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Research Article

Habitat selection of honey badgers: are they at the risk of an ecological trap?

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Abstract

Human-induced environmental changes have dramatically changed habitats worldwide, decreasing the quantity and quality of habitats for wildlife and putting wild populations at risk. In the current study habitat suitability of the honey badger (*Mellivora capensis*) across its distribution range in Southern Iran was investigated. We combined presence-only field data with environmental and anthropogenic variables, generating an ensemble model of habitat suitability based on four species distribution models. The contribution scores of anthropogenic variables (human footprint index and village density) in the model were noticeable, indicated that honey badgers do not avoid human-modified areas. The ensemble model further revealed large areas of low quality of natural habitats across the study area. Land use changes may have led honey badgers to settle in poor-quality habitats, where their fitness may be lower than in other available habitats. Therefore, there is a possible risk of an ecological trap due to the lack of protected high-quality habitats. Further research on honey badger fitness, in human-modified areas, is required to evaluate the hypothesis of ecological trap.

Introduction

Every species has a set of resource requirements and physical conditions under which it can survive and reproduce (Peterson et al., 2011). Having adequate knowledge about habitat requirements of a particular species is necessary to inform management activities aimed at conservation (Elith and Leathwick, 2009; Schwartz, 2012). Species distribution models (SDMs) are generally used to investigate basic questions regarding the potentially suitable habitats and their environmental determinants for a target species (Joy and Death, 2004; Elith and Leathwick, 2009). These models are cost effective and valuable to map the distribution of organisms (Guisan and Zimmermann, 2000; Seoane et al., 2003; Fourcade et al., 2014). However, since human activities directly and indirectly affect the quantity and quality of habitat in various ecosystems, meaning that animals increasingly come upon conditions they have not experienced in their evolutionary history (Pereira et al., 2010), information on human-related impacts such as that available in the form of maps and databases (Sanderson et al., 2002) should be implemented into predictive SDMs to inform policies and promote species conservation.

The accuracy of SDMs depends on the data analyzed, the environmental variables used for modelling, and underlying model structure (Austin, 2007). Available data used for model development may sample a restricted environmental range, preventing complete description of ecological relationships shaping habitat use (Thuiller et al., 2013). Additionally, without complete knowledge of processes underlying habitat selection, the environmental variables best used for modelling may be unclear. Finally, models often emphasize linear relationships within a resource selection framework (i.e., comparison of habitat use vs. availability), which may not adequately describe relevant ecological relationships (Austin, 2007). To deal with these uncertainties, some researchers combine predictions from multiple models using an "ensemble" approach (Araújo and New, 2007). By combining models differing in structure, explanatory variables, and data sources, ensemble predictions allow inferences that are robust to uncertainties associated with any individual model. Ensemble modelling has been used globally to predict responses to climate change (Araújo and New, 2007) and to map habitat selection of various species (Latif et al., 2013; Meller et al., 2014; Salas et al., 2017).

We used an ensemble approach to develop model-based predictions of habitat selection of one of the least studied mesocarnivores, the honey badger (*Mellivora capensis*,Schreber 1776). The honey badgers is the only species in the genus Mellivora, distributed in Africa, Southwest Asia and the Indian peninsula (Do Linh San et al., 2016). The species is listed as least concern (LC) on the IUCN Red List, owning to its wide range and its occurrence in a variety of habitats (Do Linh San et al., 2016). Ecological information, in particular habitat selection, of honey badgers is scarce, mainly due to its relatively wide range, elusive nature of the species and low densities (Begg et al., 2005). Topography and land cover types were found to be positively correlated with the honey badger presence and distance to road and villages were negatively correlated with the occurrence of the species (Gupta et al., 2012). Vegetation cover and productivity play important roles in habitat selection of the honey badger (Kheswa et al., 2018). The preference of honey badgers for denser vegetation may be a predictor of resource availability (Pettorelli et al., 2011). Species occurrence data from camera traps showed a higher occurrence of honey badgers in *Eucalyptus* plantations than in natural habitat types (Kheswa et al., 2018). Inadequate knowledge about the honey badger's ecology and quantity and quality of its habitat hampers effective conservation planning and species management. Therefore, there is an interest in understanding honey badger habitat selection and distribution to inform conservation of the species.

The current study aimed to (i) identify ecological factors affecting the spatial distribution of honey badgers in Southern Iran, and (ii) investigate the importance of human-modified areas for the species. We hypothesised that honey badger presence and habitat use would be affected by human presence, and predicted that honey badgers would avoid human-dominated areas.

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Table 1 – List of environmental variables used for distribution modelling of the honey badger in Southern Iran .

Variables	Index	Description	Source
Topography	Roughness index	Indicating the amount of elevation differences between adjacent cells of a digital elevation grid	Digital Elevation Model (DEM) USGS.org
Habitat	NDVI	Index of vegetation productivity	MODIS satellite images
Climate	BIO1	Annual mean temperature	Wordclim.org
	BIO2	Mean diurnal range	http://wordclim.org
Human impact	Human footprint index (HI)	Representing cumulative impact of population density, roads, land use/cover, infrastructures and human access	http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic
Land use	Agriculture	Cultivated lands Fallow lands Dry farming Mix farming	Iranian Department of the Environment
Land cover	Wood	Woodlands, Forests	Iranian Department of the Environment
Village density	village density	Number per area within grids of 3x3 km	Iranian Department of the Environment

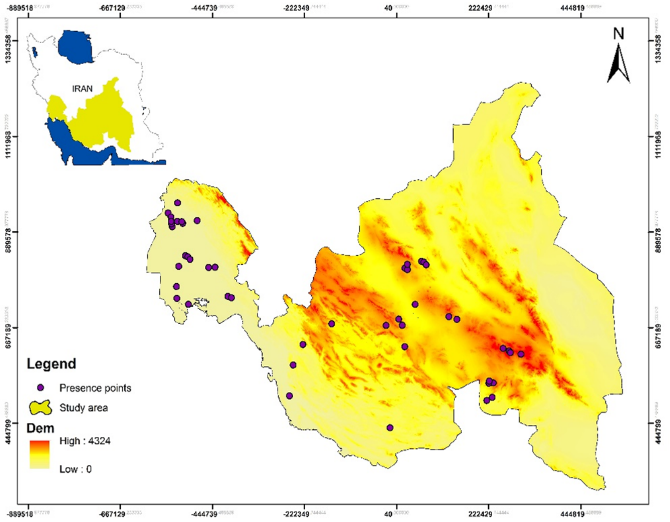

Figure 1 – Locations of collected occurrence points of the honey badger (M. capensis) in Southern Iran between 2015 and 2018.

Materials and methods

Study area and data collection

The honey badger in Iran is considered as one of the rarest mammal species. It is recorded mainly from southern half of the country (Qashqaei et al., 2015), though, there are historical records of the species from the north and the northeast (Lay, 1967; Harrington and Dareshuri, 1976). Based on the taxonomic information, honey badgers in southwest and the northeast of Iran are belong to *M. c. wilsoni* and *M. c. indica*, respectively and *M. c. buechneri* would have existed in north of Iran (Karami et al., 2008).

We surveyed Southern Iran during a period of 3 years (2015–2018). Southern Iran consists of the southern mountain ranges of Zagros, Central Iranian Range, Khuzestan Plain and the northern coasts of Persian Gulf. The occurrence data for *M. capensis* were obtained from different sources, including records of Iranian Department of the Environmental, locals' and hunters' observations, images captured by camera trap and field surveys (direct and indirect signs such as the species footprint, dung groups and den sites). In total, 58 occurrence points were collected. The possibility of recording one individual at multiple locations within its home range, known as pseudo replications is inevitable (Wordley et al., 2015), but can be diminished by considering the species home range size. For this reason, we reduced the presence points to one within every 5 km, totaling 50 points (Fig. 1), using package `dismo` in R 4.1.0 (Hijmans et al., 2020; R Development Core Team, 2014).

In 2016, a carcass of one female honey badger was recorded in Gando protected area, which was the first record of the species in Sistan and Baluchistan, southeastern Iran (Adibi et al., 2018). However, due to the lack of data from the southeastern region, this single occurrence point was not included in the modelling data set to improve model accuracy.

Environmental variables

On the basis of field knowledge and information on species biology and the limited literature available about habitat use of honey badgers (Gupta et al., 2012; Kheswa et al., 2018) a total of 25 environmental, and anthropogenic variables, expected to influence the distribution pattern of this species, were selected. Environmental variable related to climate, topography and vegetation are among the most important drivers of patterns of species distribution (Moura et al., 2016). Climate data include the 19 bioclimatic variables obtained from the Worldclim dataset at the spatial resolution of 1 km (www.worldclim.org). Climate variables were tested for correlation using principal component analysis (PCA) in ArcGIS 10.4.1 (ESRI, 2015), resulting in the reduction of the 19 variables to only two variables: annual mean temperature (`BIO1`) and mean diurnal range (`BIO2`, Tab. 1).

In order to explore the influence of topography on the *Mellivora capensis* distribution, the roughness index was used as a proxy to account for the terrain heterogeneity across the study area. The roughness index was calculated using the digital elevation model (DEM) (usgs.org) and neighborhood analysis in ArcGIS 10.4.1 (ESRI, 2015). Land use and land cover data were obtained from the Iranian Department of the Environment. Four main land cover classes including agriculture, rangeland, forests and shrublands (see Tab. 1 1 for subclasses) were extracted and Euclidean distance to each subclass were then calculated, using the Spatial Analysis Tool in ArcGIS 10.4.1 (ESRI, 2015). In addition, normalized difference vegetation index (NDVI) was used to represent vegetation greenness and therefore quality and quantity of which may be important for honey badger survival and reproduction. Twelve monthly NDVI maps were produced based on year 2015 MODIS time series data at the spatial resolution of 250 m, using Erdas Imagine v.9.3 (ERDAS, 2008).

To evaluate the anthropogenic effects on the distribution of the *Mellivora capensis*, we used the human footprint index (HI) map developed by Sanderson et al., 2002 and downloaded from the Global Human Footprint Dataset (WCS and CIESIN, 2005). This index is derived through a combination of 1 km spatial resolution data including population density and the presence of infrastructures such as roads networks, land use/cover and human access (WCS and CIESIN, 2005).The available data for the Asian part was downloaded and the corresponding values for the study area (Southern Iran) were extracted. The HI index map ranged from 0–93. The density of villages was also included, because of the coarse precision of the human footprint model. Village density was estimated from a kernel density function applied to village point layer obtained from a topographic military map of Iran (1:25000). Using the Shuttle Radar Topography Mission (SRTM) elevation model (http://srtm.csi.cgiar.org). All data layers were prepared in the raster format with a grid size of 1×1 km in ArcGIS 10.4. The final variables were tested for correlation, using the Pearson correlation coefficient. No pairs of variables showed greater correlation above the threshold of 0.8 (Tab. 1) and used to build the final distribution model of the species.

Distribution Modelling Approach

An ensemble modelling approach was employed to predict the distribution of honey badgers, using the software package biomod2 (Thuiller et al., 2009) implemented in R v.4.1.0 (R Development Core Team, 2014). This approach allowed us to simultaneously take into account results from multiple models and build a consensus model. By fitting several SDMs and exploring a range of predictions across more than one set of uncertainty sources, the ensemble modelling approach increases the accuracy of model predictions (Lauzeral et al., 2015) and thus decreases the uncertainty associated with using a single SDM. As a result of this combination, more information would be produced as compared to the utilization of a single SDM (Meller et al., 2014).

Here, an ensemble model was developed using two regression-based methods: generalized linear models (GLM), generalized additive models (GAM) and two machine learning algorithms: generalized boosting model (GBM) and maximum entropy (MaxEnt). In addition to occurrence points, all these models need background data (e.g., pseudo-absence points). Therefore, a randomly drawn set of 10000 points was generated from the extent of study area excepting occurrence cells. For model calibration, 75% of the occurrence points was used for model training and the remaining 25% of data set as test data. To combine the output of all models and obtain ensemble predictions, a weighted-averaging approach was used and each statistic model was weighted according to its predictive accuracy on test data (Thuiller et al., 2009).

Ensemble models were evaluated for their accuracy using two measures including, area under the curve (AUC) of a receiver operating characteristic (ROC) plot and true skill statistic (TSS). AUC is a threshold-independent index for evaluating the performance of niche models which is independent of species prevalence (Fielding and Bell, 1997). The AUC varies between 0 and 1. Values higher than 0.9 are considered excellent, values between 0.9 and 0.7 indicate good prediction, values lower than 0.7 considered poor prediction, and values lower than 0.5 indicate that the model is not better than a random classification (Swets, 1998). In contrast, TSS is a threshold-dependent measure ranging from -1 to 1, where 1 indicates perfect agreement between predictions and observations while zero or negative values represent model performance no better than random (Allouche et al., 2006). Models with a performance of <0.5 were discarded based on Allouche et al., 2006. Model performance was considered as "good" only if both measures (AUC and TSS) were fulfilled. The relative contribution of each environmental variable to species distribution prediction was investigated by assessing the impact on predictions of variables randomizations (Thuiller et al., 2009).

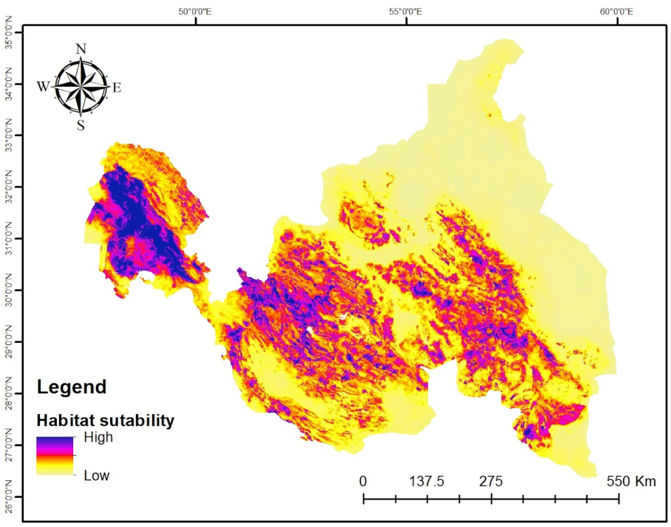

Figure 2 – Ensemble distribution model of the honey badger (*M. capensis*) in Southern Iran developed based on consensus prediction across four different distribution models including GLM: generalized linear model, GAM: generalized additive model, GBM: Generalized boosting model, and MaxEnt: maximum entropy.

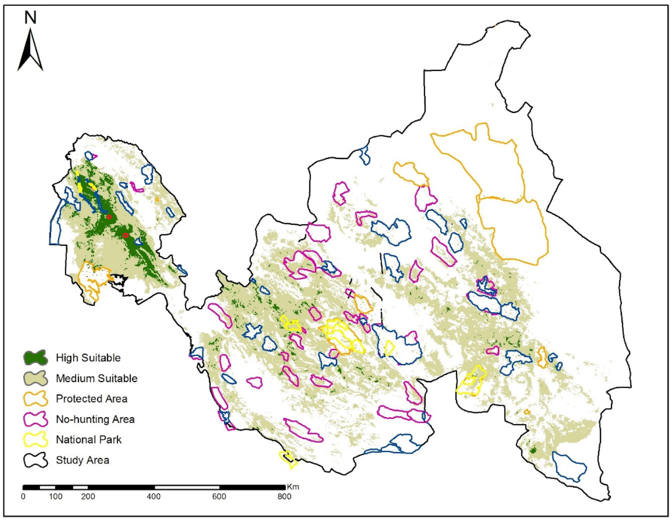

Figure 3 – Distribution map of high, medium, and low suitable habitats predicted for populations of the honey badger (*M. capensis*) across Southern Iran. Suitable areas along with the location of Iranian protected areas and no-hunting zones are presented. Red circles on the map are potential protected areas.

Results

The ensemble distribution model of honey badgers showed a patchily distributed suitable habitats for honey badgers across the study area in Southern Iran (Fig. 2). On average, GAM and GBM distribution models showed excellent predictive performance with respect to AUC metric and GLM and MaxEnt good performance (0.7<AUC<0.9). The prediction accuracy was good (e.g., TSS⩾0.6) for all models (Tab. 2). The comparison of SDMs results revealed that GBM has the highest values (AUC=0.98, TSS=0.95) while GLM had the lowest (AUC=0.79, TSS=0.6, Tab. 2).

Using the biomod2 framework, the contribution (i.e., importance) of variables in the honey badger's distribution models was estimated. The most contributing factors in the habitat suitability model of honey badgers were BIO1, HI, village density, and NDVI (Tab. 3) respectively. To evaluate the badger's response to environmental gradient, response curves were produced and compared. A similar pattern was observed between the models (Fig. 4 a-h), all indicating that annual mean temperature plays an important role in the habitat selection of the species (Fig. 4b). Difference between day and night temperatures, known as mean diurnal range (BIO2) also affected the suitability of the badger to a lesser degree (Fig. 4c). The effect of anthropogenic variables (i.e., human footprint and village density) indicated that honey badgers do not avoid human-modified areas, contrary to our prediction, and the animal's presence increased (Fig. 4d, g) with human presence. Response curves indicated a preference of the honey badger for vegetation productivity (Fig. 4e) as with increasing NDVI, the probability of honey badgers occurrence increases.

Presence/absence distribution maps were overlaid to obtain an integrated suitability map of all models. The map showed that 26% of the study area was identified as suitable habitats by at least one of the distribution models (Tab. 4). Accordingly, 74% of the study area was not identified as suitable by any of the distribution models (Tab. 4). Only 8180 ha (1.6%) of the areas was classified as highly suitable habitats, with a higher concentration in southwestern Iran (i.e. Khuzestan Plain). Moderate suitable habitats for honey badgers stretched over 118 593 km^2 representing a larger (23%) part of the study area.

A gap analysis (Scott et al., 1993) was performed by overlaying the projected maps of the badger suitable habitats and the present network of protected areas in Iran (Fig. 3,). Results showed that 59554 square

Table 2 – Performance of discrimination capacity and accuracy of four different algorithms to map honey badgers distribution in Southern Iran. Higher values indicate better model performance for each metric. AUC: the area under the curve of a receiver operating characteristic (ROC), TSS: true skill statistic, GLM: generalised linear model, GAM: generalized additive model, GBM: Generalized boosting model, and MaxEnt: maximum entropy.

	GAM	GLM	GBM	MaxEnt
AUC	0.94	0.79	0.98	0.85
TSS	0.86	0.60	0.95	0.68

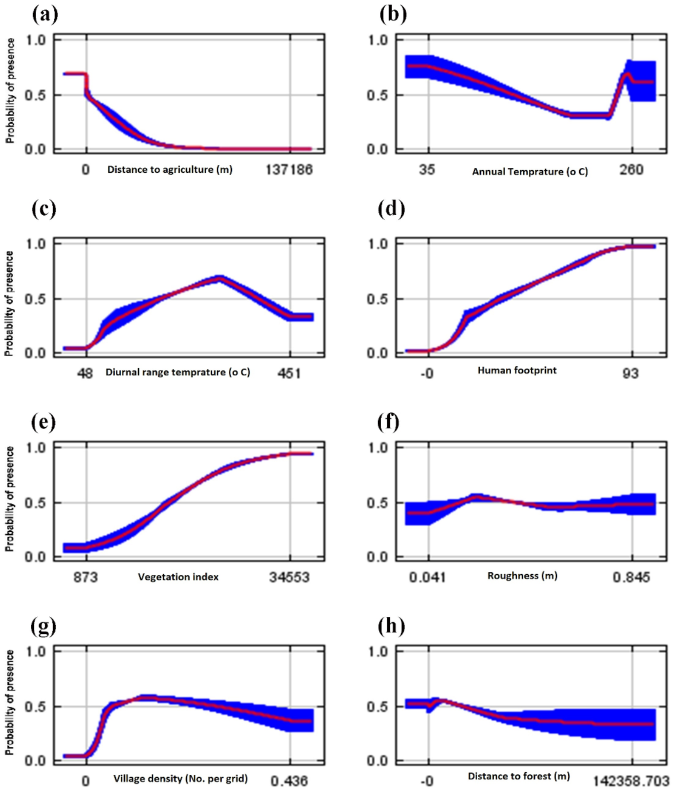

Figure 4 – Response curves of honey badgers' distribution to the gradient of the most important predictors for habitat suitability. See Table 1 for the description of variables.

kilometers (11.5%) of the study area is under protection including 7.9% of protected areas (PAs) and 3.6% of no-hunting zones (HZs), where only hunting is prohibited (Tab. 4). However, relatively large areas of low suitable habitat are present, covering, respectively, 81% of PAs and 63% of HZs. Very small parts of PAs (1.2%) and HZs (0.06%) were classified as high quality habitats for the honey badger (Tab. 4). The majority of suitable habitats, located in Khuzestan Plain were not protected (Fig. 4).

Discussion

In this study, habitat selection of honey badgers was investigated in Southern Iran, using an ensemble approach. Although most SDMs often produce good results, ensemble models (Araújo and New, 2007), combine the strength and avoid the inherent biases of different SDM algorithms (Meller et al., 2014), producing better predictions compared to a single model (Breiner et al., 2015). However, the lack of absence points is the major criticism and source of uncertainty in such presence- only methods (e.g. Senay et al., 2013). Confirmed absence data, however, are very difficult to obtain, especially for mobile and elusive species such as the honey badger. To cope with the lack of absence data, we randomly selected 10000 pseudo-absences from the extent of the study area. This strategy improve the selection of an appropriate pseudo-absence, and can yield the most reliable distribution models (Barbet-Massin, 2012). Many studies report increased accuracy using

Table 3 – Contribution of environmental variables in the honey badger's distribution models in Southern Iran. Scores are given as mean±standard deviation (SD). Contribution values were calculated based on the difference in Pearson correlation scores between general model and randomized (e.g., permuted) models for each variable. Variable descriptions are given in Tab. 1.

Variable	Score±SD
BIO1	0.27 ±0.46
Human footprint	0.26 ±0.67
Village Density	0.22 ±0.91
NDVI	0.17 ±0.23
BIO2	0.14 ±0.12
Wood	0.10 ±0.10
Roughness	0.08 ±0.14
Agriculture	0.07 ±0.38

this approach (e.g. Chefaoui and Lobo, 2008; Warton and Shepherd, 2010; Senay et al., 2013).

Based on the distribution modelling, annual mean temperature was found to be the most important climatic variable affecting the potential distribution of honey badgers. This variable is usually considered as the most important variable describing the climate of an area (Parmesan, 2006). Mean diurnal range (BIO2) also affected the suitability of the badger to a lesser degree. Climate types of Southern Iran include hot desert climate in plains and the coast of Persian Gulf and steppe climate in the mountain ranges. Honey badgers have been studied in semiarid environments of the southern Kalahari, showing that temperature is the major factor affecting honey badger activity schedules (Begg et al., 2005). Animals avoid being active during the hottest part of the day and the colder part of the night (Begg et al., 2016).

The contribution scores of anthropogenic variables (human footprint index and village density) in the model were noticeable (Tab. 3), indicated honey badgers do not avoid human-modified areas. Human-dominated regions may have ecological importance, providing more services for some species than previously thought (Tsunoda et al., 2017; Lanszki et al., 2018). In South Africa, for example, a higher occurrence of honey badgers were recorded in plantations compared to natural habitats (Kheswa et al., 2018). Mesocarnivovers such as honey badgers may benefit from conditions in human-modified landscapes, capable of using new habitat opportunities. The European badger also seems to benefit from human-modified areas such as agro-forestry and hedgerows, probably because of food availability and suitable sett locations (Chiatante et al., 2017).

Behavioural responses by animals to such environmental change, can help them adjust to new conditions. Studies in South Africa revealed that in undisturbed areas, by human, the honey badger is regularly active during the day (Begg et al., 2016). However, it has been suggested that the foraging behavior of the species has shifted to nocturnal due to human activities (Skinner and Smithers, 1990). This is likely to increase foraging costs and may place an additional stress on the survival of the species, especially in habitats with high human activity (Begg, 2001). Our ensemble model, further, revealed large areas of low qual-

Table 4 – Area and proportion of suitable/unsuitable habitats for honey badgers in Southern Iran.

Category	Area (km^2)	Percentage of study area	Protected areas km^2 (%)		No-hunting zones (%)	
Total study area	515622		41000	(7.9)	18554	(3.6)
Unsuitable areas	381560	74				
Suitable areas	134062	26				
Low suitability	7219	1.4	33254	(81.2)	11707	(63.34)
Medium suitability	118593	23	7236	(17.6)	6835	(36.6)
High suitability	8250	1.6	510	(1.2)	12	(0.06)

ity of natural habitats across the study area, covering respectively 81% of PAs and 63% of HZs. Thus, in the absence of protected high- quality habitats, some areas such as plantations, farms, and urban areas may attract honey badgers. In the current study, field evidence such as road mortalities and illegal hunting of individuals outside PAs suggested that the quality of areas under protection is not enough for supporting honey badgers (also see Qashqaei et al., 2015).

Limited availability of optimal conditions may be the reason for such a deviation from ideal habitats (Titeux et al., 2007). Environmental changes lead organisms to settle in poor-quality habitats, where their fitness may be lower than in other available habitats, known as ecological traps (Dwernychuk and Boag, 1972). An ecological trap is a habitat in low quality for reproduction and survival that cannot sustain a population. It seems valid to state that honey badger distribution often overlap with human areas and that this likely presents the risk of an ecological trap.

Ecological traps have important conservation and management implications (Sahney et al., 2010; Demeyrier et al., 2016; Hale and Stephen, 2016). For example, ecological traps are likely to increase local extinction risk (Battin, 2004). Several studies suggested that this trap phenomenon may be widespread because of human-induced rapid environmental changes (e.g. Battin, 2004; Hale and Stephen, 2016; Lamb et al., 2017. Although many species are frequently reported to breed in human-modified habitats (Sih, 2013), the data regarding fitness or demographic consequences of this shift, in habitat use, are limited. Without information on honey badger fitness in human-modified areas, the conclusion that these are ecological traps cannot be drawn.

In conclusion, model-based predictions and their implications can be used to guide future research and conservation planning. With our case study, we showed that SDMs can identify the environmental conditions and geographical areas that are used by the species, but these areas may not be the most suitable ones for the species fitness. For example, while we identified areas of high-quality honey badger habitat throughout southern Iran, we also found that honey badgers were much more frequently associated with human habitats than expected, which could potentially result in decreased fitness and reproductive potential for individuals in these areas. Increased protection of areas including high-quality honey badger habitat could also help the species avoid ecological traps. There are a couple of spots (Fig. 3) where high-quality habitats are unprotected and would be valuable in a protected area. Further research on honey badger fitness in human-modified areas are required to evaluate the hypothesis of ecological traps.

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