RESEARCH ARTICLE

# Mapping connectivity and conflict risk to identify safe corridors for the Persian leopard

Arash Ghoddousi · Benjamin Bleyhl · Clara Sichau · Delaram Ashayeri · Peyman Moghadas · Pooriya Sepahvand · Amirhossein Kh Hamidi · Mahmood Soofi · Tobias Kuemmerle

## Abstract

*Context* Many large carnivores depend on habitat patches outside protected areas, as well as safe corridors between them. However, corridor assessments typically ignore potential conflicts between carnivores and people, which can undermine corridor effectiveness and thus conservation success.

*Objectives* We identified safe dispersal corridors and conflict-prone movement bottlenecks for Persian leopard (*Panthera pardus saxicolor*) between protected areas in the Alborz Mountains, Iran, by mapping habitat, landscape permeability, and conflict risk. We then identified priority areas for conservation interventions according to the intensities of different threats.

*Methods* We mapped land cover using Landsat satellite images, gathered data on leopard and prey distributions and livestock depredation events via interview surveys in 69 cells of 6 × 6 km each. We then used occupancy modeling to identify habitat patches, used circuit theory modeling to analyze landscape permeability, and assessed human-leopard conflict risk using generalized linear models.

*Results* Leopard habitat use increased with prey availability and decreased with elevation. Prey distribution, in turn, was mostly negatively influenced by agricultural lands and distance from protected areas. Conflict risk (i.e., probability of leopard depredation on livestock) was high in landscapes where agriculture was widespread and historical forest loss high. Not

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accounting for conflicts overestimated connectivity among habitat patches substantially.

*Conclusions* Human-carnivore conflicts are an important constraint to connectivity and should be considered in corridor assessments. Our study shows how habitat analysis, connectivity assessment, and conflict risk mapping can be combined to guide conservation planning for identifying habitat networks and safe corridors for carnivores in human-dominated landscapes.

**Keywords** Alborz mountains · Connectivity · Human-wildlife conflict · Iran · Occupancy modeling · *Panthera pardus*

## Introduction

Landscapes across the globe are increasingly human-dominated (Tilman et al. 2017). This is particularly problematic for large carnivores, which are wide-ranging and require large tracts of suitable and well-connected habitat (Crooks et al. 2011; Ripple et al. 2014). Across the globe, these species are currently disappearing over large extents of their historical range as a result of habitat loss and fragmentation, as well as high mortality in human-dominated landscapes (Di Marco et al. 2014; Wolf and Ripple 2017). This is worrisome given that large carnivores play key roles in ecosystems (Ripple et al. 2014). Many protected areas are not large enough to host viable carnivore populations, driving large carnivores to seek habitat and dispersal corridors in surrounding landscapes (Crooks et al. 2011; Di Minin et al. 2016). Therefore, conservation planning to protect large carnivores and the ecological functions they provide must look beyond protected areas and identify strategies so these species can persist in human-dominated landscapes (Sanderson et al. 2002; Goswami and Vasudev 2017).

A central approach in this regard is to maintain connectivity between protected areas and habitat patches, commonly through retaining and establishing corridors (Tischendorf and Fahrig 2000; Kramer-Schadt et al. 2011). Corridors are landscape features that connect two or more habitat patches (or populations) so that individuals are able to move between the two without encountering major barriers (Tischendorf and Fahrig 2000). Therefore, identifying effective

corridors requires an understanding of the key factors limiting functional connectivity (Vasudev et al. 2015). Corridor identification typically focusses on landscape features only, such as roads, high elevation, or the inhospitable matrix surrounding habitat patches, which affect structural connectivity (Tischendorf and Fahrig 2000; Kramer-Schadt et al. 2011). However, ecological factors such as predation, competition, and prey availability (Cushman et al. 2010), as well as species' intrinsic characteristics, such as avoidance of unsafe landscapes (Ciuti et al. 2012; LaPoint et al. 2013; Gehr et al. 2017), affect behavioral responses of organisms to landscape structure and thus functional connectivity (Vasudev et al. 2015). Ignoring such ecological and behavioral constraints to dispersal might thus overestimate corridor functionality and undermine conservation efforts (Chetkiewicz et al. 2006; Scharf et al. 2018). Approaches that consider mortality risks when deriving corridors are, therefore, urgently needed.

For large carnivores, there are a number of reasons for human-caused mortality, including wildlife-vehicle collisions or poaching (Ripple et al. 2014). However, retaliatory killing in response to conflict with humans is an increasingly important mortality factor in human-dominated landscapes (Treves and Karanth 2003; Lennox et al. 2018). This conflict usually occurs in the form of livestock depredation (Chapron et al. 2014; van Eeden et al. 2018), which in turn may result in the persecution and killing of carnivores, and ultimately elevate extinction risk (Michalski et al. 2006; Jędrzejewski et al. 2017). The effects of human-carnivore conflict are more far-reaching than directly increasing mortality though. For instance, large predators in landscapes where human-related mortality is high may change their space and resource use (Bleicher 2017; Gehr et al. 2017) and may no longer exert a top-down control in food webs (Dorresteijn et al. 2015; Atkins et al. 2019). Likewise, high conflict risk can act as a barrier to movement (Vasudev et al. 2015; Goswami and Vasudev 2017). Therefore, ignoring human-carnivore conflict risk when identifying corridors may result in funneling dispersing individuals into 'ecological traps', where mortality risk is high (Little et al. 2002; Northrup et al. 2012) and thus, overestimating the effectiveness of corridors for carnivore movement (Goswami and Vasudev 2017). Conservation and corridor planning

should, therefore, consider human-wildlife conflicts (Cushman et al. 2018; Festa-Bianchet 2018).

We know of only a single study (Cushman et al. 2018) that considered conflict risk when assessing corridors for species of conservation concern. This is mainly because approaches for modeling predation risk (Hebblewhite et al. 2005) have only recently been adapted to estimating conflict risk in space (Miller 2015; Rostro-García et al. 2016). These approaches typically are based on correlating conflict occurrence or prevalence to a suite of spatial determinants (using e.g., ensemble modeling, generalized linear models, or logistic regression). Such models have great potential to provide insights into drivers of human-wildlife conflict, to predict conflict hotspots, and to understand which landscape features are associated with higher conflict than others (Miller 2015). All of this can provide worthwhile information for designing conservation strategies that mitigate conflict (Miller 2015) and could be incorporated in corridor planning (Goswami and Vasudev 2017). Cushman et al. (2018) predicted high conflict zones for lions (*Panthera leo*) from rapid declines in expected dispersal rates using cumulative kernel values from movement data. We advance this approach (Cushman et al. 2018) by using empirical data on livestock depredation events and by applying conflict risk modeling to identify conflict-prone areas in corridors that link habitat patches of large carnivores.

Our goal here was to identify safe dispersal corridors between habitat patches for the Persian leopard (*P. pardus saxicolor*), a wide-ranging large carnivore that critically depends on areas outside protected areas (Kiabi et al. 2002). We focused on the area between Golestan National Park and Jahan Nama Protected Area in the eastern Alborz Mountains, Iran, where no protected areas exist, but leopard occurrence has been reported (Kiabi et al. 2002). The area is also among the most fertile agricultural regions in notoriously drought-prone Iran, resulting in a human-dominated landscape and a high potential for further land-use changes and habitat fragmentation (Ghoddousi et al. 2017). Moreover, leopards are responsible for frequent livestock depredation in the area (Ghoddousi et al. 2016), causing widespread conflict and retaliatory killings by local people. This likely affects the survival of the leopard population in this region in major ways, which is highly problematic because the entire, critically endangered Caucasus population of Persian leopard strongly depends on immigrations from Iran (Askerov et al. 2015). Assessing where both permeable and safe corridors are found will thus contribute to leopard conservation beyond the study region, in the entire Caucasus-Hyrcanian Biodiversity Hotspot. Specifically, our objectives were (1) to identify habitat patches from estimated leopard habitat use; (2) to assess landscape permeability and movement bottlenecks across the study region; (3) to estimate human-leopard conflict probabilities using spatial risk modeling; and (4) to identify safe and high-risk corridors, and possible conservation interventions.

## Methods

### Study area

Our study area (ca. 3132 km$^2$) is situated in the eastern Alborz Mountains in northeastern Iran (Fig. 1). The area connects the Golestan National Park complex (including Golestan National Park GNP and its buffer zones Loveh Protected Area and Zav Protected Area) and Jahan Nama Protected Area (JNPA), two strongholds of the Persian leopard in southwest Asia (Kiabi et al. 2002). Only some parts of this range receive occasional patrols from the rangers of the Golestan provincial office of the Department of Environment. The main prey species of leopard in this area are bezoar goat (*Capra aegagrus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Ghoddousi et al. 2016). The study area is part of the Caucasus-Hyrcanian Biodiversity Hotspot and is covered by Hyrcanian temperate mixed forest. We focused on the mountainous part of the region (on average from 380–2300 m a.s.l.), as leopard occurrence in the lowlands is very rare and the landscape there has almost entirely been transformed into urban and agricultural areas. Moreover, there is a sharp environmental difference between the northern and southern slopes of the Alborz Mountains, with the southern slopes receiving less precipitation and thus being arid and without forests. We focused only on the northern slopes, which are more similar to the landscapes in western GNP and JNPA.
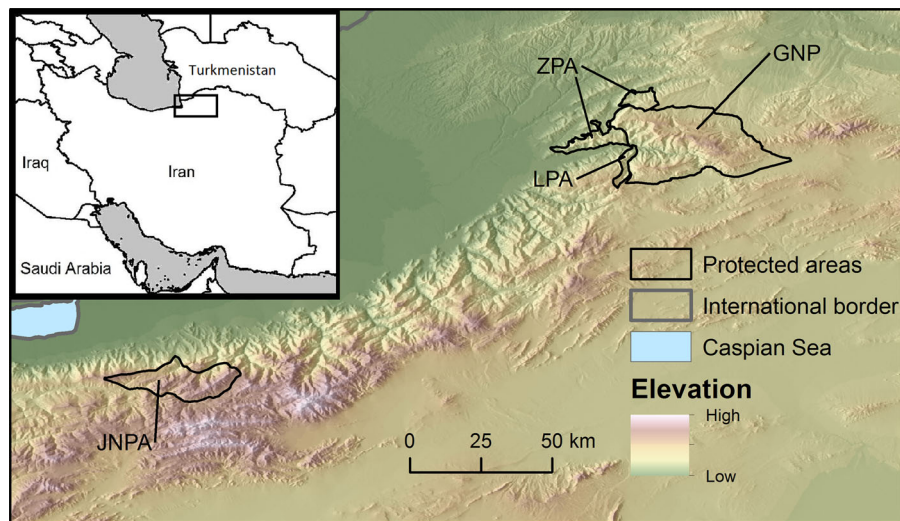
**Fig. 1** Study area in the eastern Alborz Mountains, Iran (inset map; grey: water bodies) and the location of Golestan National Park (GNP), Loveh Protected Area (LPA), Zav Protected Area (ZPA), and Jahan Nama Protected Area (JNPA)

Sampling design

We used a grid system with 6 × 6 km cells superimposed over the study area to identify sampling units (hereafter: cells). We chose this cell size following the recommendation (Beier 2019) on corridor width > 2 km when connecting habitat patches > 80 km apart (> 160 km aerial distance in our case). Moreover, such long corridors should consider a number of habitat patches where the species could temporarily reside (Beier 2019). This cell size is relevant considering the relatively large home range of Persian leopards, which is estimated at an average of around 100 km² (Farhadinia et al. 2018). Our cell size is also in accordance with recommendations on occupancy modeling approach using interview data, where cell size should be a compromise between sampling effort (i.e., the typical travel distance covered by foot by interviewees) and detectability (see below) (MacKenzie et al. 2017; Petracca et al. 2018). Finally, previous large-scale corridor planning studies for wide-ranging species used similar cell sizes (e.g., 16–36 km² for jaguar *P. onca* corridor planning in Central America; Petracca et al. 2018). We used a 50% threshold for the natural vegetation coverage in each cell based on a land-cover map (see below) derived from Landsat 8 satellite images at 30-m resolution (Bleyhl et al. 2017). We removed cells below this threshold from our analysis since highly transformed areas may function

as strong barriers to the movement of leopard and its prey (Bleyhl et al. 2017). We conducted all of our data collection and analysis in the remaining 74 cells.

Interview survey

We collected data on the presence of leopard, key prey species, and leopard depredation on livestock in our cells, using interviews with local communities from August to September 2015 and from February to October 2016. Surveys across larger landscapes can be very costly and difficult to implement using field observations of wildlife or camera trapping, and interview surveys can be a viable alternative in such situations (Zeller et al. 2011; Pillay et al. 2014; Martinez-Marti et al. 2016; Ghoshal et al. 2017). The use of interview data for wildlife surveys is especially successful when applied for relatively rare species with large body size, given appropriate statistical methods are used (Steger et al. 2017). We conducted interviews in one or two randomly chosen villages within each 36 km² cell and aimed to collect information from at least four interviewees. Each interviewee represented a replicate, providing information for the cell surrounding his/her village (Zeller et al. 2011). If other neighboring cells were visited on a monthly basis by the interviewee, we conducted a separate interview related to that cell (Taubmann et al. 2015). We conducted interviews only with individuals

who were knowledgeable about wildlife (e.g., regularly working outdoors), lived in the area for at least one year, and with a minimum residency of three months in the prior year. We gathered information from the interviewees on direct sightings of leopard and main prey species (i.e., bezoar goat, red deer, roe deer, and wild boar) and assigned them to the respective cells when the interviewee was able to distinguish the species based on pictures presented to them showing Iran's large mammals. Only direct observations by the interviewee were included, as we considered sightings by others or based on indirect evidence such as species' signs (e.g., tracks) unreliable. No other big cat or ungulate species than the study species exist in this area. Moreover, we recorded cases of leopard depredation on livestock in the prior year (Zeller et al. 2011). Wolves (*Canis lupus*) are also responsible for livestock depredation in the study area. However, we assume that the interviewees were skilled enough to distinguish between leopard and wolf depredation signs (killing by strangulation with throat bites vs. laceration of flanks and hind legs, respectively). When in doubt, we discarded ambiguous cases. Finally, we asked interviewees about their age, occupation, the period he/she has lived in the cell and the proportion of the prior year resided in the cell (Zeller et al. 2011). We received verbal consent from all interviewees before conducting interviews and assured them about the confidentiality and anonymity of their data.

Occupancy modeling

We fitted single-species, single-season occupancy models for leopard and four prey species using the *unmarked* package in R (Zeller et al. 2011; MacKenzie et al. 2017). As the assumption of population closure within the survey, required for occupancy states, could not be met due to long period of sightings (i.e., one year prior to the interview), we assumed that the occupancy states in each 36 km$^2$ cell represent the habitat use (MacKenzie and Nichols 2004). We created species detection matrices by assigning the detection/non-detection histories for leopard and prey species in different cells based on interviewees' sightings and treating each interview as a separate sampling event in that cell (Zeller et al. 2011). We addressed the potential false-positive bias from misidentifications in interviewee responses using the

*occuFP* function that allows specifying factors that may influence such detections (Fiske and Chandler 2011; Miller et al. 2011; Chambert et al. 2015; Petracca et al. 2018). We assumed that our data included both certain detections (without false-positive bias) and uncertain detections (with false-positive bias) (Miller et al. 2011), and considered sightings by rangers and hunters as having a lower probability of false-positive bias (due to higher expertise in wildlife encounters and identification) compared to other interviewees (Miller et al. 2011; Martinez-Marti et al. 2016; Ghoshal et al. 2017; Johnston et al. 2018). We marked the detections by this observer category as 'certain' in the detection matrices (Pillay et al. 2014; Chambert et al. 2015).

We developed *a-priori* hypotheses regarding factors that could affect species' detection ($\rho$) and habitat use ($\psi$). We assumed effort (i.e., days of the prior year spent in the cell) and residence (i.e., number of years of familiarity with a sampling unit) covariates to influence $\rho$ (Zeller et al. 2011). Regarding $\psi$, we hypothesized potential influence by land cover, elevation, road density, prey availability (only in leopard models), ruggedness and distance to protected areas (Petracca et al. 2014; Athreya et al. 2015; Abade et al. 2018). A detailed description of each covariate and their hypothesized effects on $\rho$ and $\psi$ are provided in Table 1. We tested all covariates for autocorrelation using the Pearson correlation test (cut-off point r = |0.60|). Moreover, we scaled all the covariates prior to the analyses to have a unit variance and minimize overdispersion (MacKenzie et al. 2017).

We tested different scenarios to calculate prey availability (bezoar goat, red deer, roe deer, and wild boar) per cell: (1) prey richness (number of prey species reported by interviewees); (2) single-species and (3) cumulative habitat use (sum of occupancy model estimates); and (4) cumulative catch-per-unit-effort (CPUE; multiplying the number of independent detections by the species' average biomass, divided by the number of interviewees) (Abade et al. 2018; Petracca et al. 2018). We obtained prey biomass figures from Lumetsberger et al. (2017). Using univariate occupancy models, CPUE performed best in explaining leopard $\psi$ (Table 2), and therefore, we used this covariate as prey availability in the leopard models.

We used a multi-step approach to specify our occupancy model parameters by first building models

**Table 1** Covariates used in the occupancy models, with the hypothesized effect of each covariate on detection probability ($\rho$) and habitat use ($\psi$) of leopard and prey species

| Model process | Covariate | Description | Data source | Hypothesized influence |
|---|---|---|---|---|
| Detection ($\rho$) | Effort | Proportion of the prior year spent in the cell | Interview data | + |
| | Residence | Number of years of familiarity with the cell | Interview data | + |
| Habitat use ($\psi$) | Prey availability[a] | The cumulative catch-per-unit-effort for three large prey species in cell[b] | Interview data | + |
| | Distance to protected areas | Nearest distance (km) to protected area borders from cell centroid | World database on protected Areas[c] | − |
| | Forest[d] | Proportion of forest in cell | Land-cover map | + |
| | Cropland[d] | Proportion of cropland in cell | Land-cover map | − |
| | Road density | Length (km) of primary roads in cell | Google earth | − |
| | Elevation | Average elevation (m) in cell | SRTM[e] | +/−[f] |
| | Ruggedness | Average ruggedness index in cell | SRTM[e] | + |

[a]Only considered in the leopard models

[b]Biomass of prey species based on Lumetsberger et al. (2017): bezoar goat 36 kg, roe deer 20 kg, red deer 99 kg

[c]Source: www.protectedplanet.net

[d]Due to the high correlation between forest and cropland layers, we only used either of them in each model

[e]Source: Shuttle Radar Topography Mission (https://search.earthdata.nasa.gov)

[f]We hypothesized that our study species could respond differently to elevation according to our field observations

using covariates influencing $\rho$ while maintaining $\psi$ as constant. Then, we held the covariates in the top $\rho$ models constant and built models that influenced $\psi$ (MacKenzie et al. 2017). We evaluated univariate occupancy models based on *a-priori* hypotheses and then made ecologically-relevant combinations of covariates to assess their influence on $\psi$ (see Online Appendix S1 for the full set of models tested). We

ranked models based on their Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). We used $\Delta$AICc < 2 criteria to select the best models and applied model averaging technique to estimate probabilities of $\psi$ and $\rho$ when more than one model fit our criteria (Burnham and Anderson 2002). We also compared a naïve model ($\psi_{naïve}$: proportion of cells with at least one detection)

**Table 2** Comparison of model performance of different prey covariate scenarios in explaining leopard habitat use ($\psi$)

| Prey covariate scenarios | K[a] | AICc[b] | ΔAICc[c] | AICc weight | Log-likelihood |
|---|---|---|---|---|---|
| CPUE | 5 | 346.99 | 0 | 0.64 | −168.02 |
| Prey richness | 5 | 350.08 | 3.09 | 0.14 | −169.56 |
| Bezoar goat | 5 | 352.20 | 5.21 | 0.05 | −170.63 |
| Cumulative prey | 5 | 352.41 | 5.42 | 0.04 | −170.73 |
| Roe deer | 5 | 352.54 | 5.56 | 0.04 | −170.80 |
| Red deer | 5 | 353.05 | 6.06 | 0.03 | −171.05 |

Scenarios: *CPUE*, cumulative catch-per-unit-effort for all prey species with biomass data from Lumetsberger et al. (2017); *cumulative prey*, cumulative habitat use estimates from occupancy models; *roe deer*, *red deer*, *bezoar goat*, single-species habitat use estimates from occupancy models; *prey richness*, number of prey species reported by interviewees per cell

[a]Number of parameters in the model

[b]Akaike information criterion corrected for small sample size

[c]Difference in AICc value relative to the best model

with and without false positive detection ($\rho_{10}$) to assess the impact of this bias on occupancy estimates (Petracca et al. 2018).

Landscape permeability

To assess landscape permeability in our study region, we estimated the landscape resistance to species movement between GNP and JNPA. First, we mapped six land-cover classes using Landsat 8 satellite images with 30-m spatial resolution: forest, rangeland, cropland, built-up, sparse vegetation, and water (see Online Appendix S2 for details on the land-cover mapping). We translated our land-cover map into a surface characterizing resistance to leopard movement (Zeller et al. 2012; Dutta et al. 2016) by assigning resistance values to land-cover classes representing vegetation formations (i.e., forest, rangeland, cropland, and sparse vegetation) based on a survey among 27 wildlife experts (Bleyhl et al. 2017). Resistance values of these vegetated land-cover classes were allowed to range from one (most permeable) to ten (least permeable). To reach a consensus across the expert group, we calculated median resistance values per land-cover class (Bleyhl et al. 2017). Next, we added paved roads as partial barriers, assigning all 30-m cells containing a major road a resistance value of 100 (a value tested previously in a similar landscape for the same study species; Bleyhl et al. 2017). Finally, we considered the land-cover classes built-up and larger water bodies as total barriers (i.e., no movement was allowed through these land covers). We averaged resistance values for each 36 km$^2$ cell.

To identify bottlenecks across the landscape at 30-m spatial resolution, we first identified the least-cost pathway between the protected areas (i.e., the single-pixel-wide path with the lowest cumulative resistance). We then mapped areas around this pathway with a cumulative resistance of < 100 times higher, which is a threshold tested and used in previous studies (Dutta et al. 2016; Bleyhl et al. 2017). We conducted both of these analyses using the Linkage Mapper Toolkit (McRae et al. 2008) in ArcGIS 10.5 (ESRI, Redlands, CA, USA). We assessed connectivity between two nodes only, as we were only interested in the linkages between two protected areas. We then applied circuit theory within our pathways to identify movement bottlenecks using the Pinchpoint Mapper tool in the Linkage Mapper Toolkit. This method measures the current (i.e., likelihood of a species passing) between nodes (in our case protected areas) across the landscape, considering the resistance of the landscape (McRae et al. 2008). High currents indicate a lack of alternative paths, and therefore, potential bottlenecks within a corridor. We defined bottlenecks as areas with a current density higher than the mean plus two standard deviations (Bleyhl et al. 2017). Finally, we calculated the number of bottlenecks for each 36 km$^2$ cell.

Conflict risk modeling

To quantify and map associations between human-leopard conflict and landscape characteristics, we used generalized linear models using the *stats* package in R (Miller 2015). We derived the binomial presence or absence of conflict (i.e., leopard depredation on livestock) in each cell from our interview data. Leopards are ambush hunters and benefit from intermediate cover levels (Balme et al. 2007). Therefore, in addition to the environmental covariates used in the occupancy modeling, we calculated variables reflecting forest type and fragmentation in each cell, as we hypothesized these variables may influence leopard feeding habitat selection, wild and domestic prey availability, and consequently the depredation risk on livestock (Balme et al. 2007; Carvalho et al. 2015; Miller 2015; Acharya et al. 2017). A detailed description of all the variables tested and their hypothesized effects on conflict risk is provided in Table 3. We used Morphological Spatial Pattern Analysis (MSPA) (Vogt and Riitters 2017) on our land-cover map to measure the share of core forest as well as connecting forest patches per cell. Core forest was defined as patches larger than 2 km$^2$ (Vogt and Riitters 2017), with an adjacent forest edge of < 300 m (10 forest pixels in our Landsat-based map). Connecting forest was assigned to those patches (> 2 km$^2$) that were > 300 m from the nearest forest patch. Additionally, we calculated the median forest patch area, forest patch density, forest patch edge, core forest patch edge, and core forest shape index per cell using FRAGSTATS (McGarigal et al. 2012) as indicators of forest fragmentation. We tested for collinearity among all covariates using the Pearson correlation test (r <|0.60|). We applied a similar model selection procedure as in our occupancy modeling. We evaluated model results using the area under the

**Table 3** Variables used in the conflict risk models, with the hypothesized effect of each variable on depredation risk of leopard on livestock

| Variable | Description | Hypothesized influence |
|---|---|---|
| Forest | Proportion of forest in cell | + |
| Cropland | Proportion of cropland in cell | − |
| Core forest | Proportion of patches larger than 2 km$^2$ with an adjacent forest edge of < 300 m (10 forest pixels in the Landsat-based map) in cell | − |
| Connect forest | Proportion of patches larger than 2 km$^2$ with an adjacent forest patch of > 300 m in cell | + |
| Forest edge | Proportion of a 300 m wide edge area of forest patch in cell | + |
| Core forest edge | Proportion of a 300 m wide edge area of core forest patch in cell | + |
| Core forest shape index | Normalized ratio of core forest patch edge (i.e., patch perimeters) to maximally clumped-shaped edge in cell | + |
| Forest patch density | Number of forest patches by the area of forest patches in cell | + |
| Forest patch area | Median forest patch area in cell | − |

receiver-operating curve (AUC) with tenfold cross-validation. We randomly split the data into 10 folds containing equal number of depredation cases, and created the training models by eliminating each fold in turn. In each turn, we used the removed fold for testing the model derived from the remaining training folds.

Identification of habitat patches and safe corridors

We used a multi-criteria approach to identify habitat patches and corridors (Fig. 2) ( Rödder et al. 2016; Cushman et al. 2018). We used Jenks natural breaks to categorize the maps of leopard habitat use, landscape resistance, bottleneck numbers, and human-leopard conflict intensity. Jenks natural breaks is a data-driven classification method that identifies natural groupings inherent in the data. We chose this method over equal or expert-based thresholds as our input surfaces were not normally distributed. We classified 36 km$^2$ cells into three categories (i.e., low, medium, high) by finding points where between-group variability was highest while within-group variability was minimized using ArcGIS 10.5. 'Habitat patches' are areas where leopards are prevalent, and thus can be the origin or destination of dispersers (Kramer-Schadt et al. 2011). Specifically, we classified habitat patches as cells with a high probability of leopard habitat use (Zeller et al. 2011) and all other cells were classified as 'matrix' (Kramer-Schadt et al. 2011; Rödder et al. 2016). We used the Wilcoxon signed-rank test to assess

differences in the levels of cumulative prey habitat use, landscape resistance and conflict probabilities between the habitat patches and the matrix.

We classified 'safe corridors' by identifying matrix cells characterized by low or medium levels of landscape resistance and low or medium levels of conflict risk. All remaining cells were relabeled as 'severed corridors' (Riggio and Caro 2017). Finally, within the severed corridors, we identified 'high-risk corridors' as areas with the highest number of bottlenecks, which require urgent conservation intervention due to the absence of alternative dispersal paths, high landscape resistance and conflict risk (Taubmann et al. 2015). To assess the sensitivity of our classification, we also did a re-classification using geometrical intervals (another data-driven classifier algorithm that minimizes the square sum of element per class) instead of natural breaks, and quantified the differences.

## Results

Interview survey

We conducted 208 semi-structured interviews in 69 cells. We were unable to collect data from five cells due to inaccessibility or lack of settlements, and therefore, those cells were removed from the analysis. Within the sampled cells, on average around 3.0
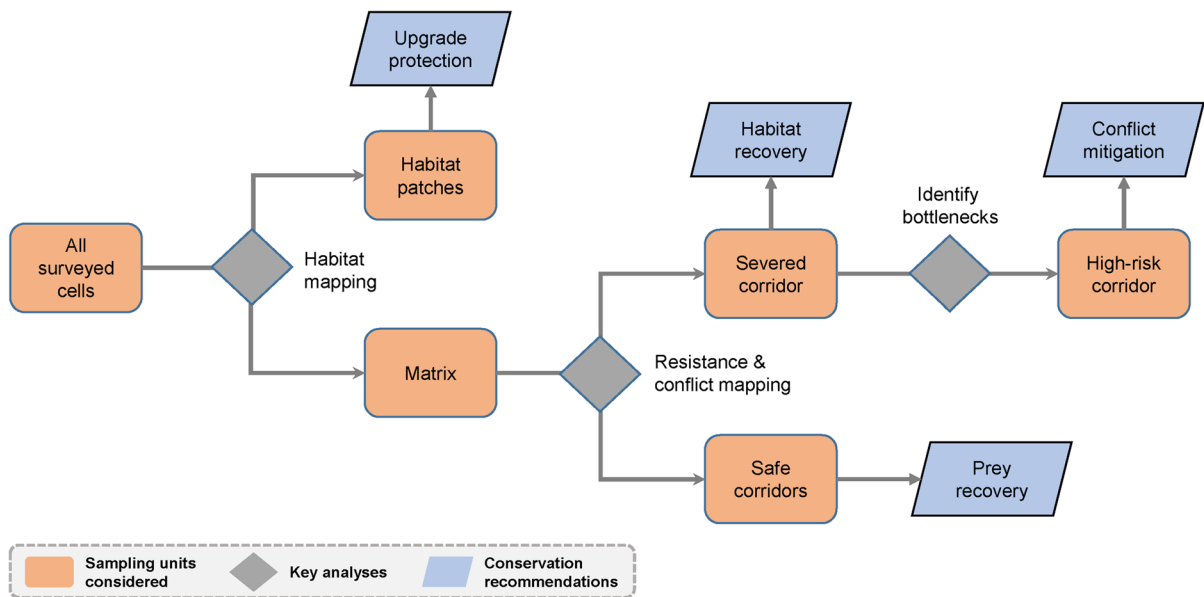
**Fig. 2** Flowchart of the step-wise multi-criteria approach to identify habitat patches, safe and high-risk corridors, and their respective conservation recommendations

questionnaires were completed. Interviewees were all male and between 17 and 80 years old with a mean age of 41.1 years. Interviewees spent on average 309 days of the year within their respective cells and had on average 38.9 years of living experience in the area. The interviewees were mostly shepherds (44.9%), but also farmers (26.8%), rangers (12.2%), foresters (6.3%), hunters (6.3%) and porters (3.4%). Leopards were sighted in 51 of the 69 cells (73.9%) and leopard depredation on livestock was reported in 24 cells (34.8%). The most often-sighted wild prey was wild boar, which occurred in all cells, followed by roe deer (63.8%), red deer (42.0%) and bezoar goat (26.1%). We removed wild boar from the analyses due to their ubiquitous distribution.

Occupancy modeling

None of the detection ($\rho$) covariates were selected in our top models. The naïve occupancy ($\psi_{naïve}$) dropped by around 14%, 9%, 1% and 5% for leopard, red deer, roe deer and bezoar goat, respectively, when considering the potential false-positive bias ($\rho_{10}$) in our interview data. The most parsimonious habitat use ($\psi$) model for leopard included prey availability and elevation covariates (Table 4). It suggests leopards avoid higher elevations and their $\psi$ increases with higher prey availability. Agriculture and distance from protected areas were the main factors negatively influencing $\psi$ for red deer and roe deer (Table 4). In addition, $\psi$ of red deer was positively associated with elevation (Table 4). The $\psi$ of bezoar goat was positively associated with the ruggedness of the cells and inversely related to the distance from protected areas (Table 4). Projecting our final model to all cells showed that high leopard habitat use ($> 0.68$) occurred in 20 cells (29% of all cells; Fig. 3). High cumulative prey habitat use ($> 1.14$; range 0–1.99) occurred in 14 cells (20%; Fig. 3). We identified habitat patches based on high leopard habitat use, and considered the remaining cells (n = 49) as matrix (Fig. 4). The cumulative prey habitat use was significantly higher ($Z = 723$, $p < 0.01$) in habitat patches compared to the matrix.

Landscape permeability

In our land-cover map, forest was the most widespread class (66.7%) followed by rangeland (18.6%), cropland (12.8%), sparse vegetation (1%), built-up (0.9%) and water ($< 0.05\%$; Fig. S1 in Online Appendix). The mean landscape resistance in each cell based on our land-cover maps ranged from 1 to 5.05, which revealed high landscape resistance in the eastern parts

**Table 4** Top occupancy models of leopard and prey species with habitat use ($\psi$) and detection probability ($\rho$) covariates

| Species | Model | Intercept (SE[a]) | Prey (SE[a]) | Elev. (SE[a]) | PA (SE[a]) | Crop (SE[a]) | Rugged (SE[a]) |
|---------|-------|------------------|--------------|----------------|------------|--------------|-----------------|
| Leopard | $\Psi$ (prey + elev.), $\rho(.)$ | 0.13 (0.64) | 1.85 (0.88) | −1.24 (0.76) | – | – | – |
| Red deer | $\Psi$ (crop + elev. + PA), $\rho(.)$ | −1.54 (0.86) | NA | 0.86 (0.46) | −0.85 (0.43) | −1.95 (1.33) | – |
| Roe deer | $\Psi$ (crop + PA), $\rho(.)$ | 1.03 (0.59) | NA | – | −2.15 (0.89) | −1.99 (0.68) | – |
| Bezoar goat | $\Psi$ (PA + rugged.), $\rho(.)$ | −9.09 (6.35) | NA | – | −7.99 (5.76) | – | 4.81 (4.43) |

The habitat use ($\psi$) covariates: *prey*, the cumulative catch-per-unit-effort for three large prey species; *elev.*, average elevation (m) in cell; *PA*, distance (km) to protected areas from cell centroid; *crop*, proportion of cropland in cell; *rugged*, average ruggedness index in cell

[a] Standard error
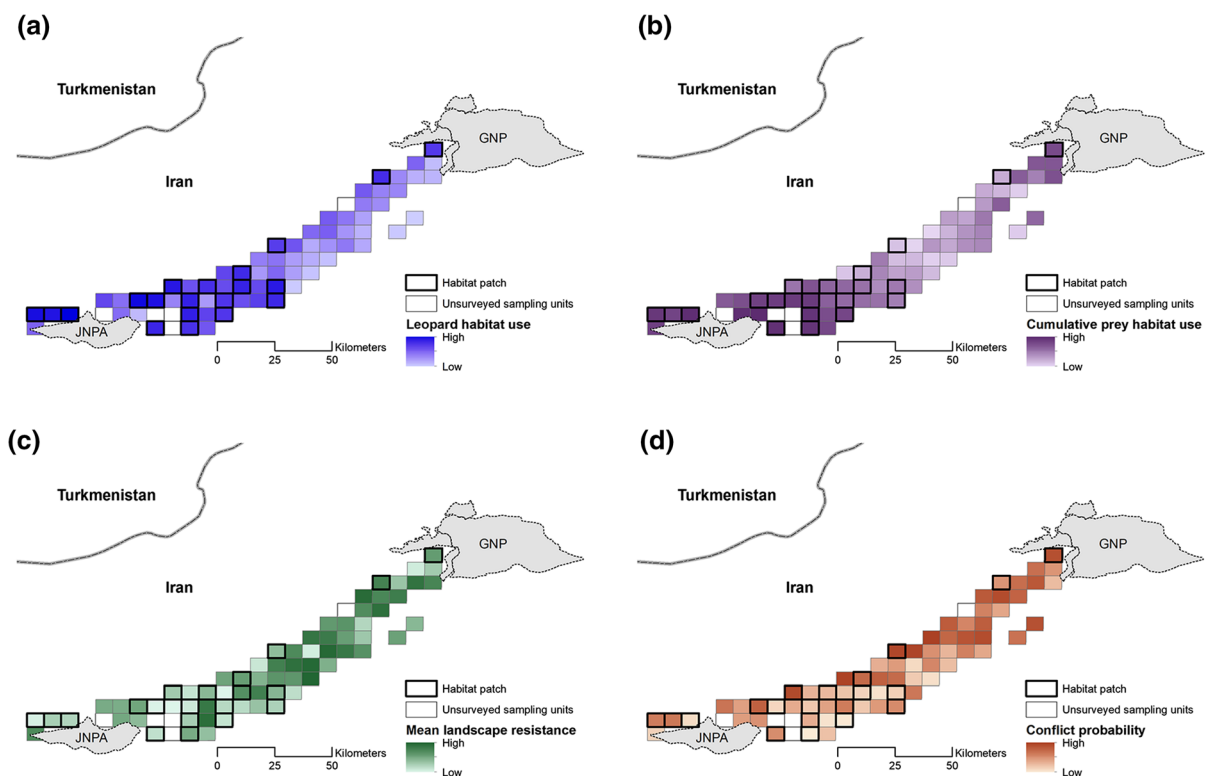


**Fig. 3** Estimated leopard (**a**) and prey (**b**) habitat uses, mean landscape resistance (**c**) and human-leopard conflict risk (**d**) between Golestan National Park (GNP) and Jahan Nama Protected Area (JNPA), Iran. Habitat patch: sampling units with high probability ($> 0.68$) of leopard habitat use. Unsurveyed sampling units: where we were unable to collect data due to inaccessibility or lack of settlements

of the study area (Fig. 3). However, the landscape resistance ($Z = 270, p < 0.01$) was significantly lower in the habitat patches compared to the matrix.

**Conflict risk**

The top conflict risk model included cropland, connecting forest and median forest patch area (Table 5). This model revealed a positive association of cropland with conflict intensity, whereas median
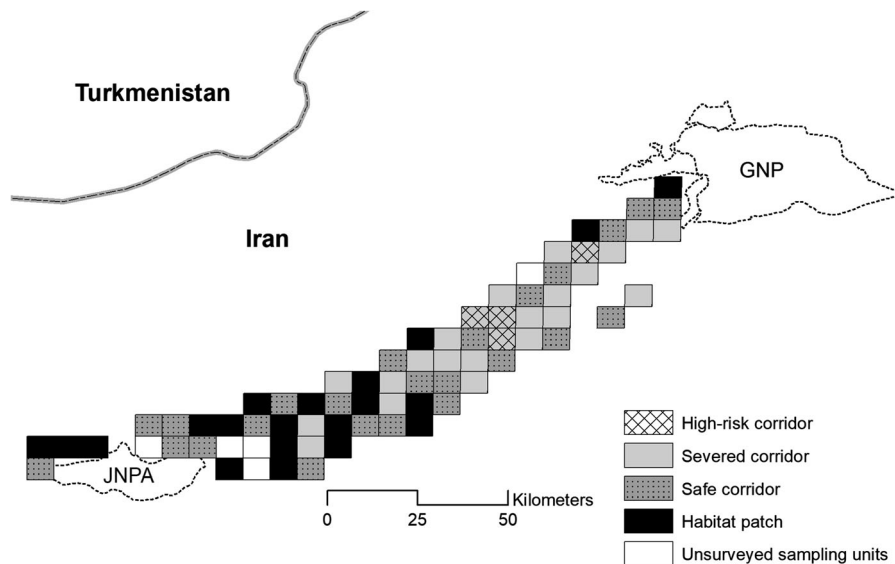
**Fig. 4** Location of habitat patches, safe, severed, and high-risk corridors between Golestan National Park (GNP) and Jahan Nama Protected Area (JNPA), Iran

forest patch area and connecting forest were associated with lower conflict rates. The AUC for the best model was 0.73. The conflict risk was lower in the habitat patches compared to the matrix but this difference was not statistically significant ($Z = 416$, $p = 0.33$).

Safe corridors

We classified 24 matrix cells (49% of all matrix cells) with low or medium conflict risk ($< 0.56$) and low or medium landscape resistance ($< 3.47$) as safe corridors and identified the remaining cells ($n = 25$) as severed corridors. The identified safe corridor cells could fill the connectivity gap between some of the habitat patches but were absent from the eastern parts of the study area (Fig. 4). When not accounting for the conflict risk and using the same landscape resistance threshold, the safe corridor cells were overestimated by 36.7%. We identified four cells with a high number of bottlenecks ($> 1377$) in the severed corridors, indicating high-risk corridors that are priority areas for conflict mitigation measures (Fig. 4). The results of the sensitivity analysis of our classification methodology showed that habitat patches and safe corridors identified based on geometrical intervals had 95% and 79% overlap with the results of the Jenks method, respectively.

**Discussion**

Large carnivores in human-dominated landscapes typically cannot persist inside protected areas alone and critically depend on habitat outside protected areas, as well as on functioning corridors between them (Ripple et al. 2014). We show how assessments of habitat, landscape permeability, and human-carnivore conflict risk can be combined to identify safe and high-risk corridors for large carnivores in human-dominated landscapes. Using the example of Persian leopards in northeastern Iran, we also demonstrate how leveraging community observations and remotely-collected data can allow for such analyses in a data-limited environment, thus ultimately guiding conservation planning for maintaining a wide-ranging threatened species outside protected areas. This is relevant, as many areas where conflict between large carnivores and people are high face such data limitations. Our analyses further provide insights on the reciprocal relationship between human-wildlife conflict and connectivity as well as the impact of agricultural land use on the persistence of ungulate species and consequently large carnivores that depend on them as prey.

A first major insight from our work was that ignoring human-leopard conflict in connectivity assessments may lead to a substantial overestimation

**Table 5** Parameters of the best-performing generalized linear model of human-leopard conflict

| Coefficient | Estimate | SD[a] | Z value | p value | Odds | 95% CI[b] |
|---|---|---|---|---|---|---|
| Intercept | 0.32 | 0.61 | 0.52 | 0.59 | – | – |
| Connecting forest | −0.13 | 0.05 | −2.51 | 0.01 | 0.87 | 0.77–0.95 |
| Cropland | 0.11 | 0.05 | 2.23 | 0.02 | 1.12 | 1.02–1.26 |
| Forest patch area | −0.24 | 0.11 | −2.14 | 0.03 | 0.78 | 0.60–0.96 |

Covariates: *connecting forest*, forest patches larger than 2 km² with > 300 m distance from the nearest forest in the land-cover map; *cropland*, proportion of cropland in cell; *forest patch area*, median forest patch area in cell from land-cover map

[a]Standard deviation

[b]Confidence intervals

of the extent of the corridor and the functional connectivity among habitat patches. Many leopard dispersal bottlenecks in the eastern Alborz Mountains were located in areas with high conflict risk (i.e., high-risk corridors), where the persecution of leopard is likely (Kiabi et al. 2002; Lennox et al. 2018), and local extinction risk is high (Jędrzejewski et al. 2017). These landscapes may act as 'ecological traps' when animals are funneled through them (Little et al. 2002; Kramer-Schadt et al. 2011; Northrup et al. 2012) and consequently, put dispersing individuals at risk of conflict. Moreover, the behavioral constraints to dispersal, such as avoidance of unsafe landscapes (Gehr et al. 2017) may limit the permeability of high-risk corridors (Goswami and Vasudev 2017). Therefore, our study reinforces other calls ( LaPoint et al. 2013; Goswami and Vasudev 2017; Festa-Bianchet 2018) for more deeply considering ecological as well as intrinsic constraints for corridor identification in human-dominated landscapes, some of which might be difficult to measure with remote sensing and conventional habitat assessment techniques (Scharf et al. 2018). Our study shows how a rapid and low-cost assessment based on local interviews can alleviate this issue and help in the identification of conservation priorities in conflict-prone landscapes.

A second insight from our analyses was a better understanding of the influence of agricultural lands and forest fragmentation on human-carnivore conflicts in human-dominated landscapes. In our study, conflict probability was clearly associated with the share of croplands in each cell, which has been reported in other human-dominated landscapes (Northrup et al. 2012). Agricultural lands on the periphery of core habitats offer domestic prey as a food source and

increase the probability of livestock depredation by leopard (Abade et al. 2018). Moreover, the prey depletion in these landscapes from habitat loss and/or poaching may trigger a higher rate of livestock depredation by big cats, as suggested in a global review (Khorozyan et al. 2015). Our results also showed a positive association between forest fragmentation and the probability of livestock depredation. Other studies ( Michalski et al. 2006; Carvalho et al. 2015; Acharya et al. 2017), similarly showed that forest fragmentation leads to the creation of heterogeneous landscapes and higher presence of livestock, both of which increase the probability of conflict between humans and large carnivores. However, the negative influence of connecting forest on conflict probabilities was contrary to our expectations, which may be due to the persistence of wild prey (roe deer and wild boar) in these forest fragments.

A third key finding of our work was the negative impact of agriculture on the occurrence of two prey species, which may have indirect negative consequences for leopards as well. Only about a third of the study area between Golestan National Park and Jahan Nama Protected Area could be considered as highly used by the leopard, and the eastern part of the study area, which has experienced a higher rate of land-use change, is likely devoid of resident leopard and prey species (except wild boar). This result stands in contrast to previous studies (Odden et al. 2014; Kshettry et al. 2017), showing that leopards may use modified landscapes and agroecosystems as habitat. Prey availability, as one of the most important drivers of leopard habitat use in our study, may explain this as it may be the true limiting factor in modified landscapes. In our study, the habitat use of prey

species was mostly negatively affected by agricultural landscapes. This reflects the importance of habitat loss from land-use change as a threat to the existence of ungulate species, especially when it coincides with poaching (Benitez-Lopez et al. 2017; Romero-Muñoz et al. 2019), which ultimately impacts large carnivores. In other human-dominated landscapes, however, prey can be abundant (Chapron et al. 2014), which can explain why our results on the impact of agricultural extent on large carnivore existence diverge from prior studies.

Despite the absence of habitat patches in the modified landscape, these areas may still be valuable as dispersal corridors (Vanbianchi et al. 2018). However, low landscape permeability due to the existence of roads and residential areas pose major barriers to leopard dispersal in the eastern part of the study area. The high potential for agricultural expansion and intensification in this fertile region (Ghoddousi et al. 2017) may further isolate protected areas, impacting habitat connectivity of leopard. These results highlight the effect of structural landscape changes on habitat use and connectivity of wide-ranging species, especially where they interplay with other threats such as poaching.

Some possible drawbacks and room for improvement of our approach need mentioning. First, integrating different methodologies across various scales is challenging and we acknowledge simplifications in the classification of habitat patches and safe corridors. However, using Jenks and geometrical intervals classification methods, we showed that the choice of algorithm had a minor influence on our final results. Second, we sought to address the potential false-positive bias by assuming a higher reliability of detections by rangers and hunters compared to other interviewees. Complete elimination of false-positive bias does not seem possible (Johnston et al. 2018), and we acknowledge that there is likely remaining misidentification error in data from rangers and hunters. However, considering the higher expertise in wildlife identifications among this group (Johnston et al. 2018) should reduce false-positive bias (Pillay et al. 2014). Moreover, we cannot completely rule out deliberate falsification of detections by interviewees (Pillay et al. 2014). However, the effects of false-positive probabilities on naïve occupancies showed the necessity of considering this bias in the analysis of interview data (Petracca et al. 2018). Third, we

acknowledge that the use of empirical movement data for parameterizing our resistance surfaces, instead of expert knowledge in our case, would have been desirable (Stevenson-Holt et al. 2014). However, such data (e.g., GPS telemetry data) were not available in our study. In the absence of such data, developing resistance layers based on expert knowledge is a viable alternative (Beier et al. 2008; Zeller et al. 2012) and often produce similar results to empirical movement models (Keeley et al. 2016; Aylward et al. 2018). Finally, the prey species in our study may use smaller areas than our cell size, which may bias our inferences by overestimating the habitat use of these species. However, such cell size has been successfully tested in multi-species settings of large carnivores and prey in previous studies (Zeller et al. 2011; Petracca et al. 2014).

Our results indicate a range of concrete conservation and landscape planning recommendations based on the intensities of species' habitat use, landscape permeability, and conflict risk. First, we recommend upgrading the protection measures in the habitat patches due to the higher habitat use of leopard. Present protected areas in Golestan Province are insufficient for the protection of the leopard's ungulate prey species (Momeni Dehghani et al. 2013), and the identified habitat patches in our study may represent suitable candidates for the expansion of the protected area network. The establishment of a protected area could provide the necessary law enforcement to curb poaching and potential land-use change. Second, safe corridors, as areas with low conflict risk and landscape resistance, require conservation interventions related to poaching mitigation, prey recovery, and protection from development (Cushman et al. 2018). Third, high-risk corridors may represent 'ecological traps' due to high conflict risk and the absence of alternative dispersal paths. These areas require urgent conflict mitigation measures to reduce the actual and perceived risk of human-leopard conflict (Broekhuis et al. 2017; Cushman et al. 2018), which are critical for the long-term persistence of leopards in the Caucasus-Hyrcanian ecoregion. Compensation to farmers for livestock losses due to leopards and/or preventive measures such as improved husbandry methods (e.g., secure night corral, education of shepherds and better guarding dogs) are recommended to reduce the chance of depredation and lethal control (Krafte Holland et al. 2018; van Eeden et al. 2018). Finally, cells identified

as severed corridors require habitat recovery and prevention of further land-use change and forest fragmentation. For the persistence of threatened wide-ranging carnivores in the human-dominated landscapes, retaining native habitat within agroecosystems is crucial (Ferreira et al. 2018). While we derive these recommendations for our case study of Persian leopards in northeastern Iran, these recommendations are likely equally valid for other regions where large carnivores depend on corridors in human-dominated landscapes, and where human-carnivore conflict may undermine the effectiveness of these corridors.

More broadly, our study highlights a low-cost and effective way to improve connectivity assessments by considering ecological and behavioral constraints to dispersal, such as human-carnivore conflict (LaPoint et al. 2013; Goswami and Vasudev 2017). Our approach can thus deliver a scientific basis for corridor planning outside protected areas by combining habitat assessment, landscape permeability, and conflict risk mapping.

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