Landscape connectivity for mammalian megafauna along the Iran-Turkmenistan-Afghanistan borderland

Mahshid Hosseini, Azita Farashi*, Ali Khani and Mohammad S. Farhadinia

• **Mahshid Hosseini**

Department of Environmental Sciences, Faculty of Natural Resources and Environment,
Ferdowsi University of Mashhad, Iran

• **Azita Farashi (Corresponding author)**

Department of Environmental Sciences, Faculty of Natural Resources and Environment,
Ferdowsi University of Mashhad, Iran, E-mail: farashi@um.ac.ir, orcid.org/0000-0001-8373-
1105.

• **Ali Khani**

Department of Biology, Faculty of Sciences, Ferdowsi University of Mashhad, Mashhad, Iran

• **Mohammad S. Farhadinia**

Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney
House, OX13 5QL, Oxford, UK

Abstract Habitat fragmentation threatens biodiversity, causes population isolation and reduces the availability of resources. When species ranges span geopolitical borders, management of transboundary populations and securing their connectivity can be compromised by different juridical efforts and priorities. Using a combination of species distribution modelling and circuit theory, we modelled suitable habitats for four conservation-dependent mammalian megafauna in northeastern Iran, bordering Turkmenistan and Afghanistan which is part of the larger Kopet Dag Ecoregion in central Asia. Our multispecies approach was aimed to identify key habitats and potential national and international corridors for Persian leopard (*Panthera pardus*), bezoar goat (*Capra aegagrus*), urial sheep (*Ovis orientalis*) and goitered gazelle (*Gazella subgutturosa*). Between 18 to 34% of the region was identified as suitable habitat for each species with a moderate variability in coverage by conservation network (14 to 43%). Importantly, we identified three key landscapes which can enhance the connectivity between main populations of the species in northeastern Iran as well as neighboring countries. Most of the suitable landscapes along the Iran-Turkmenistan borderlands are protected on the Iranian side, providing a source for species movement across the border. In contrast, the main suitable landscapes for megafauna in northeastern Iran are located far from the Afghan border. Our multispecies approach provided an empirical framework for spatial conservation planning for the mammalian megafauna across the Kopet Dag Ecoregion and can direct future survey efforts to identify critical wildlife areas in Turkmenistan and Afghanistan, two countries with scarce data on biodiversity.

Keywords: Afghanistan, landscape connectivity, Kopet Dag Ecoregion, transboundary conservation, species distribution model, Iran, Turkmenistan.

Introduction

Habitat conversion, degradation and fragmentation, mediated by growing pressures from human actions, threaten biodiversity (Tittensor et al., 2014). Future population growth and economic development are forecasted to impose unprecedented levels of extinction risk on many species worldwide, especially large mammals of tropical Africa, Asia and South America (Crist, Mora, & Engelman, 2017; Tilman et al., 2017).

Although geopolitical borderlands are typically rich in biodiversity, protecting these landscapes is often challenging. Borderlands are characterized by dynamic social, political, economic and sometimes even ecological transitions which, at extremes, involve armed conflicts and political instability (McNeely, 2003; Trouwborst et al., 2017). Expansion of border security barriers, particularly across Eurasia is recognized as a threat to wildlife because they can cause mortality, obstruct access to seasonally important resources, and reduce effective population size and viability (Linnell et al., 2016).

Borderlands between Iran-Turkmenistan-Afghanistan, which are part of the larger Kopet Dag Ecoregion (Memariani, Zarrinpour, & Akhane, 2016; Olson & Dinerstein, 1998) is a shared steppe landscape hosting various conservation-dependent mammals, such as Persian leopard (*Panthera pardus saxicolor*), bezoar goat (*Capra aegagrus*), urial sheep (*Ovis orientalis*) and goitered gazelle (*Gazella subgutturosa*) (Atamuradov, Fet, Fet, Valdez, & Feldman, 1999; Farhadinia, Moll, et al., 2018; Kaczensky & Linnell, 2015; Moheb & Bradfield, 2014). Nonetheless, national conservation programs have created a highly heterogeneous landscape across the border. There is no established network of conservation areas on the Afghan side of the border (Kanderian, Lawson, & Zahler, 2011). In Turkmenistan, although multiple reserves has been established, however they generally suffer from limited conservation resources

(Kaczensky & Linnell, 2015). On the Iranian side, the expanded network of reserves hosts populations of the mammalian megafauna (Farashi, Shariati, & Hosseini, 2017; Farhadinia, Moll, et al., 2018; Ghoddousi et al., 2016). As a transboundary biodiversity-rich landscape, the Kopet Dag Ecoregion can benefit from inter-governmental conservation initiatives.

Although some mammalian species move across the border (Farhadinia, Johnson, Macdonald, & Hunter, 2018; Kaczensky & Linnell, 2015), there is no coordinated collaboration for biodiversity conservation. Two mammalian species, Asiatic wild ass (*Equus hemionus*) and Asiatic cheetah (*Acinonyx jubatus venaticus*), both assumed to depend on transboundary movement have already disappeared from one side of the border (Farhadinia et al., 2017; Kaczensky & Linnell, 2015; D. Mallon, 2007). Developing a rigorous spatial conservation framework, along with encouraging political willingness, can facilitate a transboundary partnership between the countries.

A protective strategy in environments that are facing fragmentation is creating a network of habitats through connecting corridors (Di Minin et al., 2013; Foster, Love, Rader, Reid, & Drielsma, 2017; Moqanaki & Cushman, 2017). Corridor design improves the connectivity between isolated patches and, therefore, increases the landscape's capacity to sustain individuals, populations and meta-populations (Haddad et al., 2015; Khosravi, Hemami, & Cushman, 2018). Such a landscape-based conservation initiative requires measures that are supported by accurate information on distribution patterns and dispersal possibilities (Moqanaki & Cushman, 2017). Species Distribution Models (SDM) and circuit theory are increasingly combined to prioritize critical habitat patches and connectivity areas (Ahmadi et al., 2017; Carroll, McRAE, & Brookes, 2012; Brad H McRae & Beier, 2007).

Mammalian megafauna are known as umbrella species due to their extensive spatial and habitat requirements (Caro, 2003; Roberge and Angelstam, 2004; Rocha et al., 2018). Importantly, they can potentially be useful for conservation planning of co-occurring species (Brodie et al., 2015; Closset-Kopp, Wasof, & Decocq, 2016; Khosravi, Hemami, & Cushman, 2018). Therefore, we tailored a multiple species approach to four conservation-dependent large mammalian species which occur at all sides of the borderland between Iran, Turkmenistan and Afghanistan in central Asia.

Using a combination of species distribution modelling and circuit theory, we modelled suitable habitats for the species in northeastern Iran which is part of the larger Kopet Dag Ecoregion. Our study site was limited to the Iranian part of the landscape because species occurrence data as well as updated environmental layers were available from the Turkmen and Afghan sides. We also assessed landscape connectivity among important habitat patches. Finally, we evaluated the efficacy of the existing conservation network in safeguarding the focal mammalian community in the region. Finally, our modelling approach develops a spatial framework for launching inter-governmental transboundary partnerships across the Kopet Dag Ecoregion and can direct future survey efforts to identify critical wildlife areas in Turkmenistan and Afghanistan, two countries with scarce data on biodiversity.

Study area

We conducted our study in northeastern Iran, across two provinces of North Khorasan (28,434 km²) and Razavi Khorasan (118,854 km²) (38.28° to 33.46° E and 55.90° to 61.26° N). Our study area is part of the larger Kopet Dag Ecoregion which with an area of almost 165,000 km² mainly spans across northeastern Iran and southern Turkmenistan (Memariani et al., 2016). The region has three different climate zones that includes cold in the north, mild-semi desert in the center

and desert in the south (Bannayan, Lakzian, Gorbanzadeh, & Roshani, 2011). Elevation ranges between 300 to 3211 m.a.s.l, including two parallel mountain chains, i.e. the northern chain (Kopet Dag and Hezar Masjed mountains) and the southern chain (Binaloud, Aladagh and Golestan mountains) (Afshar-Harb, 1994). Their western extension joins the Alborz Mountains along the deforming Alpine - Himalayan orogenic belt in the south Caspian basin (Mangino & Priestley, 1998). This zoogeographical region was named as the Iranian Cradle of speciation by Misonne (1959). A total of 53 conservation areas, including 3 National Parks, 27 Protected Areas, 5 Wildlife Refuges and 18 No-Hunting Areas, and with an area of 23,103 (km²) cover 14% of the region.

Methods

Data collection

We collected species occurrence data during field samplings by authors (AKH and MSF) and rangers of the Department of Environment (DoE), spanning between 2008 and 2017. Our study species include Persian leopard, urial sheep, bezoar goat and goitered gazelle. Altogether, 108, 44, 48, and 42 occurrence points were compiled for Persian leopard, goitered gazelle, bezoar goat and urial sheep, respectively, covering most of the possible localities of the species in the region (Fig S1-S4).

Environmental variables

Optimal spatial resolution is critical for SDMs' performance (Connor et al., 2018; Guisan, Graham, Elith, Huettmann, & Group, 2007; Seo, Thorne, Hannah, & Thuiller, 2008) to avoid misleading results (Guisan & Thuiller, 2005). Therefore, we modeled each species distribution at five different spatial resolutions (1, 2, 4, 8, 16 km²).

Land cover data was obtained from the Iranian Forests, Range and Watershed Management Organization as well as DoE, prepared in 2014. The ratio of different cover types (i.e. the natural background of the landscape) in a 1-km radius from the centre of each cell was calculated using neighbourhood analysis. Normalized Difference Vegetation Index (NDVI) data was derived from 30 m Landsat TM imagery at a 1-km spatial resolution for 2017. Two of 19 bioclimatic predictors were collected from the World Clim 1.4 database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at the 1 km spatial resolution (Table 1). Topographic variables included mean and standard deviation (SD) of elevation and mean of **slope** for all raster cells in a 1 km radius, calculated based on the digital elevation model generated by the National Cartographic Center of Iran. A correlation test was performed for all pairwise combinations of environmental variables, and correlated predictor pairs with $r > 0.7$ were excluded from analysis (Table 1).

Model construction

We used an algorithm based on the maximum entropy principle (MaxEnt). MaxEnt performed best across all sample sizes of **species' occurrence points in a comparison of species distribution modeling methods** (Philips, Anderson, & Schapire, 2006). **In order to avoid autocorrelation and bias among occurrences, a simple systematic filtering was used because the simple systematic approach have proven to consistently outperform other methods (Kramer-Schadt et al., 2013; Fourcade et al., 2014). MaxEnt already discards redundant records that occur in a single cell. A grid of 5 km spatial resolution was created and randomly sampled one occurrence per grid cell. This spatial resolution was chosen based on mean of reported home range size of studied species (e.g. Stevenson-Jones, 1977; Jacobson et al., 2016).**

We used Jackknife as an efficient assessment of accuracy to evaluate the contributions of predictor variables for the best fitting model. The continuous map provided by MaxEnt was reclassified into a binary presence/absence prediction map for each species using the probability threshold corresponding to each model's maximum Kappa value. The binary maps were compared with current protected areas in IDRISI TerrSet to assess any possible overlap. Presence points were randomly divided into training and test datasets (80% and 20%, respectively). We ran 100 bootstrap replicates and used the area under the ROC-plot curve (AUC; Fielding & Bell, 1997) and the True Skill Statistics (TSS; Allouche, Tsoar, & Kadmon, 2006) to evaluate our models. AUC values between 0 and 1 mean the worst and best prediction respectively, with 0.5 corresponding to a random prediction. For TSS, -1 and 1 mean the worst and best prediction respectively, with 0 corresponding to a random prediction. The analysis was performed in MaxEnt version 3.3.3 (Philips et al., 2006) with default settings (regularization multiplier $\beta = 1$; auto features; convergence threshold = 0.0000, background points= 200).

Habitat connectivity analysis

A circuit model was used to estimate the actual connectivity inside the conservation network based on electrical circuit theory. The power of circuit theory to predict movement patterns of random walkers can be used to measure the connectivity or isolation of habitat patches (Ahmadi et al., 2017; Brad H McRae & Beier, 2007). We chose the all-to-one mode and the option to connect a cell with eight of its neighbors. In the one-to-all mode, connectivity is calculated between all focal regions. In each interaction, one focal region is connected to a source, which in this study represents protected areas (B H McRae & Shah, 2009). The connectivity maps for each species were overlapped to delineate the final connectivity within the conservation network. An isolation-by-resistance analysis was conducted using Circuitscape 3.5 (B H McRae & Shah,

2009). We also generated the inverse of the habitat suitability map for the studied species as a measure of movement resistance.

Results

Evaluation of modeling results using 14 independent environmental variables based on the TSS and AUC values showed that the MaxEnt model performed significantly better than random prediction at the five spatial resolutions (Table 1). For all four mammalian species, a spatial resolution of 2 km outperformed other resolutions (Table 1). Roughness was associated with increasing habitat suitability for all species, except the goitered gazelle. The distance to woodlands was associated with habitat suitability for all species, except bezoar goat which had less suitable habitats near woodlands (Fig 1).

Between 18 to 34% of the entire study area was modelled as suitable habitat for each mammalian species (Table 2 and Fig S1-S4). Importantly, suitable habitat coverage by conservation networks showed moderate variability between the species, varying between 14 and 43% (Table 2). In total, 58% of the study area was identified as suitable for at least one of the studied species.

Analysis of landscape connectivity revealed that large tracts of the study area provide potential corridors between suitable habitats, particularly across western parts of the region (Fig 2 and 3). Moreover, our results highlighted the existence of several pinch points (areas where animal movement is funneled within linkages) across the predicted linkages, which can constrain the species movements (Fig 2).

The Iran's leopard range is widely connected to the Turkmen side, while weak functional connectivity is seen for Persian leopards along the Iran-Afghanistan borderland (Fig S1). Similarly, for both montane dwelling ungulates, i.e. bezoar goat and urial sheep, the Iranian

populations are mainly connected to the Turkmenians (Fig S2-S3). In contrast, the suitable habitats of goitered gazelles are mainly connected to the Afghan side, along with parts of the Turkmenistan border (Fig S2). The ensemble model of cumulative current flow of the four mammalian species is shown in Figure 3.

Discussion

Our multispecies approach provided an empirical framework for spatial planning to conserve the four mammalian megafauna in northeastern Iran. We also quantified the combined effects of topographic features and law enforcement to delineate functional niches for these mammals. Finally, our modelling effort revealed the potential connectivity across dozens of conservation areas in northeastern Iran as well as across international borders with Turkmenistan and Afghanistan.

The species' response to environmental predictors supports habitat associations known from past literature for leopards (Ashrafzadeh, Naghipour, Haidarian, & Khorozyan, 2018; Ebrahimi, Farashi, & Rashki, 2017; Farhadinia et al., 2015; Khosravi, Hemami, & Cushman, 2018), urial sheep and bezoar goat (Bashari & Hemami, 2013; Makki, Fakheran, Moradi, Iravani, & Senn, 2013), and goitered gazelle (Farashi et al., 2017; Khosravi, Hemami, Malekian, et al., 2018). Accordingly, mountains provide a refugia for all species, except goitered gazelles which unsurprisingly are confined to lowlands.

On average, almost one third of each species' suitable habitats are within the existing network of conservation areas which is equivalent to 14% of the entire study area; Fig 2). Although moderate connectivity exist between the conservation areas; however, highways are a major impediment for functional connectivity across the region (Ahmadi et al., 2017; Mohammadi et al., 2018; Moqanaki & Cushman, 2017). Importantly, we identified three key

landscapes which can enhance the connectivity between main populations of study species in northeastern Iran (Fig 3): A) north of Mashhad, B) south of Sabzevar-Neyshabour and C) northern areas of Golestan National Park, close to Turkmenistan. Except areas south of Sabzevar-Neyshabour (landscape B) which are exclusively suitable for goitered gazelle, the other two landscapes (A and C) can facilitate connectivity for all focal species.

Most of the suitable landscapes along the Iran-Turkmenistan borderlands are protected on the Iranian side, providing a source for species movement across the border (Fig 3). Importantly, these border reserves can serve as sources of species transboundary movement between the two countries (Atamuradov et al., 1999; Farhadinia, Johnson, et al., 2018; Kaczensky & Linnell, 2015). The two landscapes A and C can supplement the border conservation network through providing more support for transboundary movement of the focal species. In contrast, our modeling approach showed that the main suitable landscapes for mammals in northeastern Iran are located far from the Afghan border. Equally important, there is no conservation area on the Afghan side of the border where many mammalian mega-fauna are heavily exploited (Kanderian et al., 2011). Nonetheless, Sirkhon Protected Area (Fig 3: number 46) can play as a potential source to recover mammalian megafauna, particularly goitered gazelle in western Afghanistan. Biodiversity surveys are needed to evaluate the occurrence of any of the focal species in western Afghanistan.

Although large parts of northeastern Iran are modeled as suitable habitats with a moderate percentage lying inside conservation networks, focal species are unlikely to occur outside the conservation network. As an exception, Persian leopards are widely detected outside the conservation network, perhaps due to their large spatial requirements and shortage of food resources, which drive them to occasionally raid livestock in rural areas (Farhadinia, Johnson, et

al., 2018; Farhadinia, Moll, et al., 2018). In contrast, similar to many Asian countries, ungulates are spatially confined to the conservation network since poaching and interactions with livestock threaten their persistence outside established reserves (Bashari & Hemami, 2013; Bleyhl et al., 2019; Khosravi, Hemami, Malekian, et al., 2018; D. P. Mallon & Zhigang, 2009).

Northeastern Iran is an important site for migratory mammalian species in central Asia and has an extensive network of conservation areas with moderate connectivity. Two of our focal species, Persian leopard and goitered gazelle, are listed in the Appendix II of the 1979 Bonn Convention on the Conservation of Migratory Species of Wild Animals (CMS) which is an international instrument focusing on the conservation of transboundary wildlife (Karlstetter & Mallon, 2014; Trouwborst et al., 2017). Also, they are part of the Central Asian Mammals Initiative (CAMI) priority species. Our study provides a spatial framework to expand national and transboundary conservation across the Kopet Dag Ecoregion.

Author contributions

MAHSHID HOSSEINI: data analysis, AZITA FARASHI*: study design and writing, ALI KHANI: fieldwork, MOHAMMAD S. FARHADINIA: fieldwork and writing.

References

- Afshar-Harb, A. (1994). Geology of Kopet Dagh. *Treatise on the Geology of Iran*, 11, 1–275.
- Ahmadi, M., Nezami Balouchi, B., Jowkar, H., Hemami, M. H., Fadakar, D., Malakouti-Khah, S., & Ostrowski, S. (2017). Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia. *Diversity and Distributions*, 23(6), 592–603.
- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution

models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6), 1223–1232.

Ashrafzadeh, M. R., Naghipour, A. A., Haidarian, M., & Khorozyan, I. (2018). Modeling the response of an endangered flagship predator to climate change in Iran. *Mammal Research*, 1–13.

Atamuradov, H. I., Fet, G. N., Fet, V., Valdez, R., & Feldman, W. R. (1999). Biodiversity, genetic diversity, and protected areas in Turkmenistan. *Journal of Sustainable Forestry*, 9(1/2), 73–88.

Bannayan, M., Lakzian, A., Gorbantzadeh, N., & Roshani, A. (2011). Variability of growing season indices in northeast of Iran. *Theoretical and Applied Climatology*, 105(3–4), 485–494.

Bashari, H., & Hemami, M. R. (2013). A predictive diagnostic model for wild sheep (*Ovis orientalis*) habitat suitability in Iran. *Journal for Nature Conservation*, 21(5), 319–325.

Bleyhl, B., Arakelyan, M., Askerov, E., Bluhm, H., Gavashelishvili, A., Ghasabian, M., ... Malkhasyan, A. (2019). Assessing niche overlap between domestic and threatened wild sheep to identify conservation priority areas. *Diversity and Distributions*, 25(1), 129–141.

Brodie, J. F., Giordano, A. J., Dickson, B., Hebblewhite, M., Bernard, H., Mohd-Azlan, J., ... Ambu, L. (2015). Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, 29(1), 122–132.

Carroll, C., McRAE, B. H., & Brookes, A. (2012). Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. *Conservation Biology*, 26(1), 78–87.

Closset-Kopp, D., Wasof, S., & Decocq, G. (2016). Using process-based indicator species to

297 evaluate ecological corridors in fragmented landscapes. *Biological Conservation*, 201, 152–
 298 159.

299 Connor, T., Hull, V., Viña, A., Shortridge, A., Tang, Y., Zhang, J., ... Liu, J. (2018). Effects of
 300 grain size and niche breadth on species distribution modeling. *Ecography*, 41(8), 1270–
 301 1282.

302 Crist, E., Mora, C., & Engelman, R. (2017). The interaction of human population, food
 303 production, and biodiversity protection. *Science*, 356(6335), 260–264.

304 Di Minin, E., Hunter, L. T. B., Balme, G. A., Smith, R. J., Goodman, P. S., & Slotow, R. (2013).
 305 Creating larger and better connected protected areas enhances the persistence of big game
 306 species in the Maputaland-Pondoland-Albany biodiversity hotspot. *PLOS ONE*, 8(8), 1–14.

307 Ebrahimi, A., Farashi, A., & Rashki, A. (2017). Habitat suitability of Persian leopard (*Panthera*
 308 *pardus saxicolor*) in Iran in future. *Environmental Earth Sciences*, 76(20), 697.

309 Farashi, A., Shariati, M., & Hosseini, M. (2017). Identifying biodiversity hotspots for threatened
 310 mammal species in Iran. *Mammalian Biology-Zeitschrift Für Säugetierkunde*, 87, 71–88.

311 Farhadinia, M. S., Ahmadi, M., Sharbafi, E., Khosravi, S., Alinezhad, H., & Macdonald, D. W.
 312 (2015). Leveraging trans-boundary conservation partnerships: Persistence of Persian
 313 leopard (*Panthera pardus saxicolor*) in the Iranian Caucasus. *Biological Conservation*, 191,
 314 770–778.

315 Farhadinia, M. S., Hunter, L. T. B., Jourabchian, A. R., Hosseini-Zavarei, F., Akbari, H., Ziaie,
 316 H., ... Jowkar, H. (2017). The critically endangered Asiatic cheetah *Acinonyx jubatus*
 317 *venaticus* in Iran: a review of recent distribution, and conservation status. *Biodiversity and*
 318 *Conservation*, 1–20.

319 Farhadinia, M. S., Johnson, P. J., Macdonald, D. W., & Hunter, L. T. B. (2018). Anchoring and

adjusting amidst humans: Ranging behavior of Persian leopards along the Iran-Turkmenistan borderland. *PLoS ONE*, 13(5), e0196602.

Farhadinia, M. S., Moll, R. J., Montgomery, R. A., Ashrafi, S., Johnson, P. J., Hunter, L. T. B., & MacDonald, D. W. (2018). Citizen science data facilitate monitoring of rare large carnivores in remote montane landscapes. *Ecological Indicators*, 94, 283–291.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24(1), 38–49.

Foster, E., Love, J., Rader, R., Reid, N., & Drielsma, M. J. (2017). Integrating a generic focal species, metapopulation capacity, and connectivity to identify opportunities to link fragmented habitat. *Landscape Ecology*, 32(9), 1837–1847.

Ghoddousi, A., Soofi, M., Kh. Hamidi, A. K., Lumetsberger, T., Egli, L., Khorozyan, I., ... Waltert, M. (2016). Assessing the role of livestock in big cat prey choice using spatiotemporal availability patterns. *PLOS ONE*, 11(4), e0153439.

Guisan, A., Graham, C. H., Elith, J., Huettmann, F., & Group, N. S. D. M. (2007). Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions*, 13(3), 332–340.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Collins, C. D. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), e1500052.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of*

343 *Climatology*, 25(15), 1965–1978.

344 Kaczensky, P., & Linnell, J. D. (2015). *Rapid assessment of the mammalian community in the*

345 *Badkhyz Ecosystem, Turkmenistan, October 2014*. NINA Report 1148.

346 Kanderian, N., Lawson, D., & Zahler, P. (2011). Current status of wildlife and conservation in

347 Afghanistan. *International Journal of Environmental Studies*, 68(3), 281–298.

348 Karlstetter, M., & Mallon, D. (2014). Assessment of gaps and needs in migratory mammal

349 conservation in Central Asia. In *A report for the Convention on the Conservation of*

350 *Migratory Species of Wild Animals (CMS) and the Deutsche Gesellschaft für Internationale*

351 *Zusammenarbeit (GIZ)* (p. 123).

352 Khosravi, R., Hemami, M. R., & Cushman, S. A. (2018). Multispecies assessment of core areas

353 and connectivity of desert carnivores in central Iran. *Diversity and Distributions*, 24(2),

354 193–207.

355 Khosravi, R., Hemami, M. R., Malekian, M., Silva, T. L., Rezaei, H. R., & Brito, J. C. (2018).

356 Effect of landscape features on genetic structure of the goitered gazelle (*Gazella*

357 *subgutturosa*) in Central Iran. *Conservation Genetics*, 19(2), 323–336.

358 Linnell, J. D. C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., ... Potocnik,

359 H. (2016). Border security fencing and wildlife: the end of the transboundary paradigm in

360 Eurasia? *PLoS Biology*, 14(6), e1002483.

361 Makki, T., Fakheran, S., Moradi, H., Iravani, M., & Senn, J. (2013). Landscape-scale impacts of

362 transportation infrastructure on spatial dynamics of two vulnerable ungulate species in

363 Ghamishloo Wildlife Refuge, Iran. *Ecological Indicators*, 31, 6–14.

364 Mallon, D. (2007). Cheetahs in Central Asia: A historical summary. *Cat News*, 46, 4–7.

365 Mallon, D. P., & Zhigang, J. (2009). Grazers on the plains: challenges and prospects for large

herbivores in Central Asia. *Journal of Applied Ecology*, 46(3), 516–519.

Mangino, S., & Priestley, K. (1998). The crustal structure of the southern Caspian region. *Geophysical Journal International*, 133(3), 630–648.

McNeely, J. A. (2003). Conserving forest biodiversity in times of violent conflict. *Oryx*, 37(2), 142–152.

McRae, B H, & Shah, V. B. (2009). Circuitscape user’s guide. *The University of California, Santa Barbara*.

McRae, Brad H, & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences*, 104(50), 19885–19890.

Memariani, F., Zarrinpour, V., & Akhani, H. (2016). A review of plant diversity, vegetation, and phytogeography of the Khorassan-Kopet Dagh floristic province in the Irano-Turanian region (northeastern Iran–southern Turkmenistan). *Phytotaxa*, 249(1), 8–30.

Misonne, X. (1959). Zoogeography the Mammifere de l’Iran. *Belgique. Institut Royal Des Science Naturelles de Belgique. Memoires, Deuxième Série, Fasc, 59*, 160.

Mohammadi, A., Almasieh, K., Clevenger, A. P., Fatemizadeh, F., Rezaei, A., Jowkar, H., & Kaboli, M. (2018). Road expansion: A challenge to conservation of mammals, with particular emphasis on the endangered Asiatic cheetah in Iran. *Journal for Nature Conservation*, 43, 8–18.

Moheb, Z., & Bradfield, D. (2014). *Status of the common leopard in Afghanistan. Cat News* (Vol. 61).

Moqanaki, E. M., & Cushman, S. A. (2017). All roads lead to Iran: Predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. *Animal Conservation*, 20(1), 29–41.

389 Olson, D. M., & Dinerstein, E. (1998). The Global 200: A Representation Approach to
 390 Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology*,
 391 12(3), 502–515.

392 Philips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species
 393 geographic distributions. *Ecological Modelling*, 190(3–4), 231–259.

394 Seo, C., Thorne, J. H., Hannah, L., & Thuiller, W. (2008). Scale effects in species distribution
 395 models: implications for conservation planning under climate change. *Biology Letters*, 5(1),
 396 39–43.

397 Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future
 398 threats to biodiversity and pathways to their prevention. *Nature*, 546, 73.

399 Tittensor, D. P., Walpole, M., Hill, S. L. L., Boyce, D. G., Britten, G. L., Burgess, N. D., ...
 400 Alkemade, R. (2014). A mid-term analysis of progress toward international biodiversity
 401 targets. *Science*, 346(6206), 241–244.

402 Trouwborst, A., Blackmore, A., Boitani, L., Bowman, M., Caddell, R., Chapron, G., ...
 403 Fernández-Galiano, E. (2017). International wildlife law: understanding and enhancing its
 404 role in conservation. *BioScience*, 67(9), 784–790.

405

Table 1 Environmental variables and their relative contributions to model habitat suitability for the four mammalian species at multiple spatial resolutions

			Persian leopard					Goitered gazelle					Bezoar goat					Urial sheep				
Environmental variables	Min-Max	Mean±SD	Resolution (<i>km</i> ²)					Resolution (<i>km</i> ²)					Resolution (<i>km</i> ²)					Resolution (<i>km</i> ²)				
			1	2	4	8	16	1	2	4	8	16	1	2	4	8	16	1	2	4	8	16
Climatic variables																						
Annual mean temperature	22.0-197.0	139.3±31.5	0.6	9.3	7.2	1.0	15.8	34.8	34.8	42.9	38.3	39.0	0.2	0.0	0.0	0.0	1.4	2.6	1.7	0.2	0.1	0.0
Annual precipitation	94.0-369.0	219.7±55.2	3.0	9.3	3.5	6.7	1.2	4.3	3.7	1.0	1.4	8.2	4.5	4.7	6.5	9.0	10.1	0.3	0.4	0.1	0.1	0.7
Topographic variables																						
Roughness [*]	0.6-483.1	78.4±68.8	42.1	47.6	44.6	40.1	40.7	4.9	2.9	3.3	1.5	1.1	53.8	46.2	49.8	25.0	38.8	24.1	15.8	11.2	18.4	17.3
LU/LC variables																						
Distance to urban area	0.0-106827.0	21415.8±15160.9	3.3	2.2	2.1	1.8	2.7	5.1	3.4	0.9	0.5	5.0	1.0	0.8	1.1	1.6	7.1	0.0	0.3	0.3	0.9	4.2
Distance to rural area	0.0-56384.8	3477.4±4305.3	2.0	1.6	1.6	1.6	0.6	10.6	7.1	2.8	2.4	1.4	0.7	1.0	0.7	1.9	4.3	0.1	3.0	5.5	0.3	3.9
Distance to High way	0.0-145784.0	29869.9±19125.5	2.7	2.0	2.1	0.9	0.8	5.8	7.1	6.1	15.8	8.2	0.1	0.1	0.3	0.3	1.0	0.6	0.1	0.0	0.0	0.2
Distance to Road	0.0-71310.9	11994.9±10714.0	2.6	2.8	1.9	3.2	2.3	0.6	0.2	2.9	3.2	1.0	2.3	1.0	2.7	1.2	1.2	3.6	3.2	4.7	1.9	9.5
Distance to Agriculture	0.0-67575.8	3703.4±5966.4	1.2	0.8	1.1	2.1	0.2	0.9	5.4	3.5	0.3	1.3	4.6	8.5	6.9	34.6	13.1	1.2	3.8	5.1	11.9	0.2
Distance to Scrubland	0.0-93921.5	29829.3±19943.2	1.5	0.8	1.3	2.2	0.0	4.2	5.2	3.6	6.6	0.2	1.4	0.5	1.2	0.8	0.9	3.1	1.1	0.9	2.0	0.5
Distance to Woodland	0.0-331166.5	96759.7±87353.6	8.9	12.3	11.3	3.8	27.0	18.0	15.8	18.5	18.0	13.2	24.7	29.0	21.2	19.9	9.6	54.7	60.7	64.5	59.5	53.5
Distance to Range area	0.0-19659.5	983.6±1945.5	1.0	0.9	3.4	2.9	0.2	0.5	0.7	0.1	0.5	4.9	2.4	2.6	2.5	1.4	0.7	0.5	2.1	2.5	1.3	1.0
Distance to Rocky area	0.0-96784.5	32224.0±18829.1	5.5	2.5	2.5	6.2	1.0	5.0	5.8	4.4	4.7	4.8	3.1	1.7	1.6	1.5	2.4	0.0	3.5	1.4	1.8	5.4
Distance to Mine	0.0-95770.5	23371.8±15095.3	4.0	4.5	4.5	5.0	5.1	3.6	5.2	8.5	4.3	2.7	1.1	3.0	4.7	0.5	2.9	1.7	6.2	3.0	1.0	0.1
NDVI	-0.3-0.8	0.1±0.0	21.8	3.4	12.9	22.5	2.4	1.6	2.9	1.6	2.5	9.2	0.0	1.0	0.7	2.2	6.3	1.5	0.8	0.7	0.6	3.6
Accuracy index																						
AUC	-----	-----	0.95	0.96	0.93	0.89	0.92	0.90	0.98	0.93	0.91	0.92	0.90	0.96	0.94	0.92	0.97	0.95	0.99	0.97	0.97	0.96
TSS	-----	-----	0.93	0.97	0.92	0.87	0.90	0.89	0.96	0.92	0.90	0.94	0.91	0.95	0.90	0.90	0.94	0.92	0.97	0.92	0.93	0.93

Table 2 Area and proportion of protection granted to the four mammalian megafauna in northeastern Iran

Species	% Suitable habitat	% Suitable habitats protected by conservation network
Persian leopard	34%	24%
Bezoar goat	26%	29%
Urrial sheep	18%	43%
Goitered gazelle	27%	14%

Fig 1 Response curves of MaxEnt model for the four studied species at spatial resolution of 2 km based on Jackknife test.

Fig 2 Model of cumulative current flow used to evaluate habitat connectivity for the four mammalian megafauna in northeastern Iran.

Fig 3 Ensemble model of cumulative current flow used to evaluate habitat connectivity for the four mammalian megafauna in northeastern Iran. Red capital letters denote key landscapes in the northeast of Iran which are of high importance for survival of the focal species: A) northern Mashhad, B) southern Sabzevar-Neyshabour and C) northern Golestan National Park, towards Turkmenistan.

Appendix

Fig S1. Habitat suitability of Persian leopard in northeastern Iran and gaps between suitable habitats and conservation network.

Fig S2. Habitat suitability of goitered gazelle in northeastern Iran and gaps between suitable habitats and conservation network.

Fig S3. Habitat suitability of Urial sheep in northeastern Iran and gaps between suitable habitats and conservation network.

Fig S4. Habitat suitability of Bezoar goat in northeastern Iran and gaps between suitable habitats and conservation network.