When pork is not on the menu: Assessing trophic competition between large carnivores and poachers

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A B S T R A C T

Overexploitation of wildlife for meat is a widespread phenomenon, which drives populations of many species toward extinction and may in turn affect large carnivores. Therefore, human hunters may compete with large carnivores over food resources and threaten their survival. In this study, we assessed the trophic competition of endangered Persian leopard with local poachers in Golestan National Park, Iran, where poaching has depleted populations of three ungulate species by 66–89% in the past decades. We compared leopard diet (77 scats) with prey offtake by poachers (75 poacher seizure records). In addition, we estimated prey abundance by line transect sampling (186 km), camera trapping (2777 camera days), double-observer point-counts (64 scans) and dung counts (38 km). Using interview surveys with local poachers, we also quantified their stated hunting preference. We documented a narrow hunting specialization of leopard (niche breadth 0.24) and poachers (niche breadth 0.19), and exclusivity (niche overlap 0.31) of their dietary/hunting niches, which suggest no exploitative competition between these two apex predators. This pattern likely results from the major role of wild boar in leopard diet. Due to religious beliefs, poachers avoid hunting this species and its population has increased in contrast to other ungulates. Considering the general avoidance of Suidae species across leopard range, depletion of alternative prey species may have resulted in a prey-switching strategy by leopard. The influence of religious beliefs and taboos on hunting preference and, consequently, on prey populations and predators' trophic niches shows the importance of incorporation of cultural beliefs in conservation practices.

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1. Introduction

Overexploitation of wildlife for meat is a widespread phenomenon, which drives populations of many species toward extinction (Milner-Gulland et al., 2002). This pattern in form of pursuit hunting or trapping is known to also affect natural food webs (Rowcliffe et al., 2003) as species targeted by humans may play important roles in the diet of large carnivores (Henschel et al., 2011). A recent study revealed that humans exploit shared prey at 1.9 times higher rates than all other predators combined within the human-predator-prey communities studied (Darimont et al., 2015). Therefore, human hunters may compete with carnivores over food resources, acting as an unsustainable "super predator" (Darimont et al., 2015).

Large carnivores are especially vulnerable to low density and biomass of their preferred prey (Carbone et al., 2011) and prey depletion is one of their major threats worldwide (Wolf and Ripple, 2016). When prey is scarce, large carnivores may expand their hunting effort by increasing home ranges or changing activity patterns (Schmidt, 2008). However, if competition reaches exploitative levels, switching to other prey species or extermination from habitats may be observed (Henschel et al., 2011; Rosenblatt et al., 2016). Additionally, prey depletion may force carnivores, such as big cats, to shift toward livestock depredation and trigger retaliatory persecution by humans (Khorozyan et al., 2015). Therefore, prey depletion is a vitally important factor for the survival of large carnivores, which requires further attention by conservationists (Chapron et al., 2008).

Dietary competition between different carnivores is well-studied in ecology (see Caro and Stoner, 2003). Within the large carnivore guilds, species exploit different resources if sufficient prey is available or compete when prey is limited (Karanth and Sunquist, 2000; Odden et al., 2010; Harihar et al., 2011; Jumabay-Uulu et al., 2014). The degree of

dietary niche overlap may indicate exploitative competition among predators (Caro and Stoner, 2003). However, the role of humans as an apex predator in the trophic niche of animal predators has been rarely studied (Henschel et al., 2011; Darimont et al., 2015; Foster et al., 2016). Conservation of large carnivores in a changing world requires 'coexistence' of human and animal predators, and understanding differences in their ecological niche in local context is increasingly necessary (Chapron and López-Bao, 2016).

All these aspects are relevant to preservation of big cats, such as the globally endangered Persian leopard (*Panthera pardus saxicolor*). The largest protected population of this felid (23–42 individuals) is known to exist in Golestan National Park (GNP), Iran (Hamidi et al., 2014). The main threat to leopards in GNP is thought to be road kills (Kiabi et al., 2002). However, the rapid population decline of at least three ungulate species in GNP since the 1970s may indicate that poaching of prey species is another important threat (Ghoddousi et al. in press). Such hunting pressure is targeted on ungulates, but not on leopards (Ghoddousi et al., 2016a). Understanding responses of leopards to declining prey species may help develop appropriate conservation measures for this endangered large carnivore (Lovari et al., 2013). In this study, we quantified the dietary niche overlap of leopard and poachers to assess the threat of prey depletion to leopard. We hypothesize that given high ungulate poaching rate in GNP (Ghoddousi et al. in press), prey depletion may threaten the survival of leopards in case of high dietary niche overlap between leopards and poachers.

2. Material and methods

2.1. Study area

GNP is located in northeastern Iran covering an area of 874 km^2 (Fig. 1). Elevation ranges from 450 to 2411 m above sea level and precipitation from 866 to 142 mm from west to east, respectively, creating a variety of different habitats (Akhani, 2005). The park has a mountainous terrain covered by sub-humid Hyrcanian forests in the west, and steppes and semi-deserts to the east (Akhani, 2005). GNP is the oldest national park of Iran, established in 1957, and a UNESCO Biosphere Reserve. GNP is home to six species of ungulates, most of which are affected by poaching (Ghoddousi et al. in press). Despite a long history of protection and sufficient law enforcement resources (Ghoddousi et al., 2016a), lack of acceptability of conservation laws, poverty and inefficient enforcement practices have resulted in rampant poaching in the park (Ghoddousi et al. in press). No villages exist within GNP, however, around 8660 inhabitants from different ethnicities including Turkmens, Persians, Balochs and Kurds live in 15 villages <2 km away from its boundaries. The main occupation of local communities is farming crops or livestock.

2.2. Leopard diet analysis

We collected leopard scats opportunistically from all around GNP, especially alongside main trails and near scrapes, from 2011 to 2014 and analyzed prey hair remains for assessment of leopard dietary profile (Klare et al., 2011). Additionally, other undigested remains in scats such as bones, hooves, claws and feathers were used to assist identification of prey species (Lumetsberger, 2014). We estimated consumed prey numbers using the non-linear correction factor CF_2 (Wachter et al., 2012):

$$CF_{2;i} = 3.094 \exp\left(-0.5((\text{1n}(x/16.370))/2.584)^2\right)$$

where $CF_{2;i}$ is the number of scats produced from consuming an individual of the i-th prey species against the average body mass of the species x (kg). Therefore, the number of individuals of the i-th consumed prey was equal to the number of leopard scats containing the i-th prey
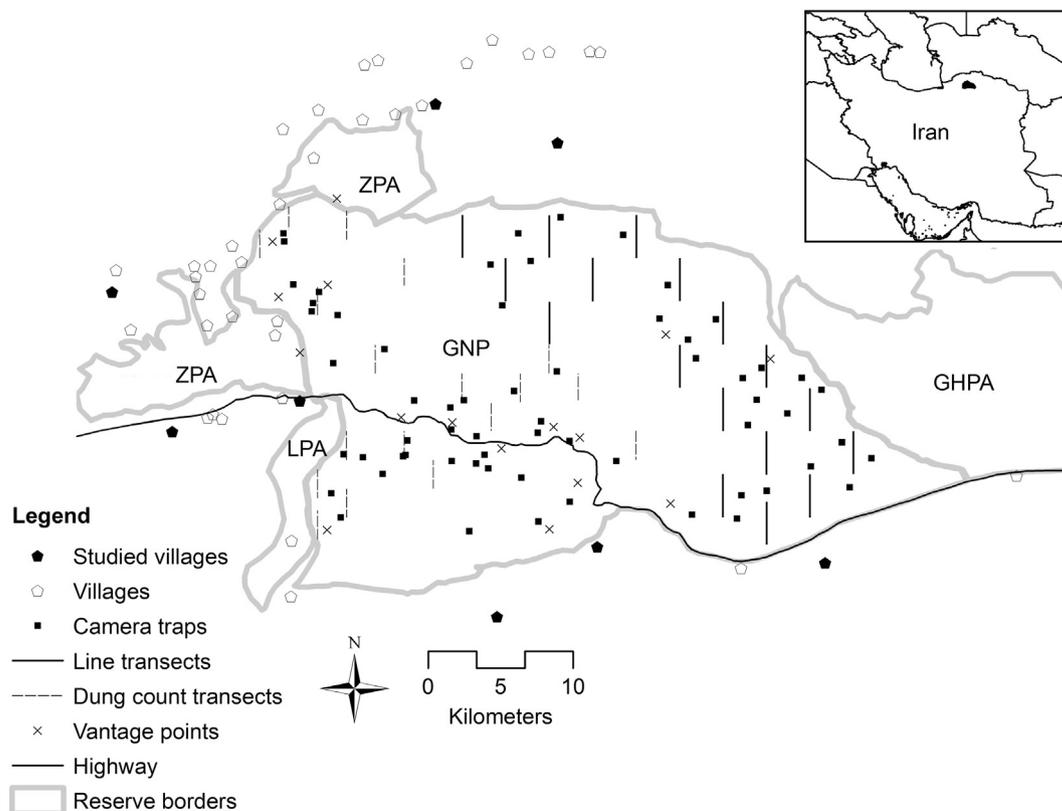

Fig. 1. Map of Golestan National Park (GNP) showing the location of line transects, camera traps, vantage points, studied villages and neighboring reserves (LPA: Loveh Protected Area; ZPA: Zav Protected Area; GHPA: Ghorkhod Protected Area).

divided by $CF_{2;i}$ (Wachter et al., 2012). The average body masses of each prey species were extracted from literature as 3/4 of average female body mass to account for predation on sub-adult individuals (Lumetsberger, 2014). Detail on methodologies is provided elsewhere (Ghoddousi et al., 2016b).

2.3. Poacher seizure data

We used official GNP poacher seizure records from 2007 to 2014 to obtain an index on the frequency of hunted species by poachers. We used only cases when hunted animals were present during a seizure and excluded cases of captures before successful hunts. We calculated the proportion of each hunted species to the total number of hunted species. To check if our sample size was sufficient to portray poachers' hunting choice in GNP, we computed the species accumulation curve using 'vegan' package in R statistical software 3.2.2. There is a potential variation in detection probability of poachers within different habitats (Keane et al., 2011). In GNP, poaching is practiced solely in form of pursuit hunting with guns and occurs throughout the year (own data, unpublished). In open landscapes, poachers normally locate ungulate herds and wait until the dusk for shooting when they can better escape potential ranger encounters (pers. obs.). In forest, poachers hunt throughout the day whenever encountering ungulates. However, red deer (Cervus elaphus) poaching peaks during the rut season (September–October) when poachers imitate stag calls and draw them to shooting distances (pers. obs.). Rangers normally use a sit-and-wait or tip-off from local informants to detect poachers (own data, unpublished). Therefore, we believe that seizure data represents a robust distribution of hunted species in GNP.

2.4. Prey abundance estimation

We assessed the abundance of the main prey species consumed by both leopards and poachers, which were identified from scat analysis and law enforcement records (see above). We used different methodologies for abundance estimation of prey species in stratified habitats due to different detection probabilities and habitat characteristics (Ghoddousi et al., 2016b). We estimated bezoar goat (Capra aegagrus) abundance using a double-observer point-count approach in 53.6 km^2 of rugged landscapes of GNP from November to December 2014 (Suryawanshi et al., 2012). Two independent observers conducted four alternating counts at 16 sampling points (Fig. 1) and the data was later analyzed using DOBSERV software (Nichols et al., 2000). We estimated urial (Ovis vignei) population size using line transects in 340 km^2 of steppes in eastern GNP (Buckland et al., 2001). We surveyed 17 3-km transects in four replicates (January to February 2013, August to September 2013 and February 2014; Fig. 1) and the data was analyzed using Distance 6.0 software (Thomas et al., 2010). For assessing the abundance of wild boar (Sus scrofa), we applied the random encounter model (REM) using camera traps (Rowcliffe et al., 2008). Data from 67 camera traps deployed across GNP (excluding a 25 km^2 arid plain; Fig. 1) from January to December 2011 was used for this purpose (Hamidi et al., 2014). Finally, red deer population size was estimated with a combination of REM using camera traps, and dung counts using fecal standing crop (FSC) approach (Buckland et al., 2001; Rowcliffe et al., 2008). Data from 37 camera traps installed from May to December 2011 (REM) and a single survey of 18 2-km transects from January to February 2013 (FSC) were gathered in 422 km^2 of forests in western parts of GNP (Fig. 1). Details on methodologies and modeling approaches related to prey abundance estimation by us are provided in other publications (Hamidi et al., 2014; Ghoddousi et al., 2016a, 2016b; Soofi et al. 2017). For estimation of ungulate abundance within GNP, we extrapolated the density of each species to the relevant stratified habitat.

2.5. Preference indices

We used Jacob's index I_j to calculate leopard and poachers' prey preference (Jacobs, 1974):

$$I_j = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

where r_i is the proportion of the number of individuals of the i-th consumed/hunted prey species to all consumed/hunted individuals and p_i is the proportion of the abundance of the i-th species to the abundance of all prey species. I_j ranges from -1 (maximum avoidance) to $+1$ (maximum preference), with $I_j > 0.3$ indicating preferred prey species and $I_j < -0.3$ as avoided prey. The index between these values suggests predation according to prey abundance (Clements et al., 2014). We calculated the proportion of prey individuals consumed/hunted using the total abundance of the four prey species described above.

2.6. Interview survey

As an independent measure of poaching preference, we used interview surveys to obtain data on self-reported preference of hunted species by local poachers (Gavin et al., 2010; Martin et al., 2012). Although different poachers may have different poaching preferences, we assumed that by interviewing a representative number of poachers we could identify the typical hunting preference of local poachers. As we initiated participatory monitoring schemes with cooperation of local communities in GNP (Hamidi et al., 2014; Ghoddousi et al., 2016a), a number of local poachers were identified through a chain referral approach (Newing, 2011). As we worked as a non-governmental group of researchers and informed local poachers about the purpose of this study, poachers agreed to attend the interview survey. On December 2012, a focus group meeting with participation of five poachers was organized and we collected data on preferred hunted species (up to three entries) using semi-structured interviews (Newing, 2011; Martin et al., 2012). We also used data on poachers' preferred hunted species from a previous social study (Ashayeri, 2014), using individual qualitative interviews from eight participants from June 2013 to February 2014 (Newing, 2011). The 13 participants were from eight different villages adjacent to GNP. The respondents' age ranged from 29 to 66 years, and all were males. Based on investigations by former GNP manager (J. Selyari pers. comm.), local informants ($n = 2$; own data, unpublished) and other poachers ($n = 4$; own data, unpublished), we calculated the total number of active hunters in villages around GNP (Martin et al., 2012). The interviewees were ensured that the anonymity and security of their identity would not be recorded nor disclosed to Department of Environment (DoE). The interviewees gave their verbal consent on the use of their data, as written consent was not possible and could affect data quality. The interview survey was in accordance to the ethical guidelines of Georg-August-Universität Göttingen and with written approval of the DoE and Golestan provincial office of DoE.

2.7. Niche breadth and overlap

By incorporating leopard diet and poacher seizure records data, Levin's dietary niche breadth index was calculated (Levins, 1968) to assess the degree of dietary/hunting specialization of leopard and poachers. We calculated a standardized dietary niche breadth (B_{sta}), because the number of prey species differed between poachers and leopard (Henschel et al., 2011):

$$B_{sta} = (1/\sum p_i^2 - 1)/(B_{max} - 1)$$

where p is the proportion of each prey species consumed/hunted (i) and B_{max} is the total number of prey species consumed/hunted. B_{sta} ranges between 0 (specialist hunter) and 1 (generalist hunter). Moreover, the

dietary/hunting niche overlap between leopard and poachers was calculated using Pianka's index (O_{pl}), which ranges from 0 (hunting exclusivity) to 1 (hunting overlap) (Pianka, 1973):

$$O_{pl} = \sum_i^n P_{ip}P_{il} / \left(\sum P_{ip}^2 \sum P_{ip}^2 \right)^{1/2}$$

where P_i is the proportion of the prey item "i" in the diet/hunting of the species "p" (poachers) and "l" (leopard).

3. Results

3.1. Leopard diet analysis

We collected 77 leopard scats containing 12 prey species (Fig. 2). The corrected proportions of prey individuals consumed showed the main contribution of wild boar (66.67%), followed by bezoar goat (18.14%), urial (13.24%) and red deer (1.97%) (Table 1).

3.2. Poacher seizure

We collected data on 75 cases of poacher seizures in GNP, reporting on 113 killed animals of eight species (Fig. 2). The corrected proportion of hunted species by poachers was highest for urial (68.75%), followed by red deer (13.54%), bezoar goat (10.42%), and wild boar (7.29%) (Table 1). The species accumulation curve reached an asymptote at approximately 80–90 hunted individuals, indicating that our sample size of 113 killed animals was sufficient to portray species diversity in poachers' hunting bags (Fig. 3).

3.3. Prey abundance estimation

During 64 scans, we observed 39 bezoar goats in seven groups. The estimated abundance was 519 individuals (coefficient of variation CV = 31.3%; 95% CI = 201–807). From 50 pellet groups, the FSC method estimated red deer abundance as 194 individuals (CV = 28.4%; 95% CI = 103–285). Also, we captured 10 photos of red deer from 1345 camera days of effort in GNP. Using REM approach, the estimated red deer population in GNP was 257 individuals (CV = 35.3%; 95% CI = 91–423). We calculated red deer abundance as 226 individuals, which is the arithmetic mean of the REM and FSC estimates. By a total survey effort of 186 km, we observed 1981 urials in 70 groups and estimated their abundance as 4275 individuals (CV = 35.5%; 95% CI = 2117–8632). Finally, we captured 386 wild boar photos during 2777 camera days of effort across GNP and estimated wild boar abundance as 6478 individuals (CV = 27.0%; 95% CI = 3050–9906).

3.4. Prey preferences

Leopard showed the highest preference for bezoar goat ($I_j = 0.62$) among the studied species (Fig. 4). Predation on wild boar ($I_j = 0.23$) and red deer ($I_j = 0.00$) was according to their abundance (Fig. 4). Urial ($I_j = -0.60$) was avoided by leopard in GNP (Fig. 4). The poachers' hunting preference using seizure records indicated red deer ($I_j = 0.80$), urial ($I_j = 0.58$) and bezoar goat ($I_j = 0.38$) as the preferred species. Wild boar ($I_j = -0.72$) was highly avoided by poachers in GNP (Fig. 4).

3.5. Interview survey

Poachers reported their highest preference for killing urial (46.4% of all records). The other species frequently mentioned as being preferred were red deer (35.7%) and bezoar goat (17.8%) (Table 2). No poachers from our sampled population stated preference for wild boar hunting. The average number of local poachers around GNP was estimated as 80 ± SE 24 individuals. Therefore, our sample size represents around 16.3% of GNP poachers.

3.6. Niche breadth and overlap

The dietary/hunting niche breadth of leopard ($B_{sta} = 0.24$) and poachers ($B_{sta} = 0.19$) confirms specialization of both predators in prey choice. Also, the dietary/hunting niche overlap of poachers and leopard ($O = 0.31$) shows exclusivity of hunted species.

4. Discussion

In this study, we documented hunting specialization of both the Persian leopard and local poachers in Golestan National Park. According to our results, dietary niche overlap of leopards and poachers is low, which suggests no exploitative competition between these two apex predators. Such pattern is likely due to the role of wild boar, which constitutes the major prey of leopard in the national park, but is widely avoided by poachers (Fig. 4). Due to the prohibition of pork consumption by Islam, this species is experiencing low poaching pressure inside Iranian protected areas (Ghoddousi et al. in press). Therefore, it appears that religious beliefs are working indirectly in favor of leopards despite rampant poaching of other ungulate species.

Religions have a high potential in conservation by protecting sacred lands, influencing people's attitude toward wildlife and channeling funding opportunities (Bhagwat and Palmer, 2009; Li et al., 2013; Bhatia et al., 2016). However, this connection is complex and followers of different faiths may show variable behaviors toward wildlife (Baker et al., 2014; Bhatia et al., 2016). As an example, while Buddhist monasteries may safeguard large tracts of snow leopard (*P. uncia*) habitat and contribute to its conservation more than protected areas, religious superstitions drove leopards in Zanzibar to extinction (Li et al., 2013; Walsh and Golman, 2007). In this study, we show the importance of cultural beliefs in wild meat consumption among local communities and its influence on the persistence of a top predator. Food taboos and religious beliefs, especially related to meat consumption, are common across the world and may significantly influence conservation of different species, including predators (Baker et al., 2014; Leroy and Praet, 2015). Therefore, incorporation of cultural beliefs in conservation practices may help disentangle the interactions between local communities, prey and apex predators (Bhatia et al., 2016).

Religious beliefs and taboos about members of the Suidae family are influential in hunting patterns of local communities in different parts of the world (Randrianandrianina et al., 2010). Under such conditions, the wild boar population has increased by 58% within four decades in
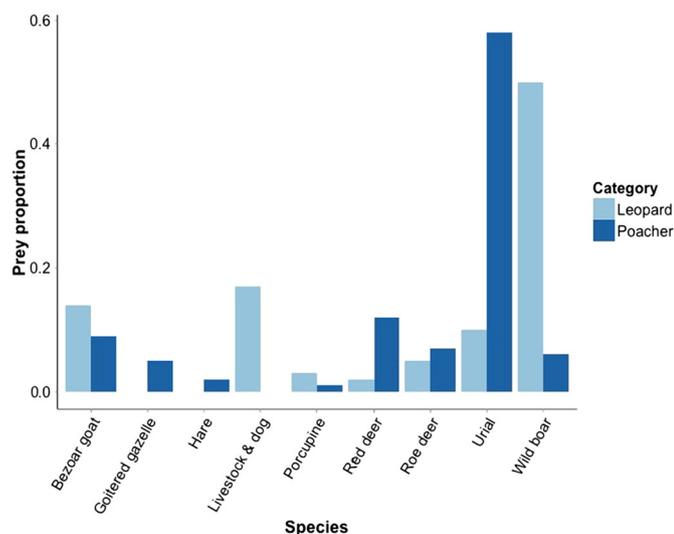

Fig. 2. Proportions of different prey species in Persian leopard diet and poacher seizure records in Golestan National Park.

Table 1
Hunting preferences of poachers and Persian leopard in Golestan National Park in relation to abundance of four studied prey species.

	Prey abundance		Leopard diet	Poacher seizure data	Hunting preference	
	No. individuals	(%)	Corrected individuals consumed (%)	Corrected individuals hunted (%)	Leopard Jacob's index (I_j)	Poachers
Bezoar goat	519	4.51	18.14	10.42	0.62	0.38
Red deer	226	1.97	1.96	13.54	0.00	0.80
Urial	4275	37.18	13.24	68.75	−0.60	0.58
Wild boar	6478	56.34	66.67	7.29	0.23	−0.72
Total	11,498	100	~100	100		

Golestan National Park (Ghoddousi et al. in press). Despite the high importance of wild boar in leopard's diet, our results suggest that wild boar is not a preferred prey, being only predated upon according to its abundance. Throughout its range, the leopard is known to avoid hunting suids due to their aggressive behavior, group living and heavy body mass exceeding the leopard's preferred prey range (1–45 kg; Hayward et al., 2006; Clements et al., 2014). However, large carnivores are capable to adapt to human interventions (Carter and Linnell, 2016) and we hypothesize that the considerable share of wild boar predation in leopard diet in Golestan National Park may be a result of a prey-switching strategy (Garrott et al., 2007) caused by the drastic decline of other ungulate species (Ghoddousi et al. in press).

Limited resource availability may influence the diet of carnivores (Lovari et al., 2013), and specialization on different prey species is one of the main strategies to avoid competition in different carnivore guilds (Karanth and Sunquist, 2000; Harihar et al., 2011). Such alteration may lead to dietary niche separation (Pianka, 1973). Current levels of ungulate over-hunting and the increasing wild boar population (Ghoddousi et al. in press) suggest that the dependence of Persian leopards on wild boars is expected to increase in Iran. Lack of alternative prey may be compensated by high densities of wild boars in Iranian forests. However, in arid parts of the country wild boar densities are low and other ungulates constitute a majority of the leopard diet (Taghdisi et al., 2013). Limited dietary niche breadth of leopard may therefore put the survival of Persian leopards at risk in the future, especially in arid areas. Moreover, given the intrinsic risks of injury and energetic costs associated with wild boar predation by leopards (Qi et al., 2015), it remains unclear how the dependence on this species would affect the long-term viability of Persian leopards.

With the current rate of rampant poaching in Golestan National Park, some ungulate species may become extinct in the near future (Ghoddousi et al. in press). This will reduce the dietary niche breadth of leopard and make the species more susceptible to prey depletion (Hayward and Kerley, 2008; Wolf and Ripple, 2016). Although

generalist predators are known to be less affected by this threat due to their ability to switch to alternative prey (Purvis et al., 2000), an overall simplification of the food web may trigger cascading effects throughout the ecosystem (Layman et al., 2007). We argue that conservation of top predators should move from simple assessments of predator and prey presence/absence to more dynamic interactions resulting from overexploitation of natural resources and their long-term effects on these species.

An earlier study by Henschel et al. (2011) indicated exploitative competition between leopards and snare-using bushmeat hunters in the Congo basin. Apparently, no such a relationship exists in our study area where poachers practice only pursuit hunting and, therefore, their preference directly affects the populations of exploited species (Rowcliffe et al., 2003). Apart from wild boar, we recorded trophic niche separation between leopard and poachers in another two prey species studied. High preference for red deer may be driven by the quantity of meat provided by this largest ungulate of the park for selling in illegal markets (Martin et al., 2012). However, seizure records indicate that poachers kill less red deer than they report (Table 2). The sharp decline of the red deer population by 89% in the past four decades and its low detection probability may have reduced the hunting success rate of this species (Ghoddousi et al. in press). This species constitutes a minor proportion of leopard diet and was predated upon according to its abundance. In contrast, urial experiences a higher poaching pressure than it was claimed by respondents. Despite higher availability, living in open landscapes may limit the success rate of urial hunting by leopards (Balme et al., 2007). Therefore, avoidance of urial by leopards in Golestan National Park is plausible. The only studied prey species preferred by both poachers and leopard was bezoar goat. This species has experienced around 88% decline due to poaching since the 1970s
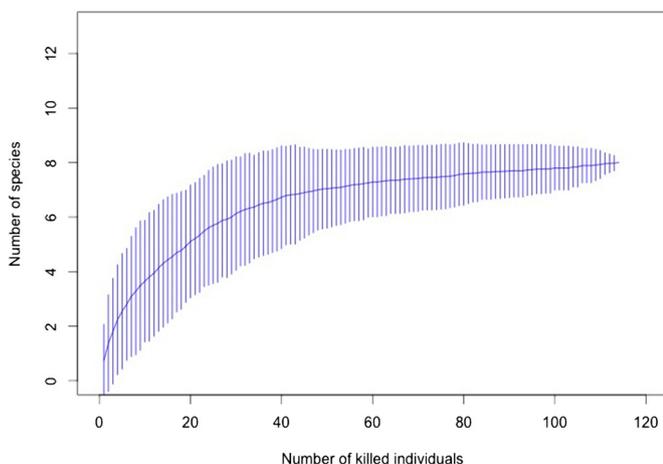
Fig. 3. The accumulation curve and 95% confidence interval of the number of species in poacher seizure records.
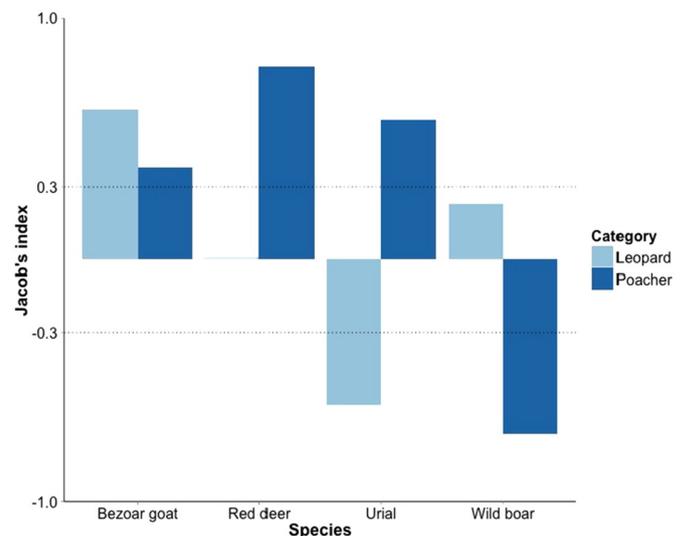
Fig. 4. Hunting preferences of Persian leopard and poachers in Golestan National Park as estimated by Jacob's index (Jacob's index >0.3 was considered as preferred and <−0.3 as avoided, with the index between these values indicating predation/hunting proportional to the abundance of prey).

Table 2
Reported hunting preferences of poachers from interview survey and seizure records in Golestan National Park.

Species	Reported preference (% of all mentions)	Proportion of hunted individuals (%)	Proportion of hunted individuals minus reported preference
Bezoar goat	17.86	10.42	−7.44
Red deer	35.71	13.54	−22.17
Urial	46.43	68.75	22.32
Wild boar	0.00	7.29	7.29
Total	100	100	–

(Ghoddousi et al. in press). Despite its rarity, bezoar goat made a remarkable share in poachers' hunts and leopard diet, and was highly preferred by leopard. Enforcement of protection of the last population patches of this species in rocky habitats is essential to secure leopard survival in the park and should be considered a conservation priority.

We are aware of some limitations of this study, which might affect our inferences. The scat sample size in this study was small ($n = 77$) and the sampling process extended over few years. A comparison of leopard diet with pooled data from a previous study in Golestan National Park showed no significant differences in the share of the main prey species in leopard diet (Ghoddousi et al., 2016b). Due to the lack of data, we did not consider two species hunted by leopard or poachers in Golestan National Park, namely roe deer (*Capreolus capreolus*) and goitered gazelle (*Gazella subgutturosa*). However, they play a minor role compared to the four studied prey species, which constitute 75% of leopard diet and 85% of poachers' successful hunts. Another limitation was that the camera trapping data used for red deer and wild boar abundance estimation came from a study that targeted leopard (Hamidi et al., 2014). As movement patterns of herbivores are independent from those of carnivores (Cusack et al., 2015), this design should not violate the assumptions of random encounter models (Rowcliffe et al., 2008). The application of random encounter model to red deer and wild boar populations in Golestan National Park produced abundance estimates similar to other tested methods (Ghoddousi et al., 2016b; Soofi et al. 2017). Moreover, there is a potential bias from the use of data on leopard diet, prey abundance and poacher seizures coming from different study periods. Apart from seizure records, which we extended to 2007 to acquire more samples, the rest of the data was collected only from 2011–2014. Finally, due to sensitivity of illegal hunting, we were not able to include more poachers in our survey. However, we attempted to spatially distribute our interviews in villages around the national park to minimize the potential bias.

5. Conclusions

Conservation of threatened carnivores requires careful consideration of their dietary requirements and solutions to alleviate depletion of their prey (Wolf and Ripple, 2016). In this study, leopard and poachers showed exclusivity in their dietary/hunting niches in Golestan National Park despite rampant ungulate poaching. This is likely due to the major role of wild boar in leopard diet, which is not preferred by leopard nor extensively hunted by poachers due to religious beliefs. Considering the general avoidance of Suidae species across the leopard range, depletion of other prey species may have resulted in a prey-switching strategy by the leopard. The influence of religious beliefs and taboos on hunting preference and, consequently, on prey populations and predators' trophic niches shows the importance of incorporation of cultural beliefs in conservation practices. We demonstrated that poachers prefer hunting prey with higher body mass (red deer), but are most successful in hunting abundant species (urial). Although in our study leopard and poachers had a low trophic niche overlap, the reduction of dietary niche breadth may threaten the long-term survival of leopard (Hayward and Kerley, 2008). Therefore, conservation initiatives should target poachers' socio-economic incentives to reverse the alarming population decline of ungulates (Ghoddousi et al. in press).

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