

Vertical relief facilitates spatial segregation of a high density large carnivore population

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Keywords: auto-correlated Kernel density estimation; elevation gradient; intraspecific competition; planimetric; predation pattern; topography.

Introduction

Animal space use and the scales at which they range, establish home ranges, and use habitat within the home ranges is fundamental to their ecology (Johnson 1980, Börger et al. 2008). A home range is integral to animals' cognitive maps of their environment (Powell and Mitchell 2012). At a more basic level, a home range is comprised of abiotic and biotic conditions that have implications for animal survival and reproduction (Burt 1943). How an animal uses different parts of that range can be quantified as a utilization distribution (UD) based on the relative probability of using different parts of the range (Worton 1989) which can provide better understanding of complex habitat dynamics (Worton 1987). Modern statistical modeling of home ranges facilitates the exploration of processes which determine the characteristics of the emergent UD (Börger et al. 2008).

The spatiotemporal availability of resources is an important factor that affects animal movement and the configuration and size of UD. Ranging patterns of large carnivores are influenced by intrinsic factors such as age and sex (Johansson et al. 2016, Morato et al. 2016) or extrinsic factors including resource availability (Allen et al. 2016, Johansson et al. 2018), topographic features (Powell and Mitchell 1998) and population density (Cooper 1978, Benson et al. 2006).

The conventional method for quantifying ranging patterns is calculating UD_s as a bivariate frequency distribution represented by a two-dimensional (X , Y) planimetric surface (Van Winkle 1975). Kernel-based nonparametric probabilistic models are widely popular for estimating home range size using relocation data (Worton 1989, Laver and Kelly 2008, Fleming and Calabrese 2017). Home ranges and core areas for large carnivores are often quantified without tangibly incorporating topography, notwithstanding being in areas with high orography (Johansson et al. 2016, 2018, Farhadinia et al. 2018a).

Topography, however, is often an important influence on animal ecology. Vertical relief can affect the animal's perception of habitat, food resources, access to mates, refugia, or escape from predators (Powell and Mitchell 1998, Stankowich and Coss 2006, Montgomery et al. 2012). Incorporating elevation can provide better insight into coexistence of sympatric large carnivores (Husseman et al. 2003, Li et al. 2018). For example, elevation gradient can have differentiating effect both on selection of habitat and location of kill sites within a guild of sympatric carnivores (Husseman et al. 2003, May et al. 2008). In environments that exhibit strong seasonality, plant phenology can drive vertical migration of herbivores and consequently, synchronize predator movement (Mysterud 2013, Spitz et al. 2018). Ignoring this factor can lead to misinterpretation of animals' ecological needs, particularly in mountainous landscapes. It also can affect our comparative understanding on density,

Home range estimates based on planimetric area, without accounting for the true surface area traversed by an animal, may underestimate home ranges and overestimate population densities in montane regions (Monterroso et al. 2013). Despite the recognized importance of including topography in the estimation of home-range sizes (Powell and Mitchell 1998), few studies endeavored to do so in terrestrial home range estimations (Campbell et al. 2004,

Monterroso et al. 2013, Powell et al. 2017). Importantly, ignoring the true surface can result in the overestimation of population parameters, inducing researchers to consider that the status of population is better than it really is (Monterroso et al. 2013). To our knowledge, no study has included the complexity of topography for terrestrial large carnivore home ranges or core areas. We address this challenge with a GPS telemetry study of the Persian leopard *Panthera pardus saxicolor* in a remote montane landscape along the Iran-Turkmenistan borderland.

Human persecution, mainly in retaliation of killing domestic animals, is a major threat to Persian leopards (Babrgir et al. 2017, Naderi et al. 2018). Their extensive spatial requirements relative to the small size of many reserves means that their persistence often relies on a mosaic of protected and human-altered landscapes (Farhadinia et al. 2018b, Hosseini et al. 2019, Soofi et al. 2019), at least for dispersal or foraging (Sharbafi et al. 2016, Farhadinia et al. 2018a). The unfolding complexities of space use in these highly heterogeneous mountains are likely to inform management plans.

We extended our previous planimetric study on ranging patterns (Farhadinia et al. 2018a) by incorporating elevation in estimating space use. Using GPS relocation data from a wide-ranging predator living in a rugged mountainous landscape, we modeled the variation between planimetric (two-dimensional) and topographic (three-dimensional) home range and core area. We also explored the association between predation patterns and elevation gradient and how they relate to ecological outcomes at population and intraguild levels. Finally, we discuss how topographic analysis can improve our understanding of the ecology of the species and the corresponding implications for conservation.

92 **Material and Methods**

93 *Ethics statement*

94 The study was conducted in Tandoureh National Park (TNP), Iran. The Iranian
95 Department of Environment reviewed all sampling, trapping, and handling procedures and
96 approved permits for the work conducted (93/16270). The trapping and handling protocols were
97 also approved by the University of Oxford’s Ethical Review Committee (BMS-ERC-160614).

98 *Study area*

99 We studied leopards in TNP, a 355 km² national park in north-eastern Iran approximately
100 20 km from the Turkmenistan border. Protected since 1968, TNP is characterized by a dry
101 climate with average annual rainfall of between 250 and 300 mm. The vegetation of the area’s
102 mountains are dominated by wormwood *Artemisia* sp. and scattered juniper trees *Juniperus* sp.
103 Elevation ranges from 1,000 to 2,600 m.

104 The primary occupation of local human communities is sheep and goat herding in
105 villages with populations typically ranging between 30 to 400 households. There are no human
106 settlements inside the park. Leopards in TNP mainly prey on urial (*Ovis orientalis*), bezoar goat
107 (*Capra aegagrus*), and wild pig (*Sus scrofa*). Apart from wild pigs, which are occasionally found
108 in multi-use areas outside of the national park, other wild medium-sized prey are available only
109 inside the park. In contrast, domestic animals are found exclusively outside the park (Farhadinia
110 et al. 2018c).

111 *Leopard collaring and monitoring*

112 We collared six leopards (5 males and 1 female; Table 1) using Aldrich foot-snare traps
113 (see Farhadinia et al. 2017a for details on capturing and immobilization procedures). Age

determination was based on dental features (see Farhadinia et al. 2017a for more details). We used GPS collars with Iridium download capabilities (LOTEK Engineering Ltd., Newmarket, ON, Canada), each equipping with a drop-off buckle activated by a timer set to 52 weeks since deployment.

To increase fix success rates, fixes were taken hourly during the last week of each month whereas for the rest of month, fixes were recorded every 3 hours. This programming schedule was adopted to facilitate the identification of spatially aggregated GPS points, or clusters indicative of kill sites (Knopff et al. 2009) while securing the battery life until the end of collar activity. Bjørneraas et al. (2010) recommended that to analyse animal movement and behaviour, fixes obtained immediately after collaring should be excluded because the animal may not behave normally. Therefore, we omitted all data from the first 4 days post-collaring, associated with the earliest known kill made by the leopards after collaring (M1) (Farhadinia et al. 2018c).

We investigated potential kill sites defined as clusters of ≥ 2 locations within 100 m of each other and separated by less than 12 hour (Knopff et al. 2009, see Farhadinia et al. 2018c for more details). We only included “medium” prey (≥ 15 kg) such as urial, bezoar goat, wild pig, domestic sheep *Ovis aries* and domestic dog *Canis familiaris* into our elevation analysis.

Home range and core area calculation

In our previous study (Farhadinia et al. 2018a), we did not detect any erroneous fixes or spikes in movement in our GPS relocation data, based on identification of locations arising from unrealistic movement patterns, using a script developed by Bjørneraas et al. (2010).

We developed UD_s to map home ranges of the leopards using an auto-correlated kernel density estimator (AKDE). Relocation data are inherently auto-correlated (i.e. an individual's position, velocity, or acceleration are statistically correlated with the same measurements in the

past and future unless inter-location intervals are long enough) (Fleming et al. 2015, Fleming and Calabrese 2017). The AKDE is a continuous-time method that accounts for auto-correlated bivariate Gaussian density estimation for relocation data (Fleming et al. 2015).

We investigated the autocorrelation structure of the relocation data for each leopard using an empirical variogram. It is defined as the estimated semi-variance in positions as a function of the time lag separating observations. Upward curvature at zero to short time lags indicates velocity autocorrelation while the long-lag behavior of the variogram illustrates space use (Fleming and Calabrese 2017). Thus, range residents are expected to reach an asymptote on a timescale that roughly corresponds to the home-range crossing time (Calabrese et al. 2016).

We implemented two movement models, Ornstein–Uhlenbeck (OU) and Ornstein–Uhlenbeck Foraging (OUF), in package ‘ctmm’ version 0.4.0 (Calabrese et al. 2016). They both accommodate auto-correlated data to quantify home range size. Accordingly, the OU process combines a random search model without space use constraint (Brownian motion) with a tendency to remain in a particular home range. Alternatively, the OUF process features both velocity autocorrelation and restricted space use (Calabrese et al. 2016, Fleming and Calabrese 2017). Initial values of the model parameters were obtained from variograms overlaid with a continuous-time movement model. For each leopard, movement models were fitted using maximum likelihood estimation to the data. We selected the best movement model using AICc weight to estimate home range for each leopard, defined as area within 95% UD isopleths of AKDE estimates.

We also estimated core areas of space use for each leopard using an individual-based quantitative approach (Vander Wal and Rodgers 2012). Thus, the UD_s were plotted against isopleths to identify the value at which the proportional home range area begins to increase at a

greater rate than the probability of use (slope = 1). The value of the corresponding isopleth determines the boundary of the core area (Vander Wal and Rodgers 2012).

Planimetric and topographic area comparison

We compared area size by first calculating the planimetric area of each home range using the geosphere package version 1.5-7 (Hijmans et al. 2017). Euclidian distances were calculated between the coordinate data values and projection information within our home range polygons. This package accounts for the semispherical bend of polygons projected on a sphere, but not topographic features on the surface.

To calculate the topographic surface area we used a method developed by Jenness (2004) for quantifying the surface area of a DEM and implemented in the sp package version 0.7-12 (Pebesma and Bivand 2005). This method estimates area by using the inherent elevation information located within a rasterized DEM and converting it to a matrix. The area is calculated by finding the straight-line distance from each matrix value to the 8 surrounding values using the Pythagorean Theorem. The resulting distances between centroids are summed to get the surface area of the polygon (Jenness 2004).

For accuracy and computational efficiency, we obtained a 30m resolution DEM of the study area from the SRTM database via <https://earthexplorer.usgs.gov>, and masked it to the spatial polygons generated by our UD estimation for both home range and core area of all leopards. These polygons were the result of mathematical formula, and therefore have smooth edges that do not perfectly match the boundaries of a raster grid. Grid cells were included in the masked raster whose centroid lay within the polygon.

Elevation predation patterns

We derived elevation values for each kill site, recorded for each GPS fix by the collar. We developed a generalized linear model to relate elevation of kills to prey type. Another generalized linear model was constructed to explore elevation variability in kill sites for each leopard. For the latter analysis, we omitted non-resident individuals for which predation can occur less-predictably in the landscape. For example, most of scavenging clusters belonged to non-resident leopards in TNP (Farhadinia et al. 2018c). For one individual (B1/Borzou), we truncated the first 5.5 months for which he showed residency behavior (see Home range and core area calculation for details on differentiating between resident and non-resident individuals). All means are reported with standard errors. We conducted all analyses in *R* (R Development Core Team 2013).

Data deposition

All locational data are publicly available on Movebank: https://www.movebank.org/panel_embedded_movebank_webapp. Project: Persian leopard Tandoureh Iran (accession number 270329098). All the data are available for download as .csv file.

Results

We monitored six leopards for between 54 and 368 days per individual (Table 1). In total, they represented a study period of 56.7 leopard months, monitored between September 2014 and May 2017. We obtained a total of 22,226 GPS locations for 1,702 leopard-days ($283.7 \pm \text{SE } 50.8$ days/leopard) with a high overall fix rate (mean $85.0\% \pm \text{SE } 7.6$).

Three adult males (M2/Bardia, M3/Borna and M4/Tandoureh) exhibited constrained space use as resident individuals, based on a clear asymptote in variograms (Fig. 1 and Supplementary material Appendix 1, Fig. 1). In contrast, both young leopards (F5/Iran and M6/Kaveh) lacked asymptotes, showing a non-residency pattern. M1/Borzou (an old male) showed a mixed ranging pattern. Following 5.5 months of residency behavior inside the national park, he started his excursions outside the park along the borderland's communities with regular returns to the national park which was associated with an increase in his semi-variance (Fig. 1 and Supplementary material Appendix 1, Fig. 1). Although M4/Tandoureh was collared when other males' collars were dropped off, photographic detections by means of camera traps or tourist encounters suggested that he was a resident male in the same area before collaring. Therefore, we used his relocation data to analyze inter-individual altitudinal differences in predation patterns.

The AKDE estimates were obtained for all six leopards equally shared between OU and OUF as best performing models based on their AICc weight (Table 1). Mean planimetric AKDE home range was calculated to be $103.4 \pm \text{SE } 51.8 \text{ km}^2$ for resident males while it increased to $133.2 \pm \text{SE } 65.5 \text{ km}^2$ when topographically analyzed. Similarly, mean core area was calculated to be $32.4 \pm \text{SE } 12.7 \text{ km}^2$ planimetrically with a mean surface area of $42.3 \pm \text{SE } 16.3 \text{ km}^2$ (Table 1). The mean isopleth for core areas were the 62% to 67% isopleths of the utility distribution.

Calculation of surface area was increased by a median of 27.8% for all collared leopards when topography was also incorporated. Specifically, home range size and core area estimates increased by $28.4 \pm \text{SE } 1.2\%$ and $29.6 \pm \text{SE } 1.8\%$, respectively (Table 1). The increase in spatial parameters for all three resident leopards was above the median line, whereas it was slightly

lower for non-residents (Fig. 2). At individual level, the leopards' ranges showed a variable factor of increase between 26.0% and 38.4% (Fig. 2).

In total, we detected 139 kill sites where leopards preyed ($n = 130$) or scavenged ($n = 9$) on 10 different prey species. The majority (93.1%) of these prey were medium sized. The elevation at which these predations took place varied between leopards ($F_{3, 91} = 28.32$, $P < 0.005$; Fig. 3). Also, various medium sized prey were killed at different elevations ($F_{4, 120} = 12.16$, $P < 0.005$), with two clear groups identifiable: lowland prey including sheep, domestic dog and wild pig (ca. 1100 meter a.s.l), and highland prey such as urial and bezoar goat (ca. 1500 meter a.s.l; Fig. 4).

Discussion

We observed that elevation is an important component in representing the home range behavior of a large carnivore. We found that failing to consider elevation in home range estimation led to a 38% bias in home range and core area estimation in our mountainous study area. We would not expect this bias to be consistent across space. Rather, it should dynamically vary given the landscape and the life history characteristics of leopards. In this case, resident male leopards showed elevation-dependent predation behavior, while non-resident leopards had high elevation variability in ranging patterns.

Topographic versus planimetric spatial analysis

The use of topographic home range estimation facilitated examination of the importance of elevation in studies of leopard space use. Our results confirmed that the incorporation of elevation into home range modeling can significantly increase the range size. Conversely, our study demonstrates the tendency for planimetric quantification of terrestrial home range to

underestimate the surface size used in montane areas; however, planimetric home range techniques are likely valid in areas with less topographic relief (Walter et al. 2013). Simulation studies suggest that planimetric estimates in areas with an average slope of 16 ° or more will incur in errors $\geq 5\%$ (Monterroso et al. 2013). Regardless of the analysis method, our home range estimates for Persian leopards are larger than those reported in previous Asian leopard ranging studies (Odden and Wegge 2005, Simcharoen et al. 2008).

The method we used here for surface area calculation, first developed by Jenness (2004), does not require a great amount of additional effort or computational efficiency, and we believe it provides a more realistic estimate of space use. We therefore encourage ecologists to incorporate elevation and topography into their movement ecology analysis in mountainous environments to obtain a more complete understanding of species spatial behavior.

Ecological outcomes along elevation gradient

Large felids in rugged landscapes show moderate home range overlap between conspecifics (Farhadinia et al. 2018a, Johansson et al. 2018). Several plausible mechanisms could explain the coexistence of multiple individuals. First, although long-term home range overlap can be relatively high, short-term home overlaps can be much smaller (Johansson et al. 2018). Second, despite high degrees of spatial overlap, predators can have exclusive hunting areas, which was seen in TNP (Farhadinia et al. 2018a). Finally, as shown in this study, different predators, despite sharing large parts of their home range, confine their hunting areas to individual-specific elevations. All these three mechanisms facilitate intraspecific competitive exclusion which is widely reported in territorial carnivores (Steyn and Funston 2009, Lopez-Bao et al. 2011, Broekhuis et al. 2018).

Leopards showed elevation predation patterns, with bezoar goat and urial as highland prey whereas lowland prey include sheep, domestic dog and wild pig. This pattern can have two implications. First, in strongly seasonal environments, plant phenology can drive elevation migration of herbivores and consequently, synchronizing predator movement (Mysterud 2013, Bleyhl et al. 2019). Thus, integrating elevation gradients of resources for prey and predators in rugged landscapes can improve ecological interpretation and management plans. Although our sample size was not large enough to evaluate the effect of season, future research with larger sample sizes can test it on prey-predator interaction across elevation gradients. Second, domestic dog and sheep were mainly killed in lowland areas, suggesting that conflict with rural people can be a problem happening at lower levels of an elevation gradient. The practices of prey recovery through establishing law enforcement as well as minimizing wild ungulate competition with livestock and associated displacement from optimal habitats are widely encouraged (Babgir et al. 2017, Karimov et al. 2018, Bleyhl et al. 2019, Soofi et al. 2019). Our findings highlight the importance of considering elevation in conflict resolution plans through elevation zoning efforts.

Elevation gradients and vertical relief can shape fine-scale processes impacting mammalian carnivore communities. Two key axes of co-occurrence include spatial and dietary overlap in a guild of large carnivores (May et al. 2008, Davis et al. 2018). For example, although wolves *Canis lupus* are rarely detected in the national park's rugged highlands; they commonly attack livestock in lowland pastures outside the park (Farhadinia et al. 2017b). In terms of dietary requirement, wolves primarily prey on lowland prey species such as plain-dwelling ungulates, livestock and anthropogenic resources (Hosseini-Zavarei et al. 2013, Chetri et al. 2017). In contrast, leopards' main prey are ungulates inhabiting higher elevations (Sharbafi et al. 2016, Farhadinia et al. 2018c, Soofi et al. 2019). Thus, differentiated patterns in human-carnivore

conflict can occur, for example in terms of livestock type raided (Babgir et al. 2017, Soofi et al. 2019) or seasonality (Hosseini-Zavarei et al. 2013, Chetri et al. 2017). Habitat segregation across elevation gradients and prey separation help to avoid intraguild interactions at the site-specific levels in mountainous environments with strong seasonal variation.

Large carnivores live in a wide range of habitat types across their global range and understanding the variability in their density and what affects it is of continuing interest for ecologists (Hearn et al. 2017, Suryawanshi et al. 2019). Although great variation in density estimates of leopards is seen across their global range (Vitkalova et al. 2018, Balme et al. 2019), they can reach exceptionally high densities in montane environments (Grey et al. 2013, Williams et al. 2017). Our findings suggest that without incorporating elevation and topographic relief in surface estimation, density measures can potentially be overestimated in mountainous landscapes. Therefore, comparing density estimates across different ecosystems types with varied levels of topographic ruggedness and elevation variability needs to be done cautiously.

Synthesis and conclusion

Our study highlighted the importance of elevation and associated evolutionary processes shaping ranging and foraging behaviour of a large carnivore in a rugged landscape. Future research might usefully explore inter-sexual differences space use and predation patterns of leopards across elevation gradients. Resident females generally have smaller home ranges (Simcharoen et al. 2008, Johansson et al. 2018) and consequently are expected to show less variability across the elevation gradients.

Mountains, covering 25% of the global land surface area, are regularly a focus of international efforts to conserve a wide range of ecosystem services and biodiversity (Körner 2007). Mountainous areas presently act as refugia for large Asian felids in many range states,

often because such habitat presents obstacles to human inhabitation. However, they are under increasing pressure from multiple threats whose function and effect can vary along the elevation gradients (Jacobson et al. 2016, Li et al. 2018, Penjor et al. 2018, Vitkalova et al. 2018, Farhadinia et al. 2019, Suryawanshi et al. 2019). Therefore, understanding the dynamic interaction between species requirement and resource availability along the elevation gradient can effectively inform protection plans.

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Author contributions - MSF, DRH and RAM conceived the ideas and designed methodology; MSF and KH collected the data; MSF, DRH, RAM and PJJ analysed the data; MSF, DRH and RAM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest – The authors have no conflicts of interest to declare.

Permit(s) – The study was conducted in Tandoureh National Park (TNP), Iran. The Iranian Department of Environment reviewed all sampling, trapping, and handling procedures and approved permits for the work conducted (93/16270). The trapping and handling protocols were also approved by the University of Oxford's Ethical Review Committee (BMS-ERC-160614).

References

- Allen, A. M. et al. 2016. Scaling up movements: from individual space use to population patterns. - Ecosphere in press.
- Babrgir, S. et al. 2017. Socio-economic consequences of cattle predation by the Endangered Persian leopard *Panthera pardus saxicolor* in a Caucasian conflict hotspot, northern Iran. - Oryx 51: 124–130.

- 360 Balme, G. et al. 2019. Big cats at large: Density, structure, and spatio-temporal patterns of a
361 leopard population free of anthropogenic mortality. - *Popul. Ecol.* in press.
- 362 Benson, J. F. et al. 2006. Regulation of space use in a solitary felid: population density or prey
363 availability. - *Anim. Behav.* 71: 685–693.
- 364 Bjørneraas, K. K. et al. 2010. Screening Global Positioning System Location Data for Errors
365 Using Animal Movement Characteristics. - *J. Wildl. Manage.* 74: 1361–1366.
- 366 Bleyhl, B. et al. 2019. Assessing niche overlap between domestic and threatened wild sheep to
367 identify conservation priority areas. - *Divers. Distrib.* 25: 129–141.
- 368 Börger, L. et al. 2008. Are there general mechanisms of animal home range behaviour? A review
369 and prospects for future research. - *Ecol. Lett.* 11: 637–650.
- 370 Broekhuis, F. et al. 2018. Feeding ecology of cheetahs in the Maasai Mara, Kenya and the
371 potential for intra-and interspecific competition. - *J. Zool.* 304: 65–72.
- 372 Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. - *J. Mammal.*
373 24: 346–352.
- 374 Calabrese, J. M. et al. 2016. ctmm: an r package for analyzing animal relocation data as a
375 continuous-time stochastic process. - *Methods Ecol. Evol.* 7: 1124–1132.
- 376 Campbell, T. A. et al. 2004. Topographic home ranges of white-tailed deer in the central
377 Appalachians. - *Southeast. Nat.* 3: 645–653.
- 378 Chetri, M. et al. 2017. Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in
379 the Central Himalayas, Nepal. - *PLoS One* 12: e0170549.
- 380 Cooper, W. E. 1978. Home range size and population dynamic. - *J. Theor. Biol.* 75: 327–337.
- 381 Davis, C. L. et al. 2018. Ecological correlates of the spatial co-occurrence of sympatric
382 mammalian carnivores worldwide. - *Ecol. Lett.* 21: 1401–1412.

- 383 Farhadinia, M. S. et al. 2017a. GPS collars reveal transboundary movements by Persian leopards
384 in Iran. - *Cat News* 65: 28–30.
- 385 Farhadinia, M. S. et al. 2017b. Wolves can suppress goodwill for leopards: Patterns of human-
386 predator coexistence in northeastern Iran. - *Biol. Conserv.* 213: 210–217.
- 387 Farhadinia, M. S. et al. 2018a. Anchoring and adjusting amidst humans: Ranging behavior of
388 Persian leopards along the Iran-Turkmenistan borderland. - *PLoS One* 13: e0196602.
- 389 Farhadinia, M. S. et al. 2018b. Citizen science data facilitate monitoring of rare large carnivores
390 in remote montane landscapes. - *Ecol. Indic.* 94: 283–291.
- 391 Farhadinia, M. S. et al. 2018c. Persian leopard predation patterns and kill rates in the Iran–
392 Turkmenistan borderland. - *J. Mammal.* 99: 713–723.
- 393 Farhadinia, M. S. et al. 2019. Belt and Road Initiative may create new supplies for illegal
394 wildlife trade in large carnivores. - *Nat. Ecol. Evol.*: 1–2.
- 395 Fleming, C. H. and Calabrese, J. M. 2017. A new kernel density estimator for accurate home-
396 range and species-range area estimation. - *Methods Ecol. Evol.* 8: 571–579.
- 397 Fleming, C. H. et al. 2015. Rigorous home range estimation with movement data: a new
398 autocorrelated kernel density estimator. - *Ecology* 96: 1182–1188.
- 399 Grey, J. N. C. et al. 2013. Evidence of a high density population of harvested leopards in a
400 montane environment. - *PLoS One* 8: e82832.
- 401 Hearn, A. J. et al. 2017. Responses of Sunda clouded leopard *Neofelis diardi* population density
402 to anthropogenic disturbance: refining estimates of its conservation status in Sabah. - *Oryx*:
403 1–11.
- 404 Hijmans, R. J. et al. 2017. Package ‘geosphere.’ - Retrieved from in press.
- 405 Hosseini-Zavarei, F. et al. 2013. Predation by grey wolf on wild ungulates and livestock in

- central Iran. - J. Zool. in press.
- Hosseini, M. et al. 2019. Landscape connectivity for mammalian megafauna along the Iran-Turkmenistan-Afghanistan borderland. - J. Nat. Conserv.: 125735.
- Husseman, J. S. et al. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. - Oikos 101: 591–601.
- Jacobson, A. P. et al. 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. - PeerJ 4: e1974.
- Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. - Wildl. Soc. Bull. 32: 829–840.
- Johansson, Ö. et al. 2016. Land sharing is essential for snow leopard conservation. - Biol. Conserv. 203: 1–7.
- Johansson, Ö. et al. 2018. Sex-specific seasonal variation in puma and snow leopard home range utilization. - Ecosphere 9: e02371.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. - Ecology 61: 65–71.
- Karimov, K. et al. 2018. Responses of snow leopards, wolves and wild ungulates to livestock grazing in the Zorkul Strictly Protected Area, Tajikistan. - PLoS One 13: e0208329.
- Knopff, K. H. et al. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation patterns. - J. Wildl. Manage. 73: 586–597.
- Körner, C. 2007. The use of ‘altitude’ in ecological research. - Trends Ecol. Evol. 22: 569–574.
- Laver, P. N. and Kelly, M. J. 2008. A Critical Review of Home Range Studies. - J. Wildl. Manage. 72: 290–298.
- Li, Z. et al. 2018. Coexistence of two sympatric flagship carnivores in the human-dominated

- 429 forest landscapes of Northeast Asia. - *Landscape Ecol.* in press.
- 430 Lopez-Bao, J. V et al. 2011. Intraspecific interference influences the use of prey hotspots. -
- 431 *Oikos* 120: 1489–1496.
- 432 May, R. et al. 2008. Habitat differentiation within the large-carnivore community of Norway's
- 433 multiple-use landscapes. - *J. Appl. Ecol.* 45: 1382–1391.
- 434 Monterroso, P. et al. 2013. Estimating home-range size: when to include a third dimension? -
- 435 *Ecol. Evol.* 3: 2285–2295.
- 436 Montgomery, R. A. et al. 2012. Importance of visibility when evaluating animal response to
- 437 roads. - *Wildlife Biol.* 18: 393–406.
- 438 Morato, R. G. et al. 2016. Space use and movement of a neotropical top predator: the endangered
- 439 jaguar. - *PLoS One* 11: e0168176.
- 440 Myrsetrud, A. 2013. Ungulate migration, plant phenology, and large carnivores: The times they
- 441 are a-changin'. - *Ecology* 94: 1257–1261.
- 442 Naderi, M. et al. 2018. Persian leopard's (*Panthera pardus saxicolor*) unnatural mortality factors
- 443 analysis in Iran. - *PLoS One* 13: e0195387.
- 444 Odden, M. and Wegge, P. 2005. Spacing and activity patterns of leopards *Panthera pardus* in the
- 445 Royal Bardia National Park, Nepal. - *Wildlife Biol.* 11: 145–152.
- 446 Pebesma, E. and Bivand, R. 2005. *sp: classes and methods for spatial data*. R package version
- 447 0.7-12. in press.
- 448 Penjor, U. et al. 2018. Identifying important conservation areas for the clouded leopard *Neofelis*
- 449 *nebulosa* in a mountainous landscape: Inference from spatial modeling techniques. - *Ecol.*
- 450 *Evol.* 8: 4278–4291.
- 451 Powell, R. A. and Mitchell, M. S. 1998. Topographical constraints and home range quality. -

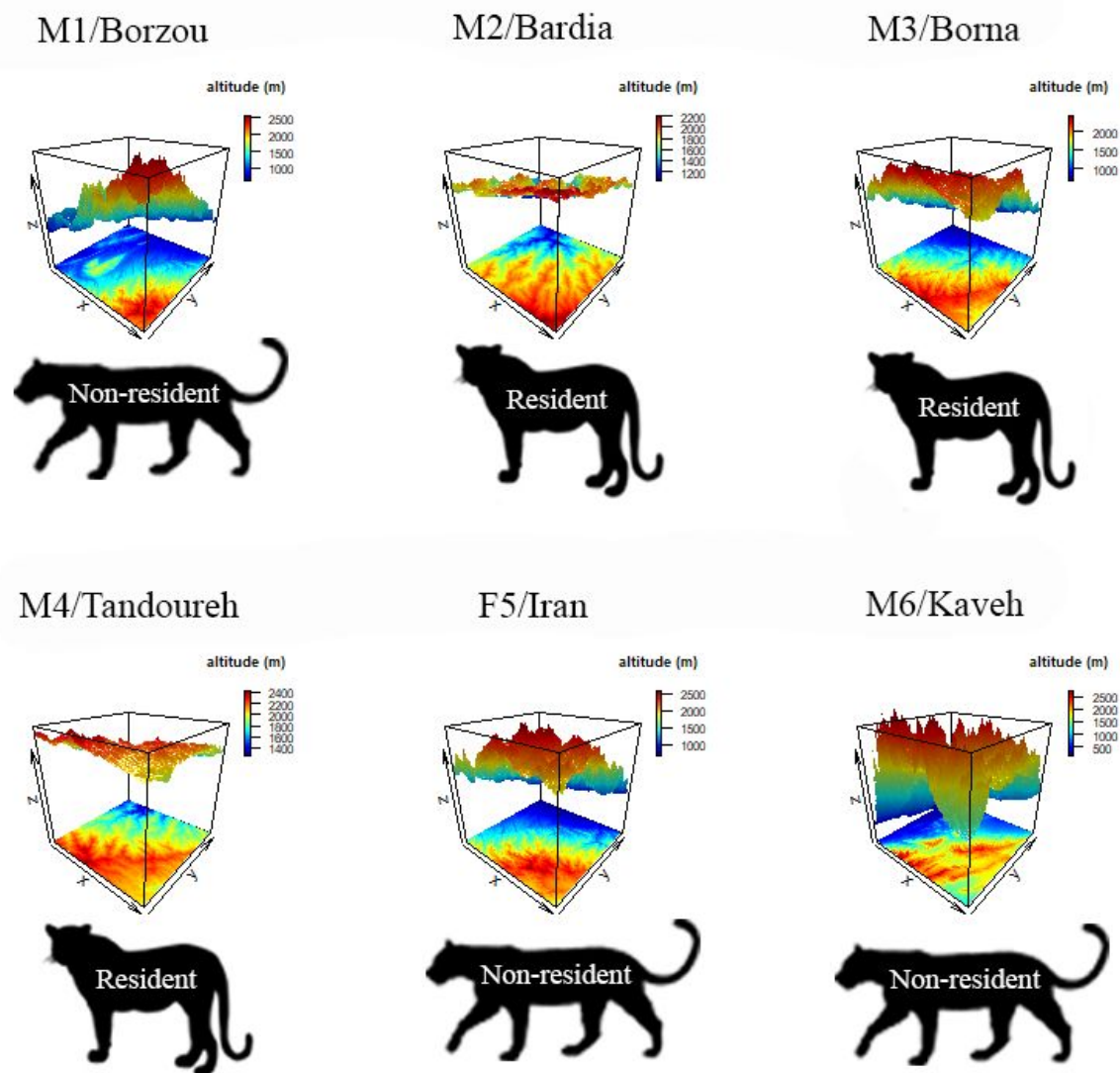
- 452 Ecography (Cop.). 21: 337–341.
- 453 Powell, R. A. and Mitchell, M. S. 2012. What is a home range? - J. Mammal. 93: 948–958.
- 454 Powell, R. A. et al. 2017. Stink or swim—techniques to meet the challenges for the study and
455 conservation of small critters that hide, swim or climb and may otherwise make themselves
456 unpleasant. - Biol. Conserv. wild musteloids in press.
- 457 R Development Core Team 2013. R: A language and environment for statistical computing. in
458 press.
- 459 Sharbafi, E. et al. 2016. Prey of the Persian Leopard (*Panthera pardus saxicolor*) in a mixed
460 forest-steppe landscape in northeastern Iran (Mammalia: Felidae). - Zool. Middle East 62:
461 1–8.
- 462 Simcharoen, S. et al. 2008. Home range size and daytime habitat selection of leopards in Huai
463 Khaeng Wildlife Sanctuary, Thailand. - Biol. Conserv. 141: 2242–2250.
- 464 Soofi, M. et al. 2019. Assessing the relationship between illegal hunting of ungulates, wild prey
465 occurrence and livestock depredation rate by large carnivores. - J. Appl. Ecol. 56: 365–374.
- 466 Spitz, D. B. et al. 2018. How plastic is migratory behavior? Quantifying elevational movement in
467 a partially migratory alpine ungulate, the Sierra Nevada bighorn sheep (*Ovis canadensis*
468 sierrae). - Can. J. Zool. 96: 1385–1394.
- 469 Stankowich, T. and Coss, R. G. 2006. Effects of risk assessment, predator behavior, and habitat
470 on escape behavior in Columbian black-tailed deer. - Behav. Ecol. 18: 358–367.
- 471 Steyn, V. and Funston, P. J. 2009. Land-use and socio-spatial organization of female leopards in
472 a semi-arid wooded savanna, Botswana. - South African J. Wildl. Res. 39: 126–132.
- 473 Suryawanshi, K. R. et al. 2019. Sampling bias in snow leopard population estimation studies. -
474 Popul. Ecol. in press.

- 475 Van Winkle, W. 1975. Comparison of several probabilistic home-range models. - J. Wildl.
476 Manage.: 118–123.
- 477 Vander Wal, E. and Rodgers, A. R. 2012. An individual-based quantitative approach for
478 delineating core areas of animal space use. - Ecol. Modell. 224: 48–53.
- 479 Vitkalova, A. V et al. 2018. Transboundary cooperation improves endangered species
480 monitoring and conservation actions: A case study of the global population of Amur
481 leopards. - Conserv. Lett. 11: e12574.
- 482 Walter, W. D. et al. 2013. Topographic home range of large mammals: is planimetric home
483 range still a viable method? - Prairie Nat. 45: 21.
- 484 Williams, S. T. et al. 2017. Population dynamics and threats to an apex predator outside
485 protected areas: implications for carnivore management. - R. Soc. Open Sci. 4: 161090.
- 486 Worton, B. J. 1987. A review of models of home range for animal movement. - Ecol. Modell. 38:
487 277–298.
- 488 Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range
489 studies. - Ecology 70: 164–168.
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495 **Table 1.** Movement parameters, home range estimates, and range size differences between planimetric and surface area of GPS
496 collared Persian leopards (*Panthera pardus saxicolor*) in Tandoureh National Park, northeastern Iran. Home range estimates were
497 calculated using 95% utilization distributions (UDs). The mean isopleth for core areas were 62% to 67% of the UD. Home ranges for
498 individuals marked with asterisk (*) were based on an Ornstein-Uhlenbeck (OU) process model, while an Ornstein-Uhlenbeck
499 Foraging (OUF) process model was fitted to the other animals based on their AICc weight. Means are only based on resident
500 individuals (M2/Bardia, M3/Borna and M4/Tandoureh).

Leopard ID/Name	Sex/age	Capture date	Last fix	# days	Planimetric AKDE 95% (km ²)	Planimetric Core area (km ²)	Topographic AKDE (km ²)	Topographic Core area (km ²)	AKDE 95% 3D/2D size difference (%)	Core area 3D/2D size difference (%)
M1/Borzou*	M/+10	5.2.2015	4.2.2016	368	563.4	224.5	709.7	287.3	26.1	27.8
M2/Bardia	M/8-10	3.10.2014	30.9.2015	362	43.9	16.5	58.8	22.8	34.2	38.4
M3/Borna*	M/5-6	28.9.2014	27.9.2015	364	206.5	57.6	177.8	74.6	28.8	30.2
M4/Tandoureh	M/7-10	16.8.2016	1.04.2017	228	59.8	23.1	76.9	29.5	28.7	27.8
F5/Iran	F/2-3	6.12.2015	29.1.2016	54	330.9	92.5	420.6	117.8	27.1	27.6
M6/Kaveh*	M/3-4	4.9.2015	26.8.2016	326	2269	775.7	2856.1	973.9	26.0	26.0
Mean (SE)				283.7 (50.8)	103.4 (51.8)	32.4 (12.7)	133.2 (65.5)	42.3 (16.3)		

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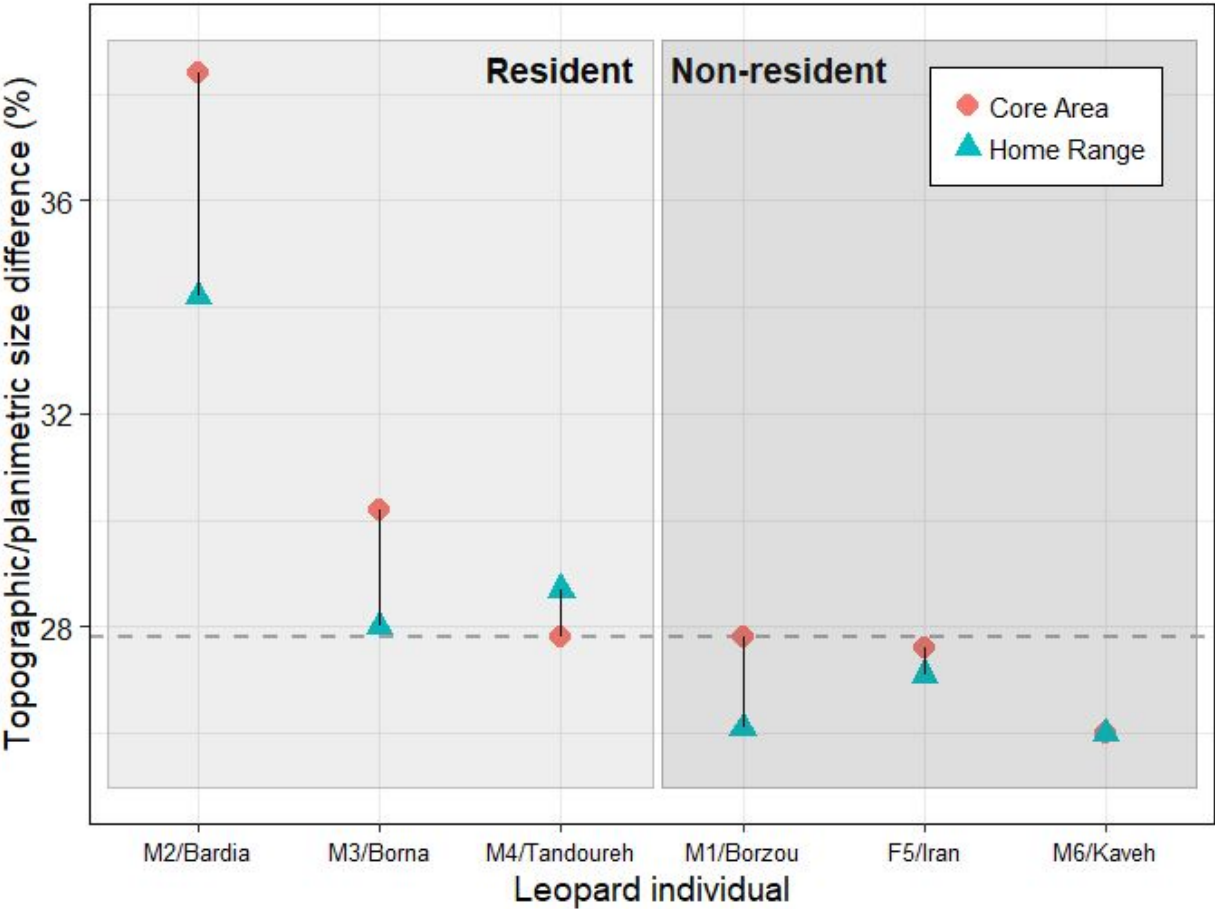


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504 **Figure 1**

505 Topographic surface areas for six collared leopards superimposed on masked three-dimensional
 506 digital elevation model (DEM) plots. Home ranges were calculated as 95% utilization
 507 distribution (UD) using auto-correlated kernel density estimator (AKDE) of GPS collar data
 508 from leopards captured in Tandoureh National Park, northeastern Iran. Individual ranges are not
 509 similarly scaled.

510



511

512 **Figure 2**

513 Combined factor of increase when comparing home range and core area of six GPS collared
514 leopards captured in Tandoureh National Park, northeastern Iran. The dashed grey line represents
515 median of topographic/planimetric size difference ratio.

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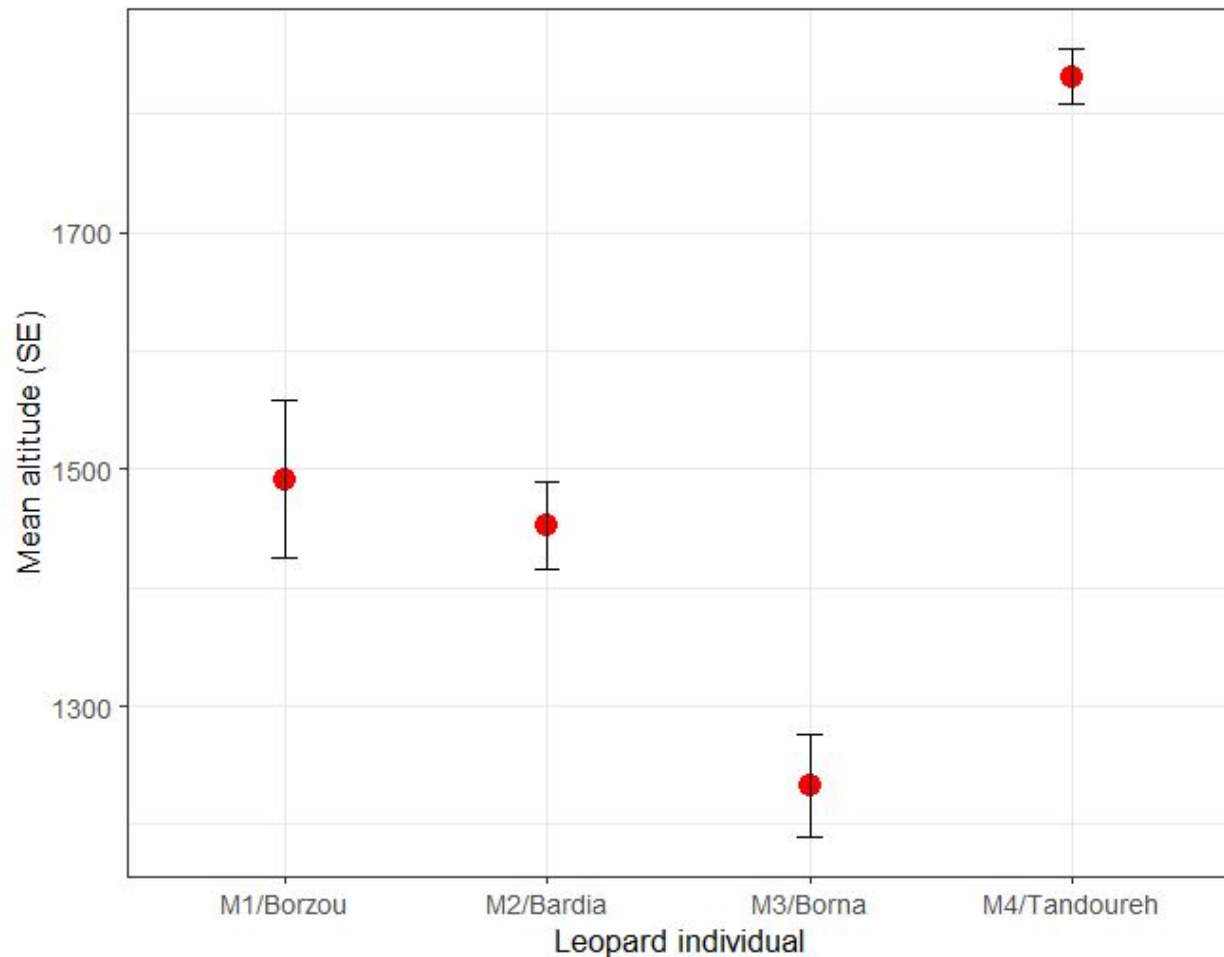
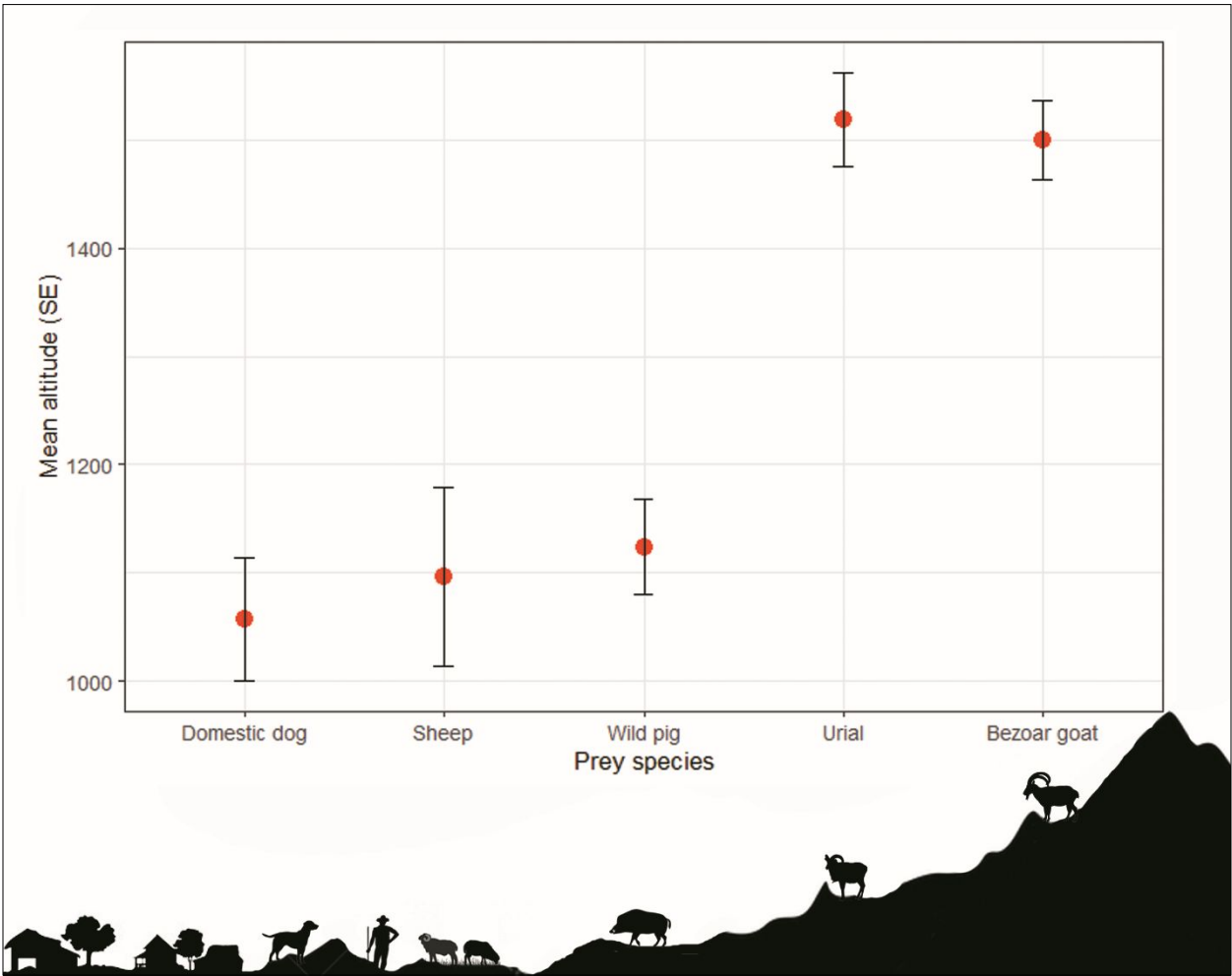


Figure 3

Inter-individual altitudinal differences in predation patterns of four adult Persian leopards in Tandoureh National Park. Predation events represent only kills made by resident leopards inside the national park, because all animals did not make kills outside the national park where most prey are lowland prey such as sheep, dog or wild pig. B1/Borzou's first 5.5 months was also included for which he showed residency behavior. Error bars represent standard errors.

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532 **Figure 4**

533 Altitudinal variability in kills, belonging to five main prey species, made by the collared Persian
534 leopards in Tandoureh National Park (2014-2017). Ranges on the graphic are not of a scale
535 relative to each other. Error bars represent standard errors.

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