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

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asiatic cheetah
caracal
carnivores co-existence
persian leopard
sand cat
wild cat

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 Soule, 1999; Frugh 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; Rodriguez-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.
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. goat-haired gazelle, Gazella subgaturosa, 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 Bitteti 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 flanland 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; Ghadrian 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 the southern boundary to 2400 m in a central peak (avg.=1045 m). The area is 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. Shahkouh 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 wild cat 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; Rodriguez-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.

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

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.

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.

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,
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.

### Sympathy areas and niche overlap

The overlap of binary models allowed the identification of potential sympathy 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-sympathy areas, the highest values of overlap occurred among caracal, leopard and wildcat (Tab. S2, Fig. 4). When three or four species are considered, the lowest values of overlap occurred with the sand cat (Tab. S2, Fig. S4). Sympathy 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 2 – Top: number of training and test samples, average training and test AUC (and standard deviation), AUC standard deviation (SD), average Specificity (and standard deviation), average Sensitivity (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.

<table>
<thead>
<tr>
<th>metrics</th>
<th>Caracal</th>
<th>Cheetah</th>
<th>Leopard</th>
<th>Sand cat</th>
<th>Wildcat</th>
</tr>
</thead>
<tbody>
<tr>
<td>N training / test samples</td>
<td>38/9</td>
<td>24/6</td>
<td>12/3</td>
<td>21/5</td>
<td>13/3</td>
</tr>
<tr>
<td>Training AUC</td>
<td>0.964</td>
<td>0.966</td>
<td>0.954</td>
<td>0.984</td>
<td>0.947</td>
</tr>
<tr>
<td></td>
<td>(0.007)</td>
<td>(0.011)</td>
<td>(0.022)</td>
<td>(0.007)</td>
<td>(0.02)</td>
</tr>
<tr>
<td>Test AUC</td>
<td>0.921</td>
<td>0.942</td>
<td>0.937</td>
<td>0.959</td>
<td>0.906</td>
</tr>
<tr>
<td></td>
<td>(0.031)</td>
<td>(0.039)</td>
<td>(0.056)</td>
<td>(0.037)</td>
<td>(0.059)</td>
</tr>
<tr>
<td>AUC SD</td>
<td>0.031</td>
<td>0.027</td>
<td>0.034</td>
<td>0.023</td>
<td>0.042</td>
</tr>
<tr>
<td></td>
<td>(0.074)</td>
<td>(0.111)</td>
<td>(0.153)</td>
<td>(0.080)</td>
<td>(0.163)</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>0.933</td>
<td>0.933</td>
<td>0.900</td>
<td>0.960</td>
<td>0.867</td>
</tr>
<tr>
<td></td>
<td>(0.074)</td>
<td>(0.111)</td>
<td>(0.153)</td>
<td>(0.080)</td>
<td>(0.163)</td>
</tr>
<tr>
<td>Specificity</td>
<td>0.751</td>
<td>0.863</td>
<td>0.759</td>
<td>0.866</td>
<td>0.833</td>
</tr>
<tr>
<td></td>
<td>(0.082)</td>
<td>(0.053)</td>
<td>(0.115)</td>
<td>(0.039)</td>
<td>(0.054)</td>
</tr>
<tr>
<td>TSS</td>
<td>0.088</td>
<td>0.094</td>
<td>0.066</td>
<td>0.076</td>
<td>0.153</td>
</tr>
<tr>
<td></td>
<td>(0.088)</td>
<td>(0.094)</td>
<td>(0.066)</td>
<td>(0.076)</td>
<td>(0.153)</td>
</tr>
</tbody>
</table>

### 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.

<table>
<thead>
<tr>
<th>variables</th>
<th>Caracal</th>
<th>Cheetah</th>
<th>Leopard</th>
<th>Sand cat</th>
<th>Wildcat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude</td>
<td>4.150</td>
<td>8.863</td>
<td>36.621</td>
<td>2.580</td>
<td>1.395</td>
</tr>
<tr>
<td></td>
<td>(2.9)</td>
<td>(8.963)</td>
<td>(13.20)</td>
<td>(2.350)</td>
<td>(2.092)</td>
</tr>
<tr>
<td>TRI</td>
<td>1.827</td>
<td>15.89</td>
<td>3.927</td>
<td>10.77</td>
<td>0.571</td>
</tr>
<tr>
<td></td>
<td>(1.854)</td>
<td>(9.603)</td>
<td>(5.360)</td>
<td>(7.239)</td>
<td>(0.760)</td>
</tr>
<tr>
<td>Rocks</td>
<td>35.532</td>
<td>34.728</td>
<td>12.08</td>
<td>4.428</td>
<td>36.453</td>
</tr>
<tr>
<td></td>
<td>(7.318)</td>
<td>(11.757)</td>
<td>(8.274)</td>
<td>(1.707)</td>
<td>(16.172)</td>
</tr>
<tr>
<td>Sand</td>
<td>11.76</td>
<td>1.268</td>
<td>6.813</td>
<td>21.25</td>
<td>6.769</td>
</tr>
<tr>
<td></td>
<td>(4.486)</td>
<td>(1.450)</td>
<td>(6.029)</td>
<td>(5.429)</td>
<td>(7.147)</td>
</tr>
<tr>
<td>Low canopy</td>
<td>2.002</td>
<td>14.775</td>
<td>0.400</td>
<td>8.422</td>
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</tr>
<tr>
<td></td>
<td>(1.956)</td>
<td>(4.116)</td>
<td>(1.470)</td>
<td>(1.603)</td>
<td>(8.343)</td>
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<tr>
<td>Woods</td>
<td>25.742</td>
<td>10.38</td>
<td>15.8</td>
<td>33.411</td>
<td>30.111</td>
</tr>
<tr>
<td>Wetlands</td>
<td>2.771</td>
<td>3.141</td>
<td>3.705</td>
<td>5.201</td>
<td>2.721</td>
</tr>
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<td></td>
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<td>(2.798)</td>
<td>(6.519)</td>
<td>(4.650)</td>
<td>(2.821)</td>
</tr>
<tr>
<td>Rivers</td>
<td>6.981</td>
<td>1.028</td>
<td>0.682</td>
<td>1.285</td>
<td>9.673</td>
</tr>
<tr>
<td></td>
<td>(4.384)</td>
<td>(1.508)</td>
<td>(1.342)</td>
<td>(1.249)</td>
<td>(6.817)</td>
</tr>
<tr>
<td>Agriculture</td>
<td>7.257</td>
<td>6.298</td>
<td>1.002</td>
<td>8.399</td>
<td>1.854</td>
</tr>
<tr>
<td></td>
<td>(4.233)</td>
<td>(4.521)</td>
<td>(1.192)</td>
<td>(5.681)</td>
<td>(2.811)</td>
</tr>
</tbody>
</table>

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...
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 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). On the other hand, the cheetah may avoid mountainous areas because of the rapidity of its pursuit and predator avoidance, thereby behaving as a sub-ordinate predator (Hunter et al., 2007; Swason et al., 2014; Rostro-García et al., 2015).

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; Khorosravi 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 sympathy 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 of 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 (Taghdi 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).
Habitat segregation within a guild of felids

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 dynamics. 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.

References


Figure 4 – Overlap between predicted suitable areas for feld 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. Sympathy indicates suitable areas for both species of the species-pair.


