








Reducing persecution is more effective for restoring large carnivores than restoring their prey

BENJAMIN BLEYHL ^{1,2,15} ARASH GHODDOUSI ¹ ELSHAD ASKEROV,^{3,4,5} GRETA BOCEDI ⁶
 URS BREITENMOSER ^{7,8} KAREN MANVELYAN,⁹ STEPHEN C. F. PALMER,⁶ MAHMOOD SOOFI ^{6,10} PAUL WEINBERG,¹¹
 NUGZAR ZAZANASHVILI,^{5,12} VALERII SHMUNK,¹³ DAMARIS ZURELL ^{1,14} AND TOBIAS KUEMMERLE ^{1,2}

¹Geography Department, Humboldt Universität zu Berlin, Unter den Linden 6, Berlin 10099 Germany

²Integrative Research Institute on Transformations of Human-Environment Systems (IRI THESys), Humboldt Universität zu Berlin, Unter den Linden 6, Berlin 10099 Germany

³WWF-Azerbaijan, 6th Boyuk Gala dongesi 11, Sabayil rayon, Baku Az 1001 Azerbaijan

⁴Institute of Zoology of Azerbaijan Academy of Sciences, Block 504, pass 1128, A. Abbaszade Str, Baku Az 1073 Azerbaijan

⁵Institute of Ecology, Ilia State University, Cholokashvili Ave 3/5, Tbilisi 0162 Georgia

⁶School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ UK

⁷KORA, Thunstrasse 31, Muri bei Bern 3074 Switzerland

⁸Centre for Fish and Wildlife Health, Vetsuisse Faculty, University of Bern, Länggassstrasse 122, Bern 3012 Switzerland

⁹WWF-Armenia, 1111 Proshyan Str., Yerevan 0019 Armenia

¹⁰Department of Conservation Biology, University of Goettingen, Bürgerstr. 50, Göttingen 37073 Germany

¹¹North Ossetian Nature Reserve, 1 Basieva Str, RSO-Alania, Alagir 363245 Russia

¹²WWF Caucasus Programme Office, Aleksidze Str. 11, Tbilisi 0193 Georgia

¹³Russian Caucasus Ecoregional Office, WWF-Russia, Kommunarov Str., No. 268, Lit. D, Krasnodar 350042 Russia

¹⁴Institute for Biochemistry and Biology, University of Potsdam, Am Neuen Palais 10, Potsdam D-14469 Germany

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Abstract. Large carnivores are currently disappearing from many world regions because of habitat loss, prey depletion, and persecution. Ensuring large carnivore persistence requires safeguarding and sometimes facilitating the expansion of their populations. Understanding which conservation strategies, such as reducing persecution or restoring prey, are most effective to help carnivores to reclaim their former ranges is therefore important. Here, we systematically explored such alternative strategies for the endangered Persian leopard (*Panthera pardus saxicolor*) in the Caucasus. We combined a rule-based habitat suitability map and a spatially explicit leopard population model to identify potential leopard subpopulations (i.e., breeding patches), and to test the effect of different levels of persecution reduction and prey restoration on leopard population viability across the entire Caucasus ecoregion and northern Iran (about 737,000 km²). We identified substantial areas of potentially suitable leopard habitat (~120,000 km²), most of which is currently unoccupied. Our model revealed that leopards could potentially recolonize these patches and increase to a population of >1,000 individuals in 100 yr, but only in scenarios of medium to high persecution reduction and prey restoration. Overall, reducing persecution had a more pronounced effect on leopard metapopulation viability than prey restoration: Without conservation strategies to reduce persecution, leopards went extinct from the Caucasus in all scenarios tested. Our study highlights the importance of persecution reduction in small populations, which should hence be prioritized when resources for conservation are limited. We show how individual-based, spatially explicit metapopulation models can help in quantifying the recolonization potential of large carnivores in unoccupied habitat, designing adequate conservation strategies to foster such recolonizations, and anticipating the long-term prospects of carnivore populations under alternative scenarios. Our study also outlines how data scarcity, which is typical for threatened range-expanding species, can be overcome with a rule-based habitat map. For Persian leopards, our projections clearly suggest that there is a large potential for a viable metapopulation in the Caucasus, but only if major conservation actions are taken towards reducing persecution and restoring prey.

Key words: *Caucasus; dispersal; Panthera pardus; Persian leopard; poaching; population viability; prioritization; RangeShifter; Spatially explicit population model.*

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¹⁵E-mail: benjamin.bleyhl@geo.hu-berlin.de

INTRODUCTION

Large carnivores have been extirpated or are declining in many world regions, owing to the combined effects of habitat loss, prey depletion, and persecution (Ripple et al. 2014). As a consequence, large carnivore populations today are small, and restricted to isolated fragments of their former range (Wolf and Ripple 2017). This is concerning, given the important role that large carnivores play in food webs and ecosystems (Estes et al. 2011, Ripple et al. 2014). Protecting and restoring large carnivore populations are therefore central goals for conservation globally, yet doing so in increasingly human-dominated landscapes is extremely challenging (Di Minin et al. 2016).

Ensuring the persistence of large carnivores requires maintaining and sometimes increasing the number and sizes of their populations (Ripple et al. 2014). Past habitat transformation and fragmentation has compromised the ability of most landscapes to accommodate currently contiguous, large populations, and protected areas are generally too small to host viable populations (Linnell et al. 2005, AkÓakaya et al. 2007). One conservation approach is therefore to promote the establishment of metapopulations comprising multiple, connected subpopulations to ensure genetic exchange in patchy landscapes and allow for recolonizations of suitable but abandoned patches (AkÓakaya et al. 2007). Understanding the potential of landscapes to maintain such metapopulations, the connectivity between available patches, and the factors determining population viability is therefore key to large carnivore conservation.

Persecution and prey depletion (and their interactions) threaten population viability of large carnivores in many regions (Ripple et al. 2014). Large carnivore persecution has been reported as a major cause of population declines and can lead to local extinctions (Balme et al. 2009, Newby et al. 2013). Despite mostly being legally protected, large carnivores remain persecuted, killed for their fur and body parts, through conflict over livestock, or because they are perceived as a danger (Liberg et al. 2012, Ripple et al. 2014). Persecution reduction has allowed carnivore populations to recover in many cases (Balme et al. 2009, Persson et al. 2015). However, prey depletion is also indirectly threatening large carnivores (Wolf and Ripple 2016). In areas with declining prey biomass, large carnivores tend to have larger home range sizes and lower net reproduction, which often leads to declining populations (Fuller and Sievert 2001, Hayward et al. 2007). Additionally, without sufficient prey, large carnivores increasingly prey on livestock, which leads to retaliatory killings (Khorozyan et al. 2015).

Spatial information on persecution and prey abundance could help to evaluate which conservation strategies are effective to promote large carnivore metapopulations better. Nevertheless, such information is lacking for most regions. At the same time, implementing conservation strategies for large carnivores is

costly because protection must cover large areas, often across international borders. Thus, large carnivore conservation needs to be well-targeted, while typically being based on scarce data. Spatially explicit metapopulation models provide promising opportunities and can be used to both assess the impact of past conservation interventions or to predict the effect of potential future interventions on large carnivore metapopulation viability (Robinson et al. 2015, LaRue and Nielsen 2016, Oveden et al. 2019). Moreover, such models are highly informative in predicting which alternative conservation strategies, such as reducing persecution or restoring prey, have a larger impact on metapopulation viability (Chapron et al. 2008).

Here, we systematically explore the relative importance of persecution reduction and prey restoration on determining metapopulation viability of the endangered Persian leopard (*Panthera pardus saxicolor*; recently revised as *Panthera pardus tulliana* by Kitchener et al. 2017) across the entire Caucasus ecoregion. The Caucasus, located between the Black and the Caspian Seas, is a global biodiversity hotspot and once hosted a larger metapopulation of the Persian leopard and its prey (Krever et al. 2001, Mittermeier et al. 2004). Diminishing support for nature conservation, reduced enforcement of conservation laws, economic hardships, and armed conflicts led to a poaching crisis and subsequently extensive wildlife declines after the Iranian Revolution (1979) and the breakdown of the Soviet Union (1991) (Zazanashvili et al. 2012, Bragina et al. 2015, Ghoddousi et al. 2019). Yet, since 2000, the Caucasus has seen a substantial expansion of its protected area network and a slight recovery of some wildlife populations, highlighting a window of opportunity for large carnivore conservation (Montalvo Mancheno et al. 2016, Breitenmoser et al. 2017).

Recent habitat models suggest potential for a larger leopard metapopulation in the Caucasus (Zimmerman et al. 2007, Gavashelishvili and Lukarevskiy 2008). If conservation measures to restore such a metapopulation were initiated, many other species could potentially benefit due to the leopard's role as umbrella species (Dickman et al. 2015). Such a recovery would very likely depend on source populations in Iran (Breitenmoser et al. 2010, Caucasus Leopard Working Group 2017). In the southern Caucasus, leopards successfully reproduce, and sightings throughout the region, including the northern Greater Caucasus, may indicate that the population is expanding its range (Yarovenko and Zazanashvili 2016, Askerov et al. 2018). The small population size (<20 individuals, excluding Iran) nevertheless requires swift and targeted conservation actions to encourage range expansion, and it remains unclear which conservation strategies are more effective for doing so.

In this study, our goal was to assess the potential of two conservation strategies—reducing leopard persecution and restoring the wild prey base for leopards—to secure a viable leopard metapopulation in the Caucasus. More specifically, we asked (1) What is the potential

spatial structure and size of a future Persian leopard metapopulation in the Caucasus? (2) How do persecution reduction and prey restoration affect leopard metapopulation viability in the Caucasus?

Exploring these questions is widely relevant, as many other species of large carnivores face similar challenges to Persian leopards in the Caucasus. For example, Amur tiger (*Panthera tigris altaica*) recovery is challenging because tigers come into conflict with livestock owners and suffer from wild prey depletion (Li et al. 2019). Likewise, jaguars (*Panthera onca*) are rapidly disappearing from the Gran Chaco in South America, one of their strongholds until recently, owing to conflicts with ranchers, probably an indirect effect of a depleted prey base and habitat destruction (Romero-Muñoz et al. 2019). Yet, how to halt these losses effectively and how best to support large carnivore populations given limited conservation funding remains unclear (Ripple et al. 2014). Additionally, data on large carnivores are often lacking because of their elusive nature and small populations, which makes it challenging to assess alternative conservation strategies (Schadt et al. 2002, Amano and Sutherland 2013). Our study aims to answer such questions for a species and region with limited data and of high conservation concern.

MATERIALS AND METHODS

Persian leopards in the Caucasus and northern Iran

Our study region comprised the Caucasus ecoregion, as delineated by the Ecoregion Conservation Plan for

the Caucasus (Williams et al. 2006), and extended across the Talysh-Alborz Mountains in northern Iran (Fig. 1). The natural vegetation of the region comprises temperate, mainly broadleaf and mixed forests along the mountain ranges, but includes large areas of steppe drylands as well as arid woodlands and semideserts in the East. Most parts of our study region are mountainous, and elevations can reach more than 5,500 m.

Until at least the mid-18th century, Persian leopards occurred throughout the entire Caucasus (Jacobson et al. 2016). Today, resident population nuclei are restricted to the southern rim of the Lesser Caucasus (Khorozyan and Abramov 2007, Stein et al. 2016, Askerov et al. 2018). This population is severely threatened and dependent on the Iranian source population, which itself is likely to decline (Moqanaki et al. 2013). Leopards in the Caucasus prey mainly on large ungulates, which are nevertheless also under pressure from poaching and competition with livestock (Mallon et al. 2007, Bleyhl et al. 2019). In the Greater Caucasus, no leopard reproduction has been detected recently (Caucasus Leopard Working Group 2017), but since 2016, six leopards have been reintroduced to the Russian Greater Caucasus (see Appendix S1).

Spatial structure of a potential leopard metapopulation

To assess the structure of a potential leopard metapopulation, we first mapped suitable habitat. Leopards can thrive in a range of environments if prey is available (Nowell and Jackson 1996, Gavashelishvili and Lukarevskiy 2008). We developed a rule-based



FIG. 1. Study area, main mountain ranges, and the location of Golestan National Park in northeastern Iran. The right panel shows two camera trap pictures of the same leopard from the Zangezur region in Nakhchivan, Azerbaijan (top) and the Khosrov Forest State Reserve in Armenia (bottom). The locations are separated by a ~170-km straight-line distance. Photo credit: WWF-Caucasus.

habitat suitability model on a 5×5 km grid (mean maximum leopard movement distance between recaptures in a camera trap study; Ghoddousi et al. 2010). We used a range of predictors related to shelter and ambushing habitat, human-induced mortality risk, and snow cover, which characterize leopard habitat suitability (Breitenmoser et al. 2007, Lukarevsky et al. 2007). Specifically, we assumed increasing habitat suitability with increasing ruggedness or increasing forest cover in areas that are distant from roads and human settlements and have a low proportion of surrounding croplands (Zimmerman et al. 2007, Gavashelishvili and Lukarevskiy 2008). Further, we excluded areas with a very high snow cover in winter (see Appendix S1 for details on the specific rules used to derive the habitat suitability map). We purposefully did not use a correlative species distribution model, because only very few leopards are left in the Caucasus, and the species is far from being in equilibrium with its environment, which could introduce substantial bias in such models (Guisan and Thuiller 2005). To validate our habitat model, we used 36 leopard locations from camera traps and 53 locations from indirect signs such as scrapes or scats from WWF's Caucasus Programme Office and from other surveys (Soofi et al. 2018). We then calculated the continuous Boyce index (Hirzel et al. 2006) and the area under the ROC curve (AUC; using 10,000 random pseudo-absence points) as a measure of accuracy (Fielding and Bell 1997). The continuous Boyce index measures the correlation between the habitat suitability prediction and the predicted to expected ratio of the frequency of validation points using a moving window of differing widths (negative values indicating an inverse model, values around zero a random model, and one a perfect model; Boyce et al. 2002, Hirzel et al. 2006). The AUC value contrasts sensitivity and specificity across all possible thresholds, with values ranging from 0 to 1 (1 indicating a perfect model; Jiménez-Valverde 2012).

To identify potential subpopulations, we first selected those cells with a habitat suitability above the 25th percentile of values at our known leopard locations (Pitman et al. 2017). We then selected continuous suitable areas of at least 250 km^2 (i.e., ~ 2.5 home ranges and large enough to host breeding populations; Farhadinia et al. 2015, 2018). Although home range sizes for female leopards are known to be smaller (Fattebert et al. 2016), no study has assessed this specifically for Persian leopards. Before applying the minimum area threshold, we split subpopulation patches to exclude potential barriers such as roads and very high ridges within subpopulations because we did not model movement within patches. Accordingly, we split subpopulation patches using main roads (categories motorways, trunk, and primary, derived from Open Street Map) and the Russian border, which roughly follows the main ridge of the Greater Caucasus and is therefore typically at high elevations ($\sim 2,700$ m). Thereby, these barriers

remained permeable (through our dispersal model) but leopards could not transfer larger distances within patches and cross major roads and highways without having to disperse. We assessed the protection status of each patch using terrestrial protected areas from the World Database on Protected Areas (IUCN and UNEP-WCMC 2019) and WWF's Caucasus Programme Office database (wwfcaucasus.net; Appendix S1: Fig. S2).

Metapopulation parametrization

We parametrized a spatially explicit metapopulation model using the software RangeShifter (Bocedi et al. 2014). RangeShifter is an individual-based modeling platform, which integrates a demographic and a dispersal model to predict metapopulation dynamics. We developed a stage-structured model with four stages and annual time steps (Caswell 2001). Survival rates were based on all known stage-structured estimates for leopard populations anywhere in the world (i.e., studies from Botswana, Namibia, and South Africa; Table 1 and Appendix S1: Table S1). Mean fecundity (i.e., number of offspring per female per year) was set to 1.92 (Daly et al. 2005) and modeled as negatively density dependent (i.e., decreasing fecundity with increasing density; Table 2). Further, males could mate with up to three females, and only adults (older than 2 yr) were allowed to breed (Lukarevsky et al. 2007). Females in our model paused for 1 yr between reproductions (Daly et al. 2005). To consider environmental stochasticity (i.e., the effects of year-to-year variation in environmental conditions on demography), we applied random variation to mean fecundity so that it fluctuated between 1 and 4 (i.e., range of number of cubs reported from captivity; Lukarevsky et al. 2007: Eqs. 5, 6). We assumed an initial population of 352 individuals for our study area (based on a population size estimate of northern Iran; Kiabi et al. 2002). Because abundance of leopards in the area is not well known, we distributed these individuals randomly amongst patches with known leopard occurrence (i.e., patches with locations matching our presence data set or a neighboring cell, and patches that overlapped with a

TABLE 1. Female and male leopard survival rates that were used to characterize the three persecution reduction scenarios in our metapopulation model (based on Daly et al. 2005, Balme et al. 2009, Swanepoel et al. 2015, Balme et al. 2017).

Stage	Survival rate (female/male)		
	Persecution reduction scenario		
	Low	Medium	High
Juvenile (0–1 yr)	0.39/0.39	0.52/0.53	0.71/0.71
Subadult (1–2 yr)	0.79/0.54	0.90/0.79	0.98/0.94
Subadult (2–3 yr)	0.79/0.54	0.90/0.79	0.98/0.94
Adult (3+ yr)	0.86/0.67	0.89/0.85	0.95/0.94

TABLE 2. RangeShifter equations and parameters used to model the stage-structured leopard metapopulation. For details on the equations refer to Appendix S1.

Parameters	Value	Appendix S1 eq. no.
Demographic		
No. of stages	4 (1 juvenile, 2 subadults, 1 adult)	
Survival rates	Scenario dependent; see Table 1	
Fecundity ϕ_0	1.92	
Density dependence in fecundity [†]	$\phi_i = \phi_{0,i} \times e^{-b \sum_{j=1}^S \omega_{ij} N_{j,t}}$	eq. (S1)
Strength of density dependence (b):	Scenario dependent, see Appendix S1: Table S2	
No. of reproductive seasons/year	1	
Probability of being male (for newborns)	0.5	
Maximum number of female mates per male	3	
No. of reproductive seasons before subsequent reproduction (in our case, one season = 1 yr)	1	
Maximum age	19	
Initial population size	352	
Dispersal[‡]		
Density-dependent emigration probability [§]	$d = \frac{D_0}{1 + e^{-(bN_{i,t} - \beta)\alpha}}$	eq. (S4)
Maximum emigration probability D_0	1.0	
α (slope)	10.0	
β (inflection point)	0.5	
Density-dependent settlement probability [¶]	$p_s = \frac{S_0}{1 + e^{-(bN_{i,t} - \beta_s)\alpha_s}}$	eq. (S5)
Maximum settlement probability S_0	1.0	
α_s (slope)	-10.0	
β_s (inflection point)	0.5	
Perceptual range	1 cell (5 km)	
Maximum number of steps	28	
Directional persistence	2.5	
Environmental stochasticity		
Noise value $\epsilon\#$	$\epsilon_{t+1} = \kappa\epsilon_t + \omega_t\sqrt{1 - \kappa^2}$	eq. (S2)
Environmental stochasticity in fecundity	$\phi_{i,t+1} = \phi_{0,i}(1 + \epsilon_{t+1})$	eq. (S3)
Minimum and maximum fecundity	1 and 4	
Temporal autocorrelation κ	0.0	
Random variable ω	$N(0, 0.25)$	

[†]For this parameter's value, ϕ_i = fecundity of stage i ; $\phi_{0,i}$ = maximum fecundity of stage i at low densities; S = number of stages; ω_{ij} = contribution of stage j to the density dependence in the fecundity of stage i ; $N_{j,t}$ = number of individuals at time t in stage j .

[‡]Limited to the subadults.

[§]For this parameter's value, D_0 = maximum emigration probability, β = inflection point, α = slope, b = strength of density dependence, $N_{i,t}$ = number of individuals in patch i at time t .

[¶]For this parameter's value, S_0 = maximum settlement probability, β_s = inflection point, α_s = slope, b = strength of density dependence, $N_{i,t}$ = number of individuals in patch i at time t .

[#]For this parameter's value, κ = the autocorrelation coefficient, ω = a random variable.

protected area that is known to host leopards) and proportionally to patch size. We distributed individuals with equal sex ratio and drew initial ages from a Poisson distribution with a mean of 7 yr so that individuals were no older than 19 yr (Balme et al. 2013). Because survival rates were higher for females than for males, the adult sex ratio in our models was slightly female-biased (1:1.10–1:1.39 m/f).

We modeled dispersal of subadults among patches using the stochastic movement simulator implemented in RangeShifter, a step-based model that accounts for interaction between individual movements and landscape structure (Palmer et al. 2011; see Appendix S1). We set our maximum dispersal distance to 170 km, based on the Euclidean distance between the Zangezur

Range in southern Azerbaijan and Khosrov Forest State Reserve in Armenia—a distance that was recently completed by an identified subadult leopard, presenting the longest documented dispersal event in the region (Askerov et al. 2018). Individuals died if they reached this distance without settling in a patch. Further, we modeled the probability for each subadult individual to disperse from a patch and to settle in a patch as a density-dependent function (see Appendix S1 and Table 2 for equations and an overview of all RangeShifter parameters used in our models). To estimate cell-wise resistance to movement, we used a leopard-specific cost surface based on the land cover of each cell from Bleyhl et al. (2017). We also tested our inverted habitat map as a cost surface (Fattebert et al. 2015b), which did not

result in substantial differences in regard to our model outcomes.

We ran 100 model replicates and calculated the mean total number of individuals per year and 99% confidence intervals for 100 simulated years. We chose 100 yr because we wanted to assess possible conservation strategies and population prospects in the long run, and initial models indicated that (sub-)population extinction sometimes occurred after more than 60 yr. Further, we calculated metapopulation extinction probability as the proportion of model replicates with no individuals after 100 yr. Finally, we calculated the probability of each patch being occupied by at least one leopard after 100 yr, by dividing the number of times a patch was occupied after 100 yr by the total number of replicate runs.

Persecution reduction scenarios

To assess the effect of persecution reduction on leopard metapopulation viability, we increased leopard survival rates of all stages (Chapron et al. 2008, Liberg et al. 2012). We used minimum, mean, and maximum values from our survival rate estimates as high, medium, and low persecution reduction scenarios (Table 1 and Appendix S1: Table S1; Daly et al. 2005, Balme et al. 2009, Swanepoel et al. 2015, Balme et al. 2017).

Prey restoration scenarios

Prey availability is an important factor in determining leopard density (Fuller and Sievert 2001, Hayward et al. 2007, Ghoddousi et al. 2017). Therefore, we simulated different prey restoration scenarios by altering possible leopard densities in relation to available prey biomass (Hayward et al. 2007). To calculate the available prey biomass, we used past and present estimates for bezoar goat (*Capra aegagrus*) and urial sheep (*Ovis vignei*) from Golestan National Park in northeastern Iran (see Appendix S1; Ghoddousi et al. 2019). From the available prey biomasses, we estimated that the leopard subpopulation patches could sustain 0.856 individuals/100 km² in a low prey restoration scenario, 3.817 individuals/100 km² in a medium prey restoration scenario, and 6.778 individuals/100 km² in a high prey restoration scenario using the following equation from Hayward et al. (2007):

$$\log_{10}(\text{leopard density}) = -2.455 + 0.456 \\ \times (\log_{10}(\text{prey biomass})) \quad (1)$$

Sensitivity analysis

First, we assessed model sensitivity to survival rates, fecundity, and strength of density dependence. Using the medium persecution reduction and medium prey restoration scenario, we conducted a sensitivity analysis

assessing how decreasing and increasing each parameter by 5% changed our two main model outcomes: extinction probability and leopard abundance after 100 yr. Second, we tested how altering the maximum dispersal distance from 170 to 47 km and 353 km (maximum dispersal distances in Fattebert et al. 2015a and in Fattebert et al. 2013, respectively) and the initial population size from 352 individuals to 200 and 500 individuals would affect model outcomes. Third, the sex ratio in leopard populations is often female biased, because males tend to have larger home ranges and are territorial (Bailey 1993, Kittle et al. 2017, Kumar et al. 2019). Additionally, subadult males tend to have lower survival rates than females due to human-caused mortality, which can lead to female-biased sex ratios (Thapa 2014). Therefore, we also tested altering the sex ratio of our initial population from 1:1 to 1:2 and 1:3 (male/female). Fourth, female leopards often tend to be more philopatric than males (Fattebert et al. 2015a). We therefore tested decreasing the maximum emigration probability (at high densities) for females incrementally from 1.0 to 0.1 (in steps of 0.1). Finally, we assessed sensitivity of our model towards the ongoing reintroductions of leopards to the Russian Greater Caucasus by having additional individuals at model initialization in Russia (see Appendix S1 for further detail on the sensitivity analyses).

RESULTS

Our habitat suitability map had a high accuracy in predicting known leopard occurrences (continuous Boyce index of 0.73 and an AUC of 0.86). Suitable leopard habitat was widespread across the study area (Fig. 2). In total, we identified 74 potential subpopulation patches that together covered 119,552 km². Patches varied greatly in size (range 250–18,478 km², mean: 1,616 km², standard deviation 2,779 km²). We identified potential subpopulation patches in all six countries of the Caucasus ecoregion. Russia had the largest total patch area (40,534 km²), followed by Iran (34,757 km²) and Georgia (16,978 km²; Table 3). Several large patches were located in the Greater Caucasus (in total 58,930 km²) and along the Talysh-Alborz Mountains in southern Azerbaijan and northern Iran (31,995 km²). Almost one quarter (23%) of the total subpopulation patch area is currently protected. The proportion of protected area differed among countries with Russia having the highest (32%) and Turkey the lowest proportion protected (8%; Table 3).

Our metapopulation model showed that we could expect the establishment of a stable population given the current initial population size under a scenario of medium persecution reduction and medium prey restoration (Fig. 3). High prey restoration (with medium persecution reduction) resulted in moderate population increases, with up to 537 individuals on average after 100 yr (53% increase over initial abundance). For the high persecution reduction scenarios, substantial

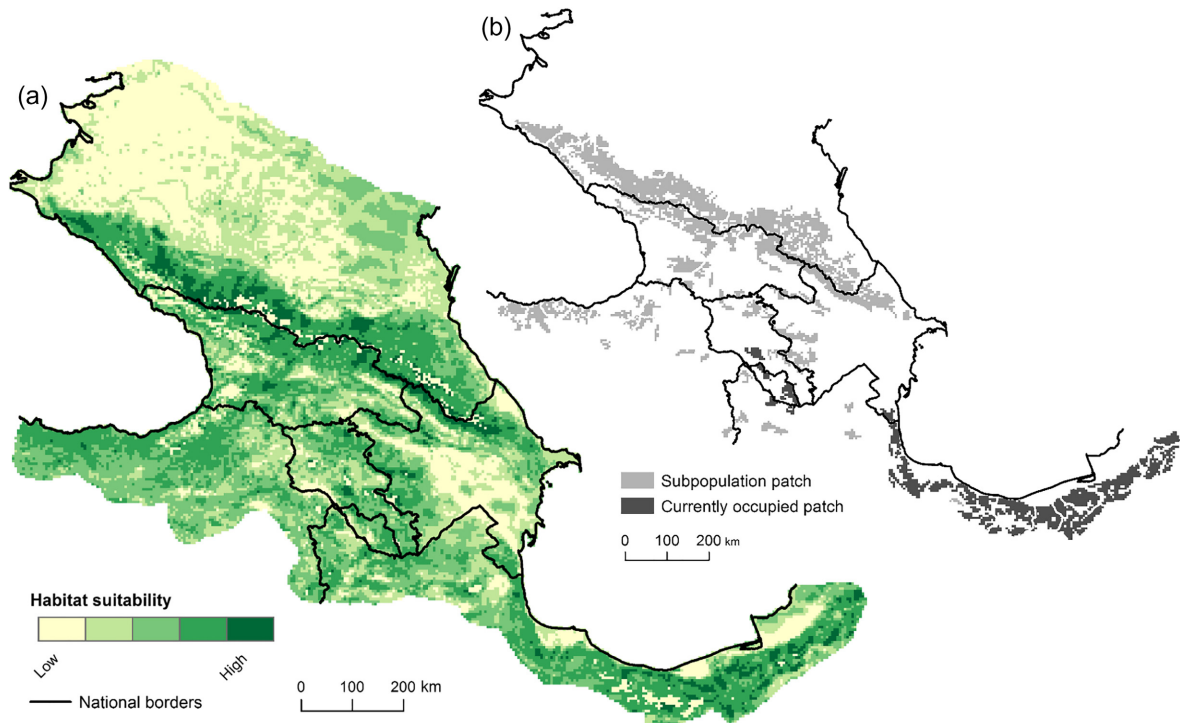


FIG. 2. (a) Distribution of suitable leopard habitat and (b) potential leopard subpopulation patches and currently occupied patches across the Caucasus ecoregion and northern Iran (see Appendix S1: Fig. S3 for details).

TABLE 3. The number and total area of subpopulation patches per country and the respective proportion of these patches that is under protection.

Country	No. subpopulation patches†	Subpopulation patch area [km ²]	Area under protection [%]
Armenia	6	3,467	14
Azerbaijan	9	13,084	27
Georgia	13	16,978	15
Iran	22	34,757	19
Russia	12	40,534	32
Turkey	15	10,732	8
Total	74	119,552	23

†Patches crossing country borders were counted if at least 250 km² were located in the respective country.

population increases were only possible when combined with medium to high levels of prey restoration. Specifically, high persecution reduction led to mean population increases of up to 1,048–2,288 individuals (3-fold to 6.5-fold increase after 100 yr) for medium and high prey restoration, respectively. Additionally, extinction probability after 100 yr was 0% for all high persecution reduction scenarios and for medium persecution reduction paired with medium prey restoration. However, extinction probability increased to 86% for low prey restoration under medium persecution reduction. Low persecution reduction led to sharp population declines

and the metapopulation went extinct after at most 60 yr, regardless of prey restoration.

The mountain range of the Greater Caucasus (northern part of our study area; Fig. 1) was colonized within 100 yr only in the high persecution reduction scenarios, assuming medium to high prey availability (Fig. 4). Nevertheless, the currently occupied patches in the Lesser Caucasus and Iran remained occupied after 100 yr also for the medium persecution reduction scenarios if prey restoration was medium or high.

Our metapopulation model was relatively robust to variations in survival rates, fecundity, and the strength of density dependence (Fig. 5). Changing the adult female survival rate had the strongest effect on mean leopard abundance after 100 yr (5% decrease in survival rate led to 53% decrease in abundance, whereas a 5% increase in survival rate led to 34% increase in abundance). Altering the maximum dispersal distance (to 47 and 353 km) did not affect extinction probability but had an effect on the resulting leopard abundance after 100 yr (Appendix S1: Fig. S4). Altering the initial population size (to 200 and 500 individuals) did not affect model outcomes markedly (Appendix S1: Fig. S4). Initial sex ratios of 1:2 and 1:3 (m/f) did not lead to notable differences in leopard abundance and extinction probability (260 individuals after 100 yr on average for sex ratios of 1:2 and 1:3 instead of 258 individuals for the mean persecution reduction and prey restoration scenario and no change in extinction probability).

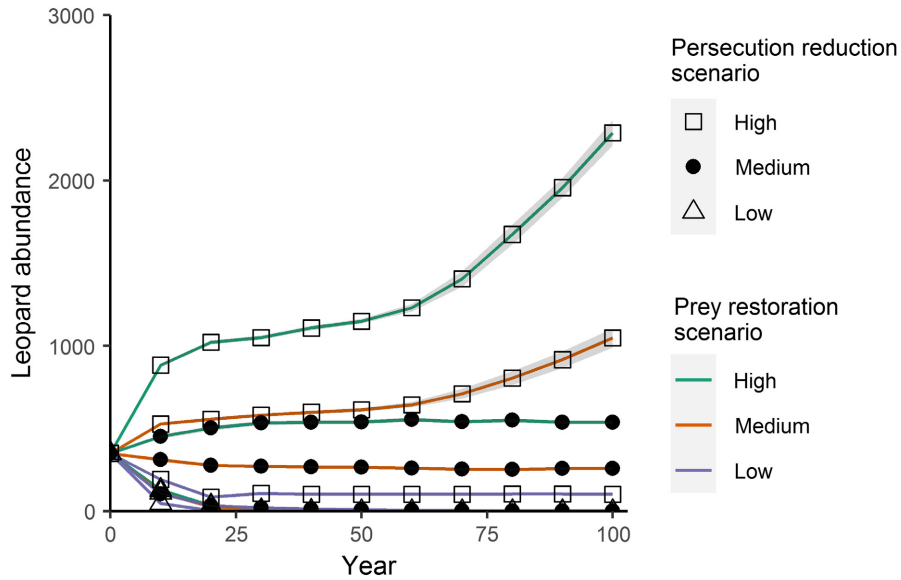


FIG. 3. Leopard total population size across the nine conservation scenarios for 100 yr. The solid lines show mean estimates and the shaded bands 99% confidence intervals. The Caucasus leopard metapopulation went extinct within 60 yr for all three scenarios with little investment into reducing persecution and therefore, those results are not visible in the graph.

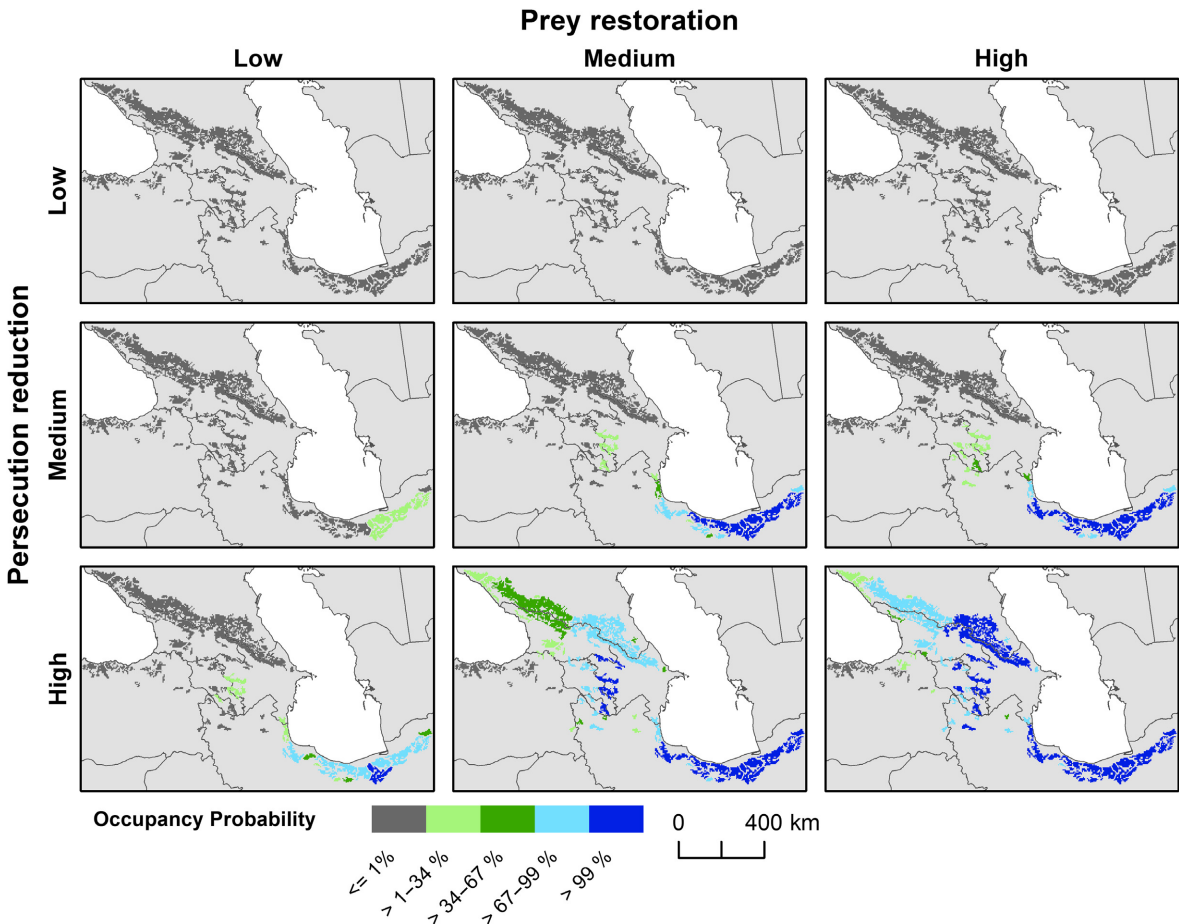


FIG. 4. Probability of leopard occurrence after 100 yr in a patch (the proportion of replicate simulations in which a patch was occupied after 100 yr) for all combinations of persecution and prey restoration scenarios.

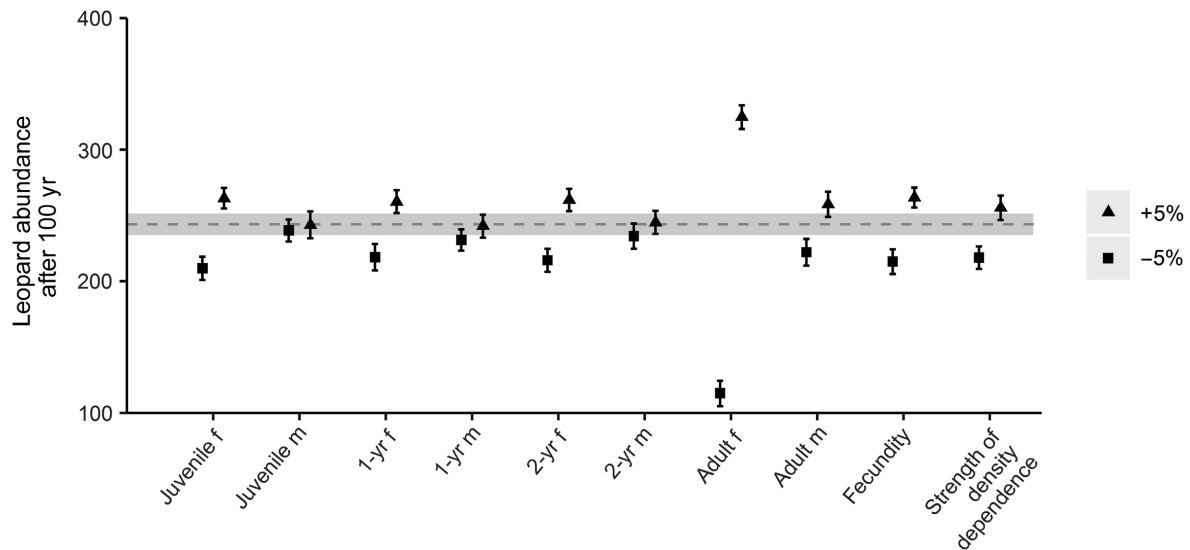


FIG. 5. Sensitivity of leopard abundance after 100 yr towards increasing and decreasing survival rates (first eight parameters), fecundity, and strength of density dependence of the medium persecution reduction and prey restoration scenario by 5% (f = female, m = male). Symbols indicate mean values; error bars show 99% confidence intervals. The dashed gray line and the shaded area show the mean value and 99% confidence interval for the medium persecution reduction and prey restoration scenario.

Decreasing the maximum emigration probability for females also did not lead to marked changes of our model outcomes (Appendix S1: Table S4). Adding additional individuals at model initialization to the Greater Caucasus to test model sensitivity to ongoing reintroductions in that area did not affect our high and low persecution reduction scenarios (no change in extinction probability, only slight changes in leopard abundance). However, we detected some effect on model outcomes for the medium persecution reduction scenarios, where 5–50 additional leopards in the Greater Caucasus led to a 10–90% higher abundance after 100 yr and a decreased extinction probability (Appendix S1: Table S4 and Fig. S8).

DISCUSSION

Given the wide-ranging nature of large carnivores, ensuring their persistence and fostering their recovery can be a colossal task: where should conservation action start, and which strategies are most effective? In our study, conservation measures to reduce persecution, and thus the killing of leopards, had a much higher impact on the long-term viability of the leopard population than that of prey restoration, underlining the often devastating effect of losing individuals in small populations and suggesting a high sensitivity of large carnivore populations to increased levels of mortality. Using the case of the endangered Persian leopard in the Caucasus, we investigated three key issues of relevance for many situations where information on large carnivore population dynamics is scarce, thereby hindering the identification of promising conservation strategies. First, we explored the relative importance of conservation actions that

target human persecution of large carnivores and depletion of their prey base, which are central drivers of large carnivore decline globally. Second, we show how an individual-based, spatially explicit simulation framework can be used to assess potential pathways for restoring large carnivores. Third, we outline an approach that works for data-deficient regions and species, which is a typical situation for large carnivores worldwide. For the Caucasus, our study clearly suggests a large potential for leopards to recolonize unoccupied habitat and establish a viable metapopulation—if conservation measures are ramped up.

Using a rule-based habitat assessment, we identified abundant potential leopard habitat across the mountain ranges of our study area (i.e., Greater and Lesser Caucasus, Talysh-Alborz Mountains). This is in line with previous studies mapping leopard habitat suitability in parts of our study area (Zimmerman et al. 2007, Gavashelishvili and Lukarevskiy 2008, Farhadinia et al. 2015, Ebrahimi et al. 2017). Our assessment highlights the importance of the Lesser Caucasus, the only region where leopard reproduction currently occurs in the Caucasus. Moreover, the Greater Caucasus could play a major role in leopard recovery, because it contains almost half of the area of all potential subpopulation patches we identified. Parts of these subpopulation patches are already under protection (32% and 15% in Russia and Georgia, respectively). However, it is unlikely that leopards are currently breeding in the Greater Caucasus, and considering the characteristics of felid populations in recolonizing their historical range, it is likely that only long-range dispersing males will arrive there from the Lesser Caucasus in the near future.

Our metapopulation analysis clearly suggests that high mortality is the principal factor constraining leopard population growth in the region. Only high persecution reduction led to a substantial population increase, whereas low persecution reduction led to sharp population decreases. All prey depletion scenarios had smaller effects on our model outcomes. Although some studies and historic hunting bags indicate that large carnivores are fairly resilient to high rates of offtake and thus low survival rates (Lindzey et al. 1992, Karanth and Stith 1999), our results suggest that leopard populations are susceptible to high mortality, at least when persecution is not sex-biased (which we did not test). This corroborates studies highlighting low survival rates as a main determinant of large carnivore declines (Dalerum et al. 2008, Balme et al. 2009, Williams et al. 2017). Historically, larger population sizes or nearby source populations could have contributed to buffer high mortality rates (Chapron et al. 2008). Today, many large carnivores occur in small and isolated populations, where the death of only a few individuals can substantially increase the extinction probability of the population, underlining the importance of effective law enforcement and conflict mitigation measures to reduce persecution (Heurich et al. 2018, Bisht et al. 2019).

Persian leopards are under marked pressure from persecution, particularly outside protected areas (Kiabi et al. 2002, Naderi et al. 2018). Several leopards have been killed in the Lesser Caucasus or observed missing a limb, indicating the use of snare and gin traps (Memarian et al. 2018), and the only confirmed transboundary leopard in the Talysh Mountains was poached in 2014 (Maharramova et al. 2018). Positive effects of persecution reduction on large carnivore populations have been shown also for other regions. For example, leopard population growth rates increased by about 15% after implementing conflict mitigation measures such as promoting alternative husbandry methods to prevent livestock depredation in South Africa (Balme et al. 2009). Likewise, preventing persecution lowered the modeled extinction probability of a lynx (*Lynx lynx*) population in the Bohemian Forest in Europe from up to 74% to <1% (Heurich et al. 2018). Although our analyses highlight avenues to lower leopard mortality in the Caucasus, it is worrying that three-quarters of the subpopulation patch area we identified are unprotected, making the implementation of measures to reduce persecution challenge effectively.

Despite the importance of persecution reduction, our results suggest that prey restoration is also needed to increase the carrying capacity for leopards, and hence their abundance and density, and to decrease their population extinction probability. The situation we found for Persian leopards is likely exemplary for many threatened large carnivores. Prey depletion is a major threat to large carnivores globally, because large herbivores, which constitute the majority of large carnivore prey, are mostly threatened themselves (Wolf and Ripple 2016). For

example, decreases in ungulate densities likely led to the absence of tigers (*P. tigris*) in the Mundanthurai reserve in India (Ramakrishnan et al. 1999). Likewise, in Central Asia, an increase in livestock numbers reduced native ungulate densities, which both led to more snow leopard attacks on livestock and in turn to more human retaliatory killings of snow leopards (Berger et al. 2013). Additionally, even our medium prey restoration scenario was based on prey abundances from a relatively prey-rich and strictly protected area in Iran (Ghoddousi et al. 2019). Therefore, current potential leopard densities are likely to lie closer to our lowest prey restoration scenario, underlining that sufficient prey is essential to prevent population declines (Zimmerman et al. 2007). Often, a combination of persecution reduction and prey restoration is needed to foster population increases of large carnivores (Jędrzejewski et al. 2017).

We used all available data on leopards to parametrize a spatially explicit metapopulation model across a large and heterogeneous biodiversity hotspot. Nevertheless, some challenges remain. First, some measures to reduce leopard persecution, such as stricter law enforcement against poaching, will likely also have a positive impact on prey availability. Yet, our model does not include such possible cobenefits. Second, neither persecution reduction nor prey restoration will act consistently across space and stage classes. For example, low survival rates of some subpopulations might be compensated by immigration from neighboring populations, which we did not consider (Chapron et al. 2008). Third, variability in survival rates, for example, due to extreme weather events, disease outbreaks, or periods of heavy poaching can have large impacts on population viability, particularly in small populations (Melbourne and Hastings 2008). Because Range-Shifters does not currently allow for variability in survival rates, we could not account for this in our model, and might therefore partly underestimate the extinction risk of leopards in the Caucasus. Finally, our habitat map possibly overestimated subpopulation patches in areas that encompass small-scale agriculture or tree crops (e.g., northern Turkey), because these were not differentiated from forest in our land-cover map (Bleyhl et al. 2017). Leopards are highly adaptable and persist well in such landscapes, but we caution that human–leopard conflict might be high (Navya et al. 2014).

Limited resources require conservation efforts to be targeted towards the most effective strategies. Three general insights for large carnivore conservation may be derived from our work. First, our study highlights the importance of preventing the loss of individuals in small populations. Reducing persecution had a much higher impact on the long-term population survival than prey restoration, making a case for actions to reduce human–carnivore conflicts that might lead to carnivore killings (e.g., compensation schemes, adapted livestock husbandry practices, promoting tolerance, and awareness raising). Second, our work shows the potential of individual-based, spatially explicit metapopulation

models to assess where large carnivores may recolonize suitable habitat, compare conservation strategies to promote such recolonizations, and quantify the long-term prospects of carnivore populations under alternative scenarios. Finally, our study outlines how data-sparse situations can be overcome, which are typical for threatened range-expanding or recovering species that are far from occupying all suitable areas (Guisan and Thuiller 2005, Fechter and Storch 2014). Our rule-based habitat map validated favorably against known leopard presence locations, highlighting the value of such a relatively simple approach for assessing and predicting large carnivore recolonizations when combined with a mechanistic population model.

For Persian leopards, our results contribute to the implementation of the objectives outlined in the Strategy for the Conservation of the Leopard in the Caucasus Ecoregion (Caucasus Leopard Working Group 2017). We clearly show that the Caucasus can indeed host a viable leopard metapopulation if appropriate conservation measures are augmented, and we highlight the patches that are likely important for establishing such a metapopulation. Measures to reduce persecution should be targeted at carnivore-adapted livestock husbandry (e.g., corralling vulnerable animals at night, guards during the day, well-trained guarding dogs; Balme et al. 2009, Khorozyan et al. 2017). Particularly since the early 2000s, many protected areas have been established in the Lesser Caucasus to prevent leopard persecution and to restore prey populations more effectively (Zazanashvili et al. 2020). Further, through the active involvement of local people, leopard and prey species monitoring has substantially increased, allowing for better predictions of population trends and conflict hotspots (Zazanashvili et al. 2020). Our results can thereby assist in identifying areas that are likely to be recolonized, and we suggest proactive actions such as improving awareness and tolerance amongst local people, and prey restorations in those patches to support leopard range expansion.

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LITERATURE CITED

- AkÓakaya, H. R., G. Mills, and C. P. Doncaster. 2007. The role of metapopulations in conservation. Pages 64–84 in D. MacDonald and K. J. Willis, editors. Key topics in conservation biology. Blackwell Publishing, Oxford, UK.
- Amano, T., and W. J. Sutherland. 2013. Four barriers to the global understanding of biodiversity conservation: wealth, language, geographical location and security. *Proceedings of the Royal Society B* 280:20122649.
- Askerov, E., T. Talibov, K. Manvelyan, N. Zazanashvili, P. Fatullayev, and A. Malkhasyan. 2018. Leopard (*Panthera pardus*) reoccupying its historic range in the South Caucasus: a first evidence (Mammalia: Felidae). *Zoology in the Middle East* 65:88–90.
- Bailey, T. N. 1993. *The African leopard*. Columbia University Press, New York, New York, USA.
- Balme, G. A., A. Batchelor, N. de Woronin Britz, G. Seymour, M. Grover, L. Hes, D. W. Macdonald, and L. T. B. Hunter. 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* 43:221–237.
- Balme, G. A., R. T. Pitman, H. S. Robinson, J. R. B. Miller, P. J. Funston, and L. T. B. Hunter. 2017. Leopard distribution and abundance is unaffected by interference competition with lions. *Behavioral Ecology* 28:1348–1358.
- Balme, G. A., R. Slotow, and L. T. B. Hunter. 2009. Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation* 142:2681–2690.
- Berger, J., B. Buuveibaatar, and C. Mishra. 2013. Globalization of the cashmere market and the decline of large mammals in Central Asia. *Conservation Biology* 27:679–689.
- Bisht, S., S. Banerjee, Q. Qureshi, and Y. Jhala. 2019. Demography of a high-density tiger population and its implications for tiger recovery. *Journal of Applied Ecology* 56:1725–1740.
- Bleyhl, B., et al. 2021. Data to the publication Reducing persecution is more effective for restoring large carnivores than restoring their prey. *Ecological Applications* e2338. Figshare, data set. <https://doi.org/10.6084/m9.figshare.12280910>
- Bleyhl, B., M. Baumann, P. Griffiths, A. Heidelberg, K. Manvelyan, V. C. Radeloff, N. Zazanashvili, and T. Kuemmerle. 2017. Assessing landscape connectivity for large mammals in the Caucasus using Landsat 8 seasonal image composites. *Remote Sensing of Environment* 193:193–203.
- Bleyhl, B., et al. 2019. Assessing niche overlap between domestic and threatened wild sheep to identify conservation priority areas. *Diversity and Distributions* 25:129–141.
- Bocedi, G., S. C. F. Palmer, G. Pe'er, R. K. Heikkinen, Y. G. Matsinos, K. Watts, and J. M. J. Travis. 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution* 5:388–396.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Bragina, E. V., A. R. Ives, A. M. Pidgeon, T. Kuemmerle, L. M. Baskin, Y. P. Gubar, M. Piquer-Rodríguez, N. S. Keuler, V. G. Petrosyan, and V. C. Radeloff. 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. *Conservation Biology* 184:456–464.
- Breitenmoser, U., E. Askerov, M. Soofi, C. Breitenmoser-Würsten, A. Heidelberg, K. Manvelyan, and N. Zazanashvili. 2017. Transboundary leopard conservation in the Lesser Caucasus and the Alborz Range. *Cat News* 65:24–25.
- Breitenmoser, U., C. Breitenmoser-Würsten, F. Mörschel, N. Zazanashvili, and M. Sylvén. 2007. General conditions for the conservation of the leopard in the Caucasus. *Cat News Special Issue* 2:34–39.
- Breitenmoser, U., I. Shavgulidze, E. Askerov, I. Khorozyan, M. S. Farhadinia, E. Can, C. Bilgin, and N. Zazanashvili. 2010. Leopard conservation in the Caucasus. *Cat News* 53:39–40.
- Caswell, H. 2001. *Matrix population models: Construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.

- Caucasus Leopard Working Group. 2017. Strategy for the Conservation of the Leopard in the Caucasus Ecoregion. Revised Version 2017. IUCN/SSC Cat Specialist Group, Muri b, Bern, Switzerland.
- Chapron, G., D. G. Miquelle, A. Lambert, J. M. Goodrich, S. Legendre, and J. Clobert. 2008. The impact on tigers of poaching versus prey depletion. *Journal of Applied Ecology* 45:1667–1674.
- Dalerum, F., B. Shults, and K. Kunkel. 2008. Estimating sustainable harvest in wolverine populations using logistic regression. *Journal of Wildlife Management* 72:1125–1132.
- Daly, B., J. Power, G. Camacho, K. Traylor-Holzer, S. Barber, S. Catterall, P. Fletcher, Q. Martins, N. Martins, and C. Owen. 2005. Leopard (*Panthera pardus*) population and habitat viability assessment. In *Proceedings of a Workshop of the Conservation Breeding Specialist Group (World Conservation Union (IUCN) Species Survival Commission)*. Endangered Wildlife Trust, Johannesburg, South Africa.
- Di Minin, E., R. Slotow, L. T. B. Hunter, F. Montesino Pouzols, T. Toivonen, P. H. Verburg, N. Leader-Williams, L. Petracca, and A. Moilanen. 2016. Global priorities for national carnivore conservation under land use change. *Scientific Reports* 6:23814.
- Dickman, A. J., A. E. Hinks, E. A. Macdonald, D. Burnham, and D. W. Macdonald. 2015. Priorities for global felid conservation. *Conservation Biology* 29:854–864.
- Ebrahimi, A., A. Farashi, and A. Rashki. 2017. Habitat suitability of Persian leopard (*Panthera pardus saxicolor*) in Iran in future. *Environmental Earth Sciences* 76:697.
- Estes, J. A., et al. 2011. Trophic downgrading of planet earth. *Science* 333:301–306.
- Farhadinia, M. S., M. Ahmadi, E. Sharbafi, S. Khosravi, H. Alinezhad, and D. W. Macdonald. 2015. Leveraging transboundary conservation partnerships: Persistence of Persian leopard (*Panthera pardus saxicolor*) in the Iranian Caucasus. *Biological Conservation* 191:770–778.
- Farhadinia, M. S., P. J. Johnson, D. W. Macdonald, and L. T. B. Hunter. 2018. Anchoring and adjusting amidst humans: ranging behavior of Persian leopards along the Iran–Turkmenistan borderland. *PLoS One* 13:e0196602.
- Fattebert, J., G. Balme, T. Dickerson, R. Slotow, and L. Hunter. 2015a. Density-dependent natal dispersal patterns in a leopard population recovering from over-harvest. *PLoS One* 10:e0122355.
- Fattebert, J., G. A. Balme, H. S. Robinson, T. Dickerson, R. Slotow, and L. T. B. Hunter. 2016. Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology* 299:153–162.
- Fattebert, J., T. Dickerson, G. Balme, R. Slotow, and L. Hunter. 2013. Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South African Journal of Wildlife Research* 43:61–67.
- Fattebert, J., H. S. Robinson, G. Balme, R. Slotow, and L. Hunter. 2015b. Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications* 25:1911–1921.
- Fechter, D., and I. Storch. 2014. How many wolves (*Canis lupus*) fit into Germany? The role of assumptions in predictive rule-based habitat models for habitat generalists. *PLoS One* 9:e0101798.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Pages 163–178 in J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. *Carnivore conservation*. Cambridge University Press, Cambridge, UK.
- Gavashelishvili, A., and V. Lukarevskiy. 2008. Modelling the habitat requirements of leopard *Panthera pardus* in west and central Asia. *Journal of Applied Ecology* 45:579–588.
- Ghoddousi, A., A. K. Hamidi, T. Ghadirian, D. Ashayeri, and I. Khorozyan. 2010. The status of the endangered Persian leopard *Panthera pardus saxicolor* in Bamu National Park, Iran. *Oryx* 44:551–557.
- Ghoddousi, A., M. Soofi, A. K. Hamidi, S. Ashayeri, L. Egli, S. Ghoddousi, J. Speicher, I. Khorozyan, B. H. Kiabi, and M. Waltert. 2019. The decline of ungulate populations in Iranian protected areas calls for urgent action against poaching. *Oryx* 53:151–158.
- Ghoddousi, A., M. Soofi, A. K. Hamidi, T. Lumetsberger, L. Egli, S. Ashayeri, I. Khorozyan, B. H. Kiabi, and M. Waltert. 2017. When pork is not on the menu: assessing trophic competition between large carnivores and poachers. *Biological Conservation* 209:223–229.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Hayward, M. W., J. O'Brien, and G. I. H. Kerley. 2007. Carrying capacity of large African predators: predictions and tests. *Biological Conservation* 139:219–229.
- Heurich, M., J. Schultze-Naumburg, N. Piacenza, N. Magg, J. Cervený, T. Engleder, M. Herdtfelder, M. Sladova, and S. Kramer-Schadt. 2018. Illegal hunting as a major driver of the source–sink dynamics of a reintroduced lynx population in Central Europe. *Biological Conservation* 224:355–365.
- Hirzel, A. H., G. Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- IUCN, and UNEP-WCMC. 2019. *The World Database on Protected Areas (WDPA)*. WCMC, Cambridge, UK.
- Jacobson, A. P., et al. 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4:e1974.
- Jędrzejewski, W., et al. 2017. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (*Panthera onca*) in Venezuela. *Biological Conservation* 206:132–142.
- Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* 21:498–507.
- Karanth, K. U., and B. M. Stith. 1999. Prey depletion as a critical determinant of tiger population viability. Pages 100–113 in J. Seidensticker, S. Christie, and P. Jackson, editors. *Riding the tiger: tiger conservation in human dominated landscapes*. Cambridge University Press, Cambridge, UK.
- Khorozyan, I. G., and A. V. Abramov. 2007. The leopard, *Panthera pardus* (Carnivora: Felidae) and its resilience to human pressure in the Caucasus. *Zoology in the Middle East* 41:11–24.
- Khorozyan, I., A. Ghoddousi, M. Soofi, and M. Waltert. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biological Conservation* 192:268–275.
- Khorozyan, I., M. Soofi, M. Soufi, A. K. Hamidi, A. Ghoddousi, and M. Waltert. 2017. Effects of shepherds and dogs on livestock depredation by leopards (*Panthera pardus*) in north-eastern Iran. *PeerJ* 5:e3049.
- Kiabi, B. H., B. F. Dareshouri, R. A. Ghaemi, and M. Jahan-shahi. 2002. Population status of the Persian Leopard (*Panthera pardus saxicolor* Pocock, 1927) in Iran. *Zoology in the Middle East* 26:41–47.

- Kitchener, A. C., C. Breitenmoser-Würsten, E. Eizirik, A. Geny, L. Werdelin, A. Wilting, N. Yamaguchi, and W. E. J. C. N. Johnson. 2017. A revised taxonomy of the Felidae: The final report of the Cat Classification Task Force of the IUCN Cat Specialist Group. *Cat News Special Issue* 11:1–80.
- Kittle, A. M., A. C. Watson, and T. S. P. Fernando. 2017. The ecology and behaviour of a protected area Sri Lankan leopard (*Panthera pardus kotiya*) population. *Tropical Ecology* 58:71–86.
- Kremer, V., N. Zazanashvili, H. Jungius, L. Williams, and D. Petelin, editors. 2001. Biodiversity of the Caucasus ecoregion: an analysis of biodiversity and current threats and initial investment portfolio. World Wide Fund for Nature, Baku, Erevan, Gland, Moscow, Tbilisi.
- Kumar, U., N. Awasthi, Q. Qureshi, and Y. Jhala. 2019. Do conservation strategies that increase tiger populations have consequences for other wild carnivores like leopards? *Scientific Reports* 9:14673.
- LaRue, M. A., and C. K. Nielsen. 2016. Population viability of recolonizing cougars in midwestern North America. *Ecological Modelling* 321:121–129.
- Li, Z., T. Wang, J. L. D. Smith, R. Feng, L. Feng, P. Mou, and J. Ge. 2019. Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia. *Landscape Ecology* 34:291–305.
- Liberg, O., G. Chapron, P. Wabakken, C. Pedersen Hans, N. T. Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B* 279:910–915.
- Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar population response to manipulation in southern Utah. *Wildlife Society Bulletin* 20:224–227.
- Linnell, J. D. C., C. Promberger, L. Boitani, J. E. Swenson, U. Breitenmoser, and R. Andersen. 2005. The linkage between conservation strategies for large carnivores and biodiversity: the view from the “half-full” forests of Europe. Pages 381–398 in J. C. Ray, K. H. Redford, R. S. Steeneck, and J. Berger, editors. *Carnivores and the conservation of biodiversity*. Island Press, Washington, D.C., USA.
- Lukarevsky, V., A. Malkhasyan, and E. Askerov. 2007. Biology and ecology of the leopard in the Caucasus. *Cat News Special Issue* 2:9–14.
- Maharramova, E., E. M. Moqanaki, E. Askerov, S. Faezi, H. Alinezhad, M. Mousavi, T. Kuemmerle, A. Heidelberg, and N. Zazanashvili. 2018. Transboundary leopard movement between Azerbaijan and Iran in the Southern Caucasus. *Cat News* 67:8–10.
- Mallon, D., P. Weinberg, and N. Kopalani. 2007. Status of the prey species of the leopard in the Caucasus. *Cat News Special Issue* 2:22–27.
- Melbourne, B. A., and A. Hastings. 2008. Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454:100–103.
- Memarian, I., S. Ostrowski, H. Kordestani, F. Khakpour, and N. Pouyanshad. 2018. The illegal use of snares and gin traps threatens endangered leopards in Iran. *Cat News* 67:10–14.
- Mittermeier, R. A., P. Robles Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. Goettsch Mittermeier, J. Lamoreux, and G. A. B. Da Fonseca. 2004. Hotspots revisited: earth’s biologically richest and most endangered terrestrial ecoregions. Cemex, Mexico City, Mexico.
- Montalvo Mancheno, C. S., N. Zazanashvili, and G. Beruchashvili. 2016. Effectiveness of the network of protected areas of the South Caucasus at representing terrestrial ecosystems after the dissolution of the Soviet Union. *Environmental Conservation* 44:158–165.
- Moqanaki, E. M., U. Breitenmoser, B. H. Kiabi, M. Masoud, and S. Bensch. 2013. Persian leopards in the Iranian Caucasus: a sinking ‘source’ population? *Cat News* 59:22–25.
- Naderi, M., A. Farashi, and M. A. Erdi. 2018. Persian leopard’s (*Panthera pardus saxicolor*) unnatural mortality factors analysis in Iran. *PLoS One* 13:e0195387.
- Navya, R., V. Athreya, D. Mudappa, and T. S. Raman. 2014. Assessing leopard occurrence in the plantation landscape of Valparai, Anamalai Hills. *Scientific Correspondence* 107:1381–1385.
- Newby, J. R., L. Scott Mills, T. K. Ruth, D. H. Pletscher, M. S. Mitchell, H. B. Quigley, K. M. Murphy, and R. DeSimone. 2013. Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. *Biological Conservation* 159:230–239.
- Nowell, K., and P. Jackson. 1996. Wild cats. Status survey and conservation action plan. IUCN/SSC Cat Specialist Group, Gland, Switzerland.
- Ovenden, T. S., S. C. F. Palmer, J. M. J. Travis, and J. R. Healey. 2019. Improving reintroduction success in large carnivores through individual-based modelling: How to reintroduce Eurasian lynx (*Lynx lynx*) to Scotland. *Biological Conservation* 234:140–153.
- Palmer, S. C. F., A. Coulon, and J. M. J. Travis. 2011. Introducing a ‘stochastic movement simulator’ for estimating habitat connectivity. *Methods in Ecology and Evolution* 2:258–268.
- Persson, J., G. R. Rauset, and G. Chapron. 2015. Paying for an endangered predator leads to population recovery. *Conservation Letters* 8:345–350.
- Pitman, R. T., et al. 2017. Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management. *Journal of Applied Ecology* 54:1687–1698.
- Ramakrishnan, U., R. G. Coss, and N. W. Pelkey. 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation* 89:113–120.
- Ripple, W. J., et al. 2014. Status and ecological effects of the world’s largest carnivores. *Science* 343:1241484.
- Robinson, H. S., et al. 2015. Linking resource selection and mortality modeling for population estimation of mountain lions in Montana. *Ecological Modelling* 312:11–25.
- Romero-Muñoz, A., et al. 2019. Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Diversity and Distributions* 25:176–190.
- Schadt, S., F. Knauer, P. Kaczensky, E. Revilla, T. Wiegand, and L. Trepl. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications* 12:1469–1483.
- Soofi, M., et al. 2018. Livestock grazing in protected areas and its effects on large mammals in the Hyrcanian forest, Iran. *Biological Conservation* 217:377–382.
- Stein, A. B., et al. 2016. *Panthera pardus*. The IUCN Red List of Threatened Species, IUCN, Gland, Switzerland.
- Stein, A. B., V. Athreya, P. Gerngross, G. Balme, P. Henschel, U. Karanth, D. Miquelle, S. Rostro, J. F. Kamler, and A. Laguardia. 2016. *Panthera pardus*. The IUCN Red List of Threatened Species 2016: e.T15954A50659089. IUCN, Gland, Switzerland.
- Thapa, T. B. 2014. Human caused mortality in the leopard (*Panthera pardus*) population of Nepal. *Journal of Institute of Science Technology* 19:155–159.
- Williams, L., N. Zazanashvili, G. Sanadiradze, and A. Kandarov, editors. 2006. Ecoregional conservation plan for the Caucasus. WWF, KfW, BMZ, CEPF, MacArthur Foundation, Tbilisi, Georgia.
- Williams, S. T., K. S. Williams, L. P. Bradley, and R. A. Hill. 2017. Population dynamics and threats to an apex predator

- outside protected areas: implications for carnivore management. *Royal Society Open Science* 4:161090.
- Wolf, C., and W. J. Ripple. 2016. Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science* 3:160252.
- Wolf, C., and W. J. Ripple. 2017. Range contractions of the world's large carnivores. *Royal Society Open Science* 4:170052.
- Yarovenko, Y., and N. Zazanashvili. 2016. Recent hard evidence for the occurrence of the Leopard, *Panthera pardus* (Mammalia: Felidae), in the Eastern Greater Caucasus. *Zoology in the Middle East* 62:88–90.
- Zazanashvili, N., M. Garforth, H. Jungius, and T. Gamkrelidze, editors. 2012. *Ecoregion conservation plan for the Caucasus. 2012 revised updated edition.* WWF, KfW, BMZ, Tbilisi, Georgia.
- Zazanashvili, N., K. Manvelyan, E. Askerov, and A. Heidelberg. 2020. *Leopard in the South Caucasus.* WWF-Caucasus, Tbilisi, Georgia.
- Zimmerman, F., V. S. Lukarevsky, G. Beruchashvili, C. Breitenmoser-Wuersten, and U. Breitenmoser. 2007. Mapping the vision—potential living space for the leopard in the Caucasus. *Cat News Special Issue* 2:28–33.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2338/full>

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Data (Bleyhl et al. 2021) are available in Figshare. <https://figshare.com/s/b9f79b71cd01019f4ede>