abundance (N) and detection probability (p) models
756 respectively.

Model parameters	Estimate (β)	CI (95%)
Abundance		
$\beta_{\text{unemployment rate}}$	1.26	(0.51, 2.01)
$\beta_{\text{ungulate abundance}}$	0.08	(0.07, 0.09)
$\beta_{\text{ranger stations}}$	–0.02	(–0.10, 0.15)
$\beta_{\text{protected area (Cat. V)}}$	0.16	(0.09, 0.23)
$\beta_{\text{no-hunting area (non-IUCN)}}$	0.14	(0.07, 0.21)
$\beta_{\text{elevation}}$	–0.08	(–0.30, 0.15)
$\beta_{\text{road density}}$	0.22	(0.12, 0.31)
β_{yr2010}	–5.93	(–7.20, –4.66)
β_{yr2011}	–4.93	(–5.80, –4.07)
β_{yr2012}	–4.28	(–5.01, –3.55)
β_{yr2013}	–2.64	(–3.24, –2.04)

β_{yr2014}	–2.37	(–2.96, –1.78)
β_{yr2015}	–2.43	(–3.02, –1.84)
β_{yr2016}	–2.65	(–3.25, –2.05)
β_{yr2017}	–2.58	(–3.17, –1.98)
β_{yr2018}	–2.59	(–3.19, –2.00)
Detection		
α_{0} intercept	–0.81	(–1.62, –0.00)
$\alpha_{ranger\ stations}$	1.89	(0.28, 3.49)
$\alpha_{elevation}$	0.22	(–0.13, 0.57)
AIC	5668.15	

765 Table 2. Summary of the simulations for estimating true poaching events. Estimated
766 mean is the values of the simulated realizations based on 200 simulations. True value is
767 the parameter values that were used for the simulations. N_{true} is the number of true
768 poaching events and $N_{estimate}$ is the estimated mean poaching events. $N_{observed\ poaching}$ is the
769 number of observed poaching events. CI coverage is the fraction of the 95% confidence
770 interval which included the True value. P is Poisson, NB is the negative binomial and

771 NB_1 is the negative binomial mixture with moderate alpha.

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Parameters	Mean (P)	Mean (NB)	Mean (NB_1)	True value (P)	True value (NB)	True value (NB_1)	CI coverage (P)	CI coverage (NB)	CI coverage $(NB)_1$
Abundance									
$\lambda_{intercept}$	–1.25	–1.52	–1.50	–1.23	–1.66	–1.66	0.96	0.89	0.95
$\lambda_{unemployment\ rate}$	1.99	2.47	2.49	1.90	2.16	2.16	0.93	0.89	0.98
Detection									
$a_{intercept}$	–2.81	–2.47	–2.50	–2.80	–2.16	–2.16	0.94	0.90	0.98
$a_{ranger\ stations}$	1.59	2.08	2.02	1.56	1.91	1.91	0.96	0.87	0.99
a_a		–2.22	1.25		–2.25			0.96	
N_{true}				10383		8230			
					8217				
$N_{estimate}$	10454	8112	8221						
$N_{observed}$ *poaching events*	1034								

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775 Table 3. The estimated population trajectory metrics, historical, and the current population
776 sizes of ungulate species in Iran. The IUCN-g and IUCN-r indicate the global and the
777 regional status of species (Yusefi et al., 2019), respectively. The historical population size
778 represents the overall population of urial, mouflon, and central Alborz red sheep. EN,
779 endangered; CR, critically endangered; LC, least concern; NT, near threatened; VU,
780 vulnerable.

Scientific name	Historical population size	Population size 2018	Population trajectory (λ)	IUCN-g	IUCN-r	Reference for the historical population estimate
Ovis vignei	75000	25284	1.06	VU	VU C2a(i)	(De-Vos, 1975)
O. gmelini						(De-Vos, 1975)
		36939		VU	VU C2a(i)	
O. gmelini × *O. vignei*		21374		VU	VU C2a(i)	(De-Vos, 1975)
Equus h. onager	1300	1218	0.97	NT		(De-Vos, 1975)
					EN B2ab, C2a(i)	
Capra aegagrus	75000–85000	66328	0.91			(De-Vos, 1975)
				LC	VU C2a(i)	
Cervus e. maral	3750–4950	744	0.41			(Kiabi 1978,
				LC	EN C2a(i)	Kiabi et al., 2004)
Capreolus capreolus	–	–	–	LC	EN C2a(i)	
Gazella bennettii	7000	2742	0.63	LC	EN C2a(i)	(De-Vos, 1975)
Gazella s. subgutturosa	35000	26479	0.87	VU	EN C2a(i)	(De-Vos, 1975)

Dama mesopotamica	611	272	0.67	EN	CR B1ab, B2ab, C2a(i)	(DoE, 2009)

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