



Research Article

Using ecological models to explore niche partitioning within a guild of desert felids

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Abstract

Mammalian carnivores play a fundamental role in ecosystem structure and function. Arid ecosystems of the Central Iranian plateau host a high diversity of carnivore species for which patterns of habitat selection and co-existence are poorly understood. We evaluated habitat correlates and segregation for five felid species in a mountainous arid region in central Iran: the sand cat, wildcat, caracal, Asiatic cheetah and Persian leopard. We produced ecological niche models (ENMs) and metrics of niche overlap to identify the most important drivers of habitat selection and patterns of species co-existence within the felids guild. We found three distinct patterns of habitat use, implying niche partitioning among the five felid species: (1) specialised use of sand dunes and desert woodlands by sand cat; (2) specialised use of flat and foothills desert areas in the case of the cheetah; and (3) broad, more generalised use of numerous habitat types in wildcat, caracal, and leopard. Together, these results indicate that mountains within vast, flat deserts (a.k.a. 'sky islands') are a cornerstone for maintaining ecological communities and predator-prey dynamics in south-western Asia. By increasing our understanding of coexistence in an understudied carnivore guild, our work provides critical information for the conservation of arid ecosystems.

Introduction

Mammalian carnivores are among the rarest and most threatened species across the world and require large and contiguous areas of habitat with abundant prey to meet their energetic requirements (Roemer et al., 2009; Ripple et al., 2014). Additionally, low population density and conflict with human activities make carnivores highly vulnerable to extinction, with risk of extinction increasing with increased body size (Carroll et al., 2001). Meso-carnivores, which are small to medium-sized carnivore species (Roemer et al., 2009), are equally important as large carnivores in determining community structure and function because they are more diverse and abundant than their larger counterparts (Crooks and Soulé, 1999; Prugh et al., 2009). Hence, quantifying the niche characteristics of both large and meso-carnivores is key to understanding many ecological processes, such as habitat segregation, competitive interactions, and predator-prey dynamics (Carroll et al., 2001; Roemer et al., 2009).

Competitive interactions strongly influence population dynamics (Hunter et al., 2007) and spatial distribution of carnivore species (Carroll et al., 2001; Rostro-García et al., 2015). Niche partitioning principally occurs along three dimensions (spatial, trophic, and temporal) and is an important mechanism for avoidance and reduction of the negative effects of competition especially when coexisting carnivore species are either phylogenetically related (Schoener, 1974; Donadio and Buskirk, 2006) or of similar size and morphology (Farlow and Pianka, 2003;

Donadio and Buskirk, 2006). Other factors such as resource availability (Hayward et al., 2007; Soykan and Sabo, 2009), habitat heterogeneity (Ford et al., 2014), and habitat security (Bashari and Hemami, 2013) can also influence niche partitioning. Nevertheless, the spatial (habitat) dimension of the niche is the most important and most frequently partitioned, particularly when spatial patterns are considered at finer scales (Schoener, 1974; Hemami et al., 2004). Habitat characterises different environmental parameters or niche attributes (e.g. food, water, cover) of a set of species (Begon et al., 1996); thus, understanding habitat selection provide a lens through which niche partitioning can be studied.

The combination of Geographical Information Systems (GIS) and Ecological Niche-based Models (ENMs) has revolutionised our understanding of spatially explicit ecological processes (Peterson et al., 2011). ENMs allow identification and mapping of the range of conditions and resources which an organism needs to survive and reproduce (Elith and Leathwick, 2009). ENMs have become an important tool for estimating realised niches (Audusseau et al., 2017; Ralston et al., 2016), thereby assisting managers in conservation planning (Zwiener et al., 2017; Fontaine et al., 2017). On the other hand, GIS allows for the manipulation and comparison of ENM outputs, which in turn increases our ability to understand ecological processes such as niche partitioning among species (Peterson et al., 2011). Although several studies have employed ENM and GIS to assess habitat suitability for carnivores (e.g. Brito et al., 2009; Rodríguez-Soto et al., 2011; Ahmadi et al., 2017; Khalatbari et al., 2018), the application of these tools to infer patterns of coexistence among sympatric species has rarely been considered, particularly in arid ecosystems.

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The arid and semi-arid deserts of central Iran are characterised by mountainous areas separated by expansive flat desert areas, together hosting a diversity of mammalian carnivores (at least 14 species, Ziaie, 2008). Desert ecosystems in central Iran provide habitats for flatland-dwelling ungulates (e.g. goitered gazelle, *Gazella subgutturosa*, and Indian gazelle, *G. bennettii*) and foothill-dwelling ungulates (e.g. wild sheep, *Ovis orientalis* and wild goat, *Capra aegagrus*), as well as many rodents (e.g. *Hystrix indica*, and species of Muridae, Dipodidae and Cricetidae families) and lagomorphs (e.g. *Lepus europeus*, *Ochotona rufescens*) (Ziaie, 2008). Consequently, the prey in this rich ecosystem supports seven medium- to large-bodied felids, including five species that are sympatric (i.e. share the same geographic region): the Asiatic cheetah (*Acinonyx jubatus venaticus*), caracal (*Caracal caracal*), Persian leopard (*Panthera pardus saxicolor*), sand cat (*Felis margarita*), and wildcat (*Felis silvestris*).

Current knowledge of factors influencing the ecology and distribution of felids in central Iran and elsewhere suggests that these species are exhibiting niche partitioning (see Pettorelli et al., 2010; Di Bitetti et al., 2010; Khosravi et al., 2018a). For instance, the geographic range of the three largest felids (i.e. cheetah, leopard, and caracal) overlap extensively (Bothma and Walker, 2013; Ziaie, 2008), but they differ in finer-scale habitat preferences (Khosravi et al., 2018a). Information regarding broad scale, regional patterns of habitat use indicate: (1) cheetahs occur mostly in lowlands and their distribution is strongly influenced by availability of gazelles (Swason et al., 2014; Khalatbari et al., 2018), (2) leopards inhabit mountain ranges where wild goat are present (Sanei et al., 2016), (3) caracals are present in both flatland and mountainous landscapes where they prey on a diversity of birds and mammals (Moqanaki et al., 2016), (4) wildcats inhabit forests, steppes, and bushy habitats where they feed on a diversity of small mammals (Phelan and Sliwa, 2005; Can et al., 2011), and (5) sand cats dwell in extremely arid desert environments where they also prey on small mammals (Sunquist and Sunquist, 2002; Ghadirian et al., 2016). For most of these species, however, fine-scale knowledge of habitat selection is scarce, especially in areas where they occur in sympatry (Ripple et al., 2014; Breitenmoser and Breitenmoser, 2016). Thus, knowledge of the fine-scale habitat preferences of these felids, three of which are considered as species of conservation concern, is necessary to better understand niche partitioning and to support management and conservation decisions regarding their populations and habitats.

By combining ENM and GIS tools with a comprehensive dataset of presence records for these five felid species, we aim to identify key factors contributing to their spatial distribution and coexistence in a protected area of the central Iranian plateau. The specific goals of this work were to understand: 1) what environmental factors influenced species occurrence, 2) what environmental factors could allow for species coexistence, 3) what regions of the protected area might support coexistence or the lack thereof. By addressing these questions, we will also provide baseline information in support of local conservation and management of these species and their habitats.

Materials and methods

Study area

The Abbasabad Wildlife Refuge (hereafter AWR) occupies an area of 3054 km² and is located in the central Iranian plateau (33°11'45" N to 33°38'15" N; 54°2'30" E to 55°8'25" E). The region has been officially protected (i.e., no hunting) since 2005 and was upgraded to a wildlife refuge in 2008. The general landscape of the area is characterised by a central mountain range (110 km length and 23 km width) and peripheral hills and plateaus. Elevation within the area ranges from 620 m in southern boundary to 2400 m in a central peak (avg.=1045 m). The climate is hot and dry with an average annual precipitation of 106 mm and average annual temperature of 18 °C (Hemami et al., 2007a). The refuge is dominated by rocky areas and xeric vegetation communities (*Artemisia* spp.) with low to moderate coverage, but woodlands (e.g. *Haloxylon* spp., *Ephedra* spp., *Zygophyllum* sp.) are sparsely distributed throughout the study refuge (Hemami et al., 2007a). Two small villages (≈84 habitants) subsisting on agriculture and livestock exist within the AWR.

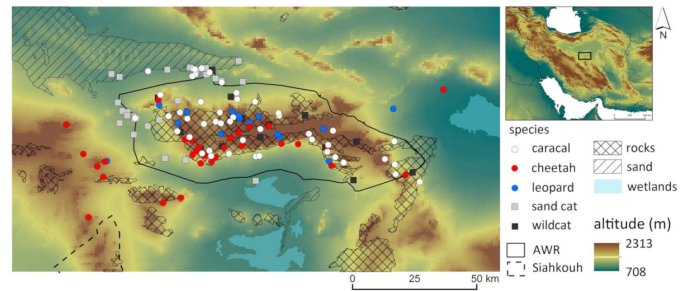


Figure 1 – Distribution of the five felid species in the study area and location of the study area in Iran (small rectangle in the right map). The extension of the Abbasabad Wildlife Refuge (AWR) and the Siahkhouh National Park, and three major types of habitats are signalled as polygons. Altitudinal range is also depicted.

Because there were records of wild felid occurrence just outside the boundaries of the AWR, and to capture a greater amount of habitat heterogeneity, we extended the study area to a 20 km buffer around the AWR (Fig. 1). This area accounts for 24380 km² and contains north parts of other protected areas (e.g. Siahkhouh National Park).

Species and distribution data

The presence of the five felid species (i.e. Asiatic cheetah, caracal, Persian leopard, sand cat, and wild cat) was recorded across the study area since 2005 when a number of studies on the conservation status of Abbasabad WR's species were started (e.g. Hemami et al., 2007a,b). Game guards assisted in data collection and we encouraged them to continue recording their observations of the target species after the end of the surveys. For the current study, we performed additional extensive field work during 2014–2015 to record species occurrences through a suite of methods, including camera trapping, daylight and night time direct observations, and identification of field signs (mainly for sand cat, caracal, and cheetah) including scats, tracks and dens (Tab. S1). The presence of each species based on field signs was confirmed only when at least two different presence signs could be recognised in one spotting site. Most of the cheetah signs were recorded after sighting reports by local people. Very little anthropogenic (i.e. infrastructures development) and climatic changes were noticed in and around Abbasabad WR during 2005–2015 (precipitation variation over this period was part of long-term fluctuations). Therefore, we pooled all occurrence data collected in different years for modelling.

Geographical coordinates (WGS 1984 datum) were recorded with a handheld GPS device and visualised in ArcGIS 10 (ESRI, 2006) to remove duplicates (i.e. records falling inside the same pixel). After filtering out duplicates, 137 records remained, including 47 for caracal, 30 for cheetah, 15 for leopard, 29 for sand cat, and 16 for wildcat (Fig. 1).

Spatial biases in sampling effort can negatively influence ENMs by producing over-fitting problems in areas with high numbers of presences (see Merow et al., 2013; Radosavljevic and Anderson, 2014). To reduce biases caused by sampling effort, we evaluated the level of spatial clustering within presence datasets for each species using the Nearest Neighbour Index (NNI; see Brito et al., 2009, 2011). Presence records for the caracal, the cheetah and the sand cat presented a random distribution (NNI<1.06), while records for the leopard and the wildcat showed a dispersed distribution (NNI<1.46), suggesting that all the data were acceptable to perform ecological models. Calculations were performed in the Spatial Analyst extension of ArcGIS.

Environmental variables

A total of ten slightly correlated variables ($r<0.7$) that are likely to influence the distribution of all five felid species (Sunquist and Sunquist, 2002; Klar et al., 2008; Pettorelli et al., 2010; Durant et al., 2010; Rodríguez-Soto et al., 2011) were used to perform ecological niche modelling. These variables accounted for two sets of descriptors (Tab. 1): (1) two topographic variables, encompassing altitude (ASTER GDEM ver. Wilson et al., 2007) and terrain roughness index (TRI); and (2) eight landscape variables, including rocky outcrops

Table 1 – Variables used to develop ENMs for each of the five felid species in the Abbasabad Wildlife Refuge. Type, name, meaning, range and units, and source for each variable are depicted.

Type	Name	Meaning	Range	Units	Source
Topographic	altitude	altitude	700–2300	m	ASTER GDEM ver. 2
Topographic	TRI	terrain roughness index	0–17.95		derived from altitude
Landscape, barelands	rocks	distance to rocks	0–0.5	°	land use map (IFRWMO)
Landscape, barelands	sand	distance to sand dune	0–0.9	°	land use map (IFRWMO)
Landscape, vegetation	low canopy	distance to low vegetation canopy, <10	0–0.5	°	rangeland map (IFRWMO)
Landscape, vegetation	mod canopy	distance to moderate vegetation canopy, 25–50	0–0.53	°	rangeland map (IFRWMO)
Landscape, vegetation	woods	distance to woodlands	0–0.55	°	land use map (IFRWMO)
Landscape, hydrographic	wetlands	distance to wetlands	0–0.92	°	land use map (IFRWMO)
Landscape, hydrographic	rivers	distance to rivers	0–0.21	°	waterway map (IFRWMO)
Landscape, anthropogenic	agriculture	distance to agriculture	0–0.66	°	land use map (IFRWMO)

(9.54% of the study area), sandy areas (7.42%), vegetation with low (6.44%) and moderate canopy (14.69%), woodlands (7.81%), wetlands (3.27%), dry riverbeds/gullies (22.92%), and agriculture areas (0.4%) (Iranian Forests, Range, and Watershed Management Organisation (IFRWMO), resampled at a resolution of 30 arc seconds ($\approx 1 \text{ km}^2$). We measured the Euclidean distance to each landscape variable using the “Euclidean Distance” tool of ArcGIS.

Ecological niche-based models

The low detection probabilities of the five felid species studied here precluded the use of presence-absence ecological niche models. For this reason, ecological niche-based models were performed using the Maximum Entropy approach on the presence-only Maxent 3.3.k software (Phillips et al., 2006). This modelling technique performs particularly well with low sample sizes (Elith et al., 2006; Hernandez et al., 2006), and has been successfully implemented in other carnivore species from arid ecosystems (e.g. Brito et al., 2009; Vale et al., 2016).

Presence data for each species and the ten variables were imported to Maxent. Twenty replicate models were run, each with a random seed, providing a different, randomised 80% training / 20% testing data partition in each run. Observations for each model replicate were chosen by bootstrap, allowing sampling with replacement. Models were then run with auto-features (Phillips et al., 2006). We used two metrics to measure individual models performance: (1) the Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) plot, which ranges from 0, low performance, to 1, high performance (Fielding and Bell, 1997); and (2) the True Skill Statistic (TSS) metric, which relates the proportion of observed presences that are predicted as presences (Sensitivity) and the proportion of observed absences that are predicted as absences (Specificity), and ranges from -1, low performance, to 1, high performance (Allouche et al., 2006). Model replicates were added to generate a mean forecast of probability of each species occurrence (Martínez-Freiría et al., 2008; Marmion et al., 2009). Standard deviation between individual model probabilities of presence was used as an indication of prediction uncertainty (Buisson et al., 2010).

The weight of each variable for describing the distribution of the species was determined by its average percentage's contribution to the models. The relation between the occurrence of each species and magnitude of each variable was determined by the visual examination of response curves profiles from univariate models (Phillips et al., 2006). When two or more species exhibited high values of contribution for a given variable, similar profiles for this variable were taken as an indication of parallel relationships between the occurrence of these species and the range of variation of the variable (e.g. (Martínez-Freiría et al., 2008; Brito et al., 2009, 2011). This indicates also the possible occurrence of sympatry and eventual competition within the range of values of the variable equally selected by species. Conversely, a dissimilar profile between species was taken as an indication of divergent relationships and possible allopatry.

Sympatry areas, geographical niche breadth, and overlap

Probability surfaces were imported to ArcGIS, where they were converted to binary models (i.e. absence/presence pixels) using the “Min-

imum Training Presence logistic threshold” (Liu et al., 2005). Then, the presence-absence surfaces were overlaid and summed to identify areas where two or more species could coexist (i.e. sympatry areas).

Values of niche breadth and niche overlap for each species and between species pairs, respectively, were calculated in the ENMtools 1.4.4 software (Warren et al., 2010), deriving average values from the 20 Maxent model replicates for each species. The Levins' Index, used as a measure of niche breadth for each of the species, ranges from 0 to 1, having specialist species the lowest values and generalist the highest (Levins, 1968). The Schoener's D Index also ranges from 0 to 1, being the niche overlap between species pairs as higher as the index (Schoener, 1974).

Results

Environmental factors related to species occurrence

The ROC plots exhibited high average AUCs with low standard deviations for both training and test datasets in all species models (Tab. 2). Similarly, average values for Sensitivity, Specificity and TSS metrics were high, showing low standard deviations in most species models (Tab. 2).

The ecological models facilitated identification of environmental variables that significantly influence species distribution patterns (Tab. 3): (1) caracal, cheetah and wildcat presences are associated with rock cover, but caracal and wildcat were also associated with woodlands, while cheetah were associated with TRI and low vegetation canopy; (2) leopard presence was primarily associated with altitude and secondarily with a moderate level of vegetation canopy; and (3) sand cat presence was associated with woodland and sandy areas.

There were common variables related to the distribution of most species, such as woodland and rock cover, or to the distribution of some species pairs, such as TRI, sand or moderate canopy (Tab. 3). When profiles of response curves for these variables are visualised, particular patterns across species can be identified (Fig. 2): (1) all species except the sand cat have high preference for rocky areas; (2) the caracal, leopard, wildcat and sand cat frequently occur in woodlands, whereas cheetah mostly occurs in the surrounding steppe areas; (3) the sand cat occurs in areas with low TRI, whereas cheetah selects areas with moderate levels of TRI; (4) the sand cat occurs in sandy areas, whereas the caracal mostly occur in grass-scrub lands and mountainous steppes far from these areas; (5) both the leopard and the wildcat mostly occur in areas with moderate canopy.

Potential areas for species occurrence and niche breadth

Probabilistic ecological models identified suitable cells for the occurrence of the five felids mostly in areas where these species were known to occur but also in areas where the species were not recorded previously (Fig. S3). Binary models allowed the identification of three major spatial patterns of distribution linked to the strict (leopard and cheetah), moderate (caracal and wildcat) and no occurrence (sand cat) in rocky areas (Fig. 3). The leopard is the species with the largest availability of potentially suitable cells (30% of study area), while sand cat showed the most restricted distribution (ca. 12%, Tab. 2). Average values of Levin's Index for the five species are lower than 0.26 and thus,

Table 2 – Top: number of training and test samples, average training and test AUC (and standard deviation), AUC standard deviation (SD), average Sensitivity (and standard deviation), average Specificity (and standard deviation) and average TSS (and standard deviation) for ENM developed for each of the five felid species in the Abbasabad Wildlife Refuge. Bottom: number of cells and % of cells in relation to the whole study area predicted by binary ENMs developed for each of the five felid species in the Abbasabad Wildlife Refuge. Estimates of Levins' I, average (and standard deviation), measuring niche breadth are depicted for each of the species.

metrics	Caracal	Cheetah	Leopard	Sand cat	Wildcat
N training / test samples	38 / 9	24 / 6	12 / 3	21 / 5	13 / 3
Training AUC	0.964 (0.007)	0.966 (0.011)	0.954 (0.022)	0.984 (0.007)	0.947 (0.02)
Test AUC	0.921 (0.031)	0.942 (0.039)	0.937 (0.056)	0.959 (0.037)	0.906 (0.059)
AUC SD	0.031	0.027	0.034	0.023	0.042
Sensitivity	0.933 (0.074)	0.933 (0.111)	0.900 (0.153)	0.960 (0.080)	0.867 (0.163)
Specificity	0.751 (0.082)	0.863 (0.053)	0.759 (0.115)	0.866 (0.039)	0.833 (0.054)
TSS	0.685 (0.088)	0.797 (0.094)	0.692 (0.066)	0.826 (0.076)	0.700 (0.153)
N cells	4478	3561	7451	2873	5501
% area	18.368	14.606	30.562	11.784	22.564
Levins' I	0.189 (0.037)	0.195 (0.047)	0.236 (0.081)	0.097 (0.036)	0.253 (0.087)

all species are recognised as specialist (Tab. 2). The wildcat and leopard appear to be specialists to the least degree (highest Levins' Index value), whereas the sand cat shows the lowest index value of the five species.

Sympatry areas and niche overlap

The overlap of binary models allowed the identification of potential sympatry areas between two or more species (Fig. 4, S4). By species-pairs, leopard and wildcat showed the highest level of area overlap, whereas cheetah and sand cat the lowest levels (Tab. S2, Fig. 4). For triple-sympatry areas, the highest values of overlap occurred among caracal, leopard and wildcat (Tab. 4, Fig. 4). When three or four species are considered, the lowest values of overlap occurred with the sand cat (Tab. S2, Fig. S4). Sympatry areas among the five species were scarce and corresponded to less than 1% for the extension of the study area (Tab. S2, Fig. S4).

Species-pairs presented a considerable variation in Schoener's D Index, ranging from low to moderate niche overlap (Tab. 4). The wildcat, caracal and leopard showed the highest levels of niche overlap, whereas the sand cat and cheetah exhibited the lowest.

Discussion

This work describes fine scale spatial patterns and topographic and habitat factors associated with the occurrence of five sympatric felids in an arid region of central Iran. Correlates from ecological models, and particularly the analysis of the response curve profiles, suggest competition for some habitats (i.e. rocky areas, woodlands and moderate canopy), and the occurrence of habitat segregation in others (i.e. TRI and sand). Spatial predictions allowed measuring niche breadth and overlap, reinforcing the distinct degree of specialisation that each species has acquired, and furthermore, suggesting important areas for the conservation and management of these populations and their ecosystem in the central Iranian plateau.

Environmental factors related to species occurrence

Although, prey availability is a primary factor affecting patterns of habitat use in carnivores (Crooks and Soulé, 1999; Hayward et al., 2007; Vanak et al., 2013), detailed information on the presence of prey species was not available for our modelling purpose. Nevertheless, we rely on vegetation structure as a proxy to infer availability of food and cover with species distributional patterns (Mueller et al., 2008).

Table 3 – Average contribution of variables (and SD) in ENM developed for each of the felid species in the Abbasabad Wildlife Refuge. The most important variables in bold.

variables	Caracal	Cheetah	Leopard	Sand cat	Wildcat
Altitude	4.150 (2.9)	8.863 (8.963)	36.621 (13.20)	2.580 (2.350)	1.395 (2.092)
TRI	1.827 (1.854)	15.89 (9.603)	3.927 (5.360)	10.77 (7.239)	0.571 (0.760)
Rocks	35.532 (7.318)	34.728 (11.757)	12.08 (8.274)	4.428 (1.707)	36.453 (16.172)
Sand	11.76 (4.486)	1.268 (1.450)	6.813 (6.029)	21.25 (5.429)	6.769 (7.147)
Low canopy	2.002 (1.956)	14.775 (4.116)	0.400 (14.70)	8.422 (1.603)	0.304 (8.343)
Woods	25.742 (6.236)	10.38 (6.693)	15.8 (4.654)	33.411 (4.378)	30.111 (9.999)
Wetlands	2.771 (1.567)	3.141 (2.798)	3.705 (6.519)	5.201 (4.650)	2.721 (2.821)
Rivers	6.981 (4.384)	1.028 (1.508)	0.682 (1.342)	1.285 (1.249)	9.673 (6.817)
Agriculture	7.257 (4.233)	6.298 (4.521)	1.002 (1.192)	8.399 (5.681)	1.854 (2.811)

The diversity of habitats across the study area resulted in different patterns of habitat use. The five felid species are all identified as habitat specialist, with different degrees of specialisation. Sand dunes, a very restricted landscape feature in the study area, seem to be a key habitat for sand cat, the most specialised felid in our study area; yet sand dunes hamper the presence of other species. For instance, caracals prefer hilly terrains and foothills with good vegetation cover, where they can find food (mainly rodents) and cover (Moqanaki et al., 2016), but avoid sparsely vegetated sand dunes.

Sand cat is known by its preference for sandy deserts along of a wide distributional range (Serra et al., 2007; Mallon et al., 2011; Cole and Wilson, 2015). In our study area, sand cat occurrence is related to sand dunes that are sparsely covered with *Haloxylon* spp. and *Zygophyllum* spp. (i.e. woodland in our model). *Haloxylon* woods make the soil more stable and likely influence the occurrence of many rodent species (Hemami et al., 2011; Traba et al., 2016). The stability of soil is also important for the sand cat as it must establish stable dens in relatively soft, sandy soil. Absence of sand cat in other habitat types is therefore likely due to a lack of preferred prey (Cole and Wilson, 2015) and suitable cover terrain.

Compared to sand cat, all other species showed broader levels of habitat selection. In addition to rocky and woodland habitats, the preference of the wildcat and the Persian leopard to moderate canopy covers (mixture of grass-scrub lands with canopy <50%) explains their wider habitat use, which in turn results in the highest niche breadth values among the studied felid species. With a relatively large home range (Jerosch et al., 2017), wildcats prey on a variety of small to medium-sized vertebrates (Apostolico et al., 2016), which are available in different habitats. Although the primary prey species of leopards in Iran are wild goat, wild sheep, and wild boar (*Sus scrofa*), they also prey

Table 4 – Estimates of Schoener's D Index (average, bottom left; standard deviation, top right) measuring niche overlap between species pairs in the Abbasabad Wildlife Refuge.

D (Avg /SD)	Caracal	Cheetah	Leopard	Sand cat	Wildcat
Caracal	—	0.054	0.062	0.06	0.045
Cheetah	0.433	—	0.07	0.051	0.061
Leopard	0.586	0.48	—	0.065	0.088
Sand cat	0.321	0.148	0.219	—	0.086
Wildcat	0.66	0.444	0.638	0.255	—

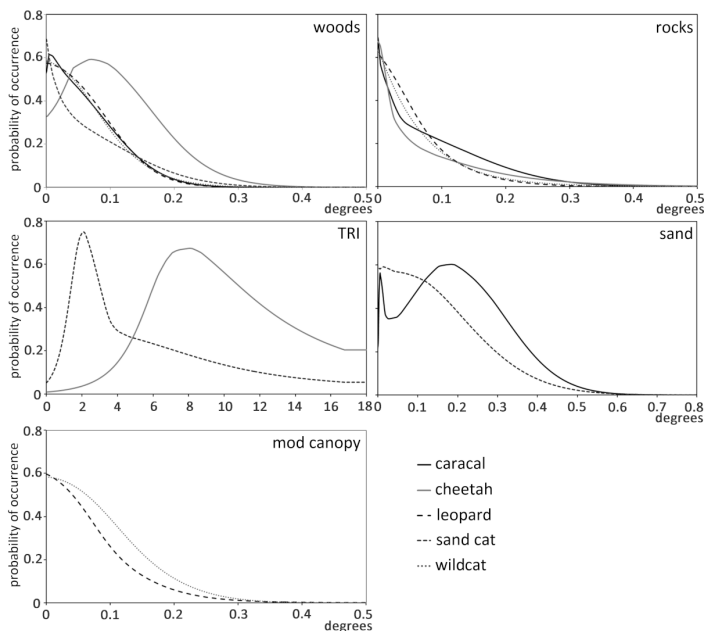


Figure 2 – Response curves for the most important common variables in ecological models developed for the five felid species in the Abbasabad Wildlife Refuge. See Tab. 1 for variable names.

on livestock (Lumetsberger, 2014; Farhadinia et al., 2014; Sanei et al., 2016; Ghoddousi et al., 2016). In fact, food items found in scats of leopard in Iran suggest a high variable diet as incorporated a diversity of vertebrates from domestic horses (*Equus caballus*) and large carnivores to birds and reptiles (Taghdisi et al., 2013; Lumetsberger, 2014; Farhadinia et al., 2014). A similar pattern of using a wide range of habitat types has been reported for the wildcat in southern Iberian Peninsula (Monterroso et al., 2009), as well as, for the Persian leopard in southern Armenia (Khorozyan, 2003).

Terrain roughness index (TRI) strongly influenced the habitat use for the sand cat and the cheetah. The sand cat belongs to flat plains; the response curve profile for the TRI variable reported its occurrence at the lowest values (i.e. flat areas located at low elevations). In Iran, sand cats mainly occur in sandy flat plains, but can also be seen in sparsely vegetated flat steppes (Hemami et al., 2011; Ghadirian et al., 2016). In the case of the cheetah, the response curve profile, suggests its occurrence in foothills and undulating grounds, which are located in vicinity to mountainous areas. The historical distribution of the Asiatic cheetah is believed to closely follow those of plain-dwelling ungulates (e.g. goitered gazelle and Indian gazelle) as they comprise its most preferred prey (Mallon, 2007; Farhadinia and Hemami, 2010; Khalatbari et al., 2018). Recent studies on prey selection by cheetah in central Iran, however, suggest a shift from these currently rare prey species to mountain-dwelling ones, such as wild sheep and wild goat (Farhadinia and Hemami, 2010). Our ecological models suggest that low canopy flat areas with higher occurrence of gazelles are still the main drivers of cheetah distribution. Accordingly, cheetah's preference of open African savannah has formerly been documented (Broekhuis et al., 2013; Swason et al., 2014).

The leopard is the only species for which elevation plays an important role in its distribution, being mostly restricted to high elevations. Preference to high-elevation landscapes allow leopards to prey on wild sheep and wild goat. This result fits well with the perception that the Persian leopard is a carnivore of remote alpine regions with high availability of large ungulates (Khorozyan, 2003; Gavashelishvili and Lukarevskiy, 2008). In Armenia leopards occupy higher elevations from late spring to late autumn and move down to foothills when there is snow (Khorozyan et al., 2010). It is documented that in arid regions of the Middle East leopards keep away from desert areas and human settlements (Gavashelishvili and Lukarevskiy, 2008). In open steppes, predation on plain-dwelling ungulates such as gazelles may only be

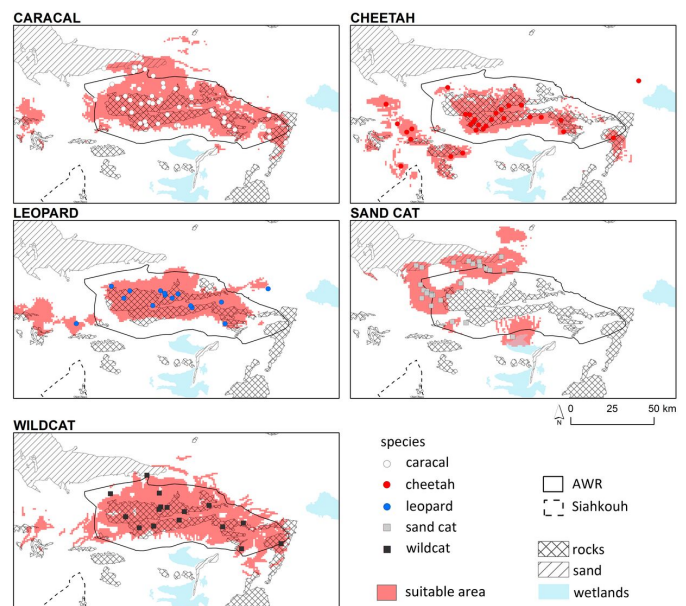


Figure 3 – Suitable areas for each of the five felid species in the Abbasabad Wildlife Refuge derived from ecological models. Species presence records and three major habitat types are shown.

economic for cheetahs that have acquired the evolutionary adaptations for very fast chases.

Sympatry areas and niche overlap

Based on the configuration of habitat suitability maps and areas of sympatry, environmental correlates and their response curves, and niche breadth values, three patterns of habitat selection and niche overlap can be discerned for the five studied felids. The first pattern corresponds to the sand cat, which is identified as the most specialist species exhibiting the minimum Schoener's D and the lowest level of sympatry with the remaining felid species. This suggests that competition among the sand cat and the other studied felid species is very low. Within the study area, dissimilarity of sand cat habitat selection with the other felid species appears to depend upon the availability of sand dunes as an exclusive habitat for the species (Serra et al., 2007; Mallon et al., 2011; Cole and Wilson, 2015), avoided by other felids.

The second pattern corresponds to the Asiatic Cheetah, for which ecological models demonstrated a patchy distribution of suitable habitats and a high level of habitat overlap with leopard. Cheetahs patrol over open areas covered by sparse halophytes in rough landscapes in the centre and south-west of the study area. This spatial pattern of habitat suitability likely reflects cheetah's focus on flatland-dwelling gazelles, and secondary preference for mountain-dwelling wild sheep and wild goat in foothill habitats. Use of foothills by cheetahs in central Iranian deserts might be a consequence of a change in their hunting strategy (Farhadinia and Hemami, 2010; Khalatbari et al., 2018) in response to the reduction of their preferred prey (*Gazella subgutturosa* and *Gazella bennettii*) in open flatlands and hilly terrain (Hemami and Groves, 2001; Khosravi et al., 2018b). Consequently, the niche overlap between the Persian leopard and the Asiatic cheetah is notable. On the other hand, the cheetah may avoid mountainous areas because of the potential of being preyed upon by leopard (Hayward et al., 2006). A similar spatial pattern has been reported for the African cheetah, where its habitat selection is driven by trade-offs between resource acquisition and predator avoidance, thereby behaving as a sub-ordinate predator (Hunter et al., 2007; Swason et al., 2014; Rostro-García et al., 2015).

The third pattern corresponds to the three species with the most similar habitat use: the caracal, leopard and wildcat. These are the less specialised species associated with rocky and woodland habitat types, which are common in the study area. Thus, the three species show a high degree of sympatry and spatial niche overlap. However, distinct size-dependent prey preferences of these species might be translated in low overlap in the trophic niche. In Iran caracals prey on a variety

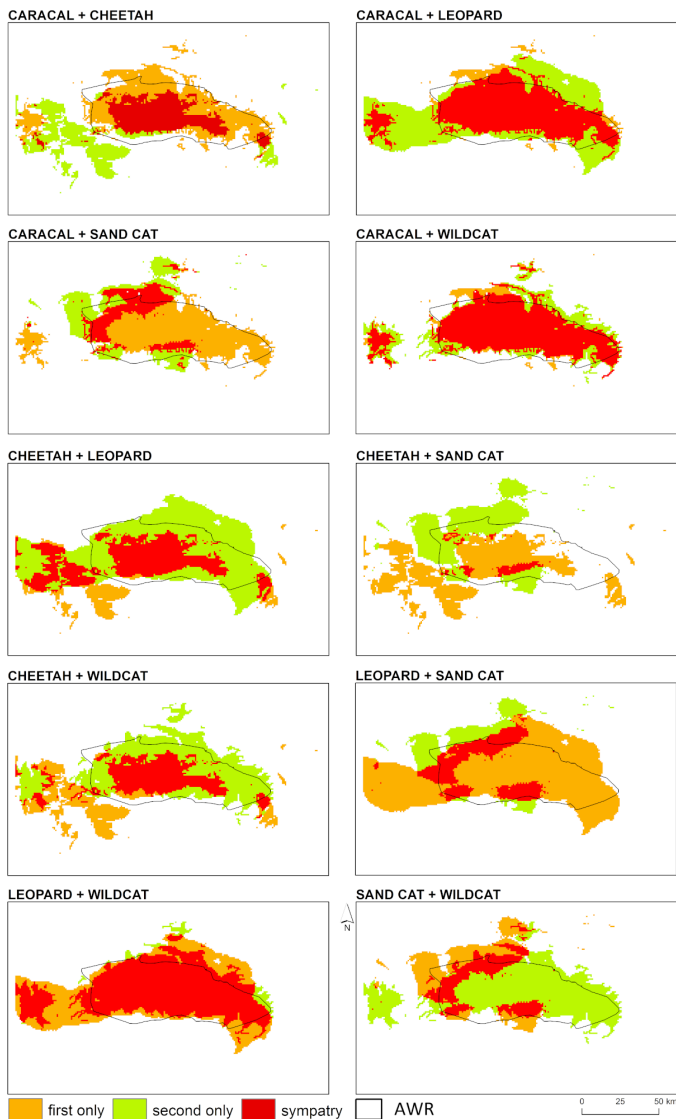


Figure 4 – Overlap between predicted suitable areas for felid species-pairs in the Abbasabad Wildlife Refuge derived from ecological models. First indicates suitable areas for the left species of the species-pair, while second indicates suitable areas for the right species of the species-pair. Sympatry indicates suitable areas for both species of the species-pair.

of small to medium-sized mammals and birds (Moqanaki et al., 2016), whereas leopards and wild cats use larger and smaller prey respectively (Sunquist and Sunquist, 2002).

Species habitat selection results form a hierarchical order of selection processes occurring at different spatial scales (Johnson, 1980). This hierarchical selection occurs from geographical range (1st order) and selection from individual's or social group's home range (2nd order) to differential use within home range (3rd order) and selection of feeding sites and food items (4th order). The results of this study indicate spatial overlap of two small to medium-sized (i.e. wildcat and caracal) and two large-bodied (Asiatic cheetah and Persian leopard) felids in geographic range (i.e. 1st order). In addition, relative body size of predators primarily influences direct competition for prey and intra-guild interference (Donadio and Buskirk, 2006). Therefore, we suggest that these species may show temporal variation in their activity or segregation in high orders (e.g. 3rd and 4th) of habitat selection process. Further work involving telemetry studies could provide comprehensive information of species habitat selection and their interspecies interactions through different spatial scales.

Conservation implications

Overall, our work reinforces the role of mountain areas dispersed throughout the vast, flat deserts of the central Iranian plateau as sanctuaries that protect the ecological communities and predator-prey dynam-

ics. Through providing security from human disturbance (e.g., hunting and livestock grazing), especially in the dry season, the AWR is a biological refuge for large-bodied herbivores, which in turn supports carnivore species.

Our predictions can be used for distinct purposes related to conservation management. Designating micro-reserves, corridors or particular habitats frequently used by one or more felid species; establishing monitoring networks for estimating and predicting population sizes and trends or understanding spatial behaviour both at intra-specific (e.g. detecting reproduction spots) and interspecific level (e.g. competitive interactions). Leopards and wildcats showed dispersed distributions with very few records; this work can hence establish further monitoring areas to understand factors affecting such distributional patterns. Predictions are particularly relevant for some species which are at the edge of extinction such as the cheetah (less than 50 individuals remain in Iran; Khalatbari et al., 2018). Restoring gazelle populations in this and other cheetah habitats could be effective in maintaining the last populations of this species. In addition, maintaining habitat diversity to support a range of small- to large-bodied prey species is essential for survival of carnivore communities in central Iranian deserts.

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Supplemental information

Table S1 Number of records used to perform ecological niche-based models for the five felid species in central Iran.

Table S2 Number of sympatry cells and % of sympatry area in relation to the whole study area for different assemblages of two, three, four and five felid species in the Abbasabad Wildlife Refuge, derived from ecological models.

Figure S3 Suitable areas for each of the five felid species in the Abbasabad Wildlife Refuge derived from average suitability ecological models.

Figure S4 Selected cases of predicted sympatry areas among three, four and five felid species in the Abbas-Aabad Wildlife Refuge, derived from ecological models.